POPULATION SCALE AND INTER-INDIVIDUAL, SPATIAL PROXIMITY VARIATION IN BARBARY MACAQUES (*MACACA SYLVANUS)*

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Having read and understood the University's definition of plagiarism, I confirm that this dissertation is my own original and – except insofar as explicitly indicated – unaided work, and that it does not contain material that has already been used to any substantial extent for a comparable purpose.

This dissertation was submitted in partial fulfilment of the requirements for the degree of BA (Hons) in Archaeology, specialization in Biological Anthropology, 2024-2025.

Acknowledgments

Thank you to my supervisor for this project, Sylvain Lemoine, who introduced me to the macaques in Gibraltar and without whose support this would have been possible. Thank you to my family and to my friends at St John’s Road for engaging with my constant conversations about monkeys.

Abstract

Proximity may be used as a proxy to investigate social relationships between primates. Using social network analysis and generalised linear mixed models, this study investigated the variation in inter-individual proximity in five groups of Barbary macaques (*Macaca sylvanus*) and whether this was influenced by seasonality, grooming and rank differences in the groups. Proximity has not previously been explored in Gibraltar.

This study found that grooming and proximity were associated in most groups, indicating that those in closer proximity were more likely to groom. In some groups, male-male dyads were shown to be more spread than female-female dyads in winter compared to summer. Most groups showed that male-male dyads were more spread than female-female dyads, likely reflecting kinship between philopatric females. Rank difference had a significant effect on proximity in one group, where higher food competition may have resulted in stricter hierarchies. Group differences in spread were shown to reflect home-ranges and the importance of the anthropogenic environment in which the macaques live.

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Introduction

In primatology, spatial proximity is recognised as being an important indicator of the social relationships between individuals in a group (Cords, 1997). Indeed, it is an integral prerequisite for any interaction that occurs between individuals in a group (Crofoot et al, 2011). Spatial proximity can be defined as how close an individual is to another individual in space. The patterns of association between dyads (pairs of individuals in a group) in primate groups are influenced by many factors including kinship, rank difference, sex and the social and ecological environment they live in. Proximity offers a measurable behaviour with which to assess group dynamics and the relationships between individuals which can then be compared against other behaviours. Affiliative and agonistic behaviours underpin the maintenance of social dynamics within a group. One such affiliative behaviour is grooming, which is often used alongside proximity as a measure of the closeness of social relationships between individuals (Cords, 1997). Grooming concerns the inspection and cleaning of another individual's fur (Roubová et al, 2015). Agonistic behaviour, equally, has an influence on dyadic proximity in primates. It is unlikely that an individual will remain in close proximity with an individual from which it experiences frequent aggression as this could cause psychological stress, risk of injury or death (Mason and Mendoza, 1993). In this study, we consider the variation in inter-individual proximity in Barbary macaques (*Macaca* sylvanus) and how this is influenced by the seasons, grooming and rank difference.

Barbary macaques (*Macaca sylvanus*) are an ideal species in which to study these dynamics. They are typical diurnal primates that form multi-male, multi-female groups. Males in the group are always dominant over females, forming their own hierarchy, and the groups are characterised by female philopatry and male dispersal. Females form matrilineal dominance hierarchies which can remain stable for years (Kapsalis, 2004). Matrilines are subgroups of relatives which provide coalitionary support for one another in contests (Thierry et al, 2004). These hierarchies are intrinsic to the sociality of macaques. This species is 'egalitarian' as opposed to 'despotic' like Rhesus and Japanses macaques (Thierry, 1990): females show less bias towards kin in affiliative behaviour and mothers will rank above their daughters until they reach reproductive age, with younger females unable to rank above their older sisters (Paul and Kuester, 1987). Ranks between individuals are therefore clearly differentiated. Grooming behaviour occurs frequently in primate species, and can engage up to 20% of an individual's time per day so can be observed often (Henzi and Barrett, 1999). Mating is seasonal, occurring in winter, which leads to changes in behaviour, particularly aggressions, depending on the season (Henkel et al, 2010).

The Barbary macaques that inhabit the rock of Gibraltar represent a particularly unique case of human-primate interface. In Europe they are the only free-ranging non-human primates (Unwin and Smith, 2010). They are referenced in records from 1740 but it is possible that they may have been present on the rock from as early as 711 CE (Fa and Lind, 1996). Gibraltar was captured by the British in 1704, and the British Army oversaw the macaques until 1992 when control was passed over to the Gibraltarian government (Zeuner, 1952; Fa and Lind, 1996). Under the British Army, provisioning of the macaques began to prevent them from entering the town, stealing from and damaging properties. Provisioning had been continued until today under the Gibraltar Ornithological and Natural History Society (GONHS) and the Ministry of Environment and Tourism to maintain the macaques as one of the main tourist attractions of Gibraltar (Fa, 1984; Pères and Bensusan, 2005; Fuentes et al, 2007). North African populations of these macaques have been observed consuming a diet including fruits, leaves, seeds, grass, arthropods and tree bark (O'Leary, 1996). The Gibraltar macaques, in contrast, consume much lower levels of arthropods in their diet and high levels of food from tourists and, while intake of food from tourists varies across the groups, provisioned food from the macaque management consistently provides most of their daily diets (O'Leary, 1996). Studies on the ratio of carbon and nitrogen isotopes from macaque hair have shown significant differences between the groups that are exposed to tourists frequently compared to those with much reduced contact, which is likely due to the differences in access to tourist food (Schurr, 2012; Saiyed et al, 2024). While the effects on the health of the macaques is not currently clear, future studies will surely reveal the impact this food has had.

Three quarters of a million people visit the macaques in the Upper Rock Nature Reserve every year, with taxis and buses offering tourists tours of the reserve (GONHS, 2008). Most of the macaque groups experience this large flow of tourism and so are highly habituated to humans, since tourists will often interact with them. Their behaviour has undoubtedly been influenced by this exposure. While feeding the macaques is illegal, this rule is rarely enforced and tourists are often observed feeding the macaques with highly processed foods like ice cream, crisps, chocolate and biscuits (S. Lemoine, pers. comm.). The macaques have also learnt to steal food from the tourists, so can access even more of this food. Taxi drivers use peanuts to encourage the macaques to jump on tourists' shoulders for photos at groups like the Cable Car troop, located near the cable car station on the top of the rock. This illegal provisioning sometimes results in aggressive behaviour from the macaques (Fa, 1992).

Much of the research on the Gibraltar macaques has focussed on the reproductive behaviour, diet and the impact that the anthropogenic environment has had on the macaques (Kümmerli and Martin, 2008; Saiyed et al, 2024; Fuentes, 2006). None of the studies conducted thus far have focussed on inter-individual variation in proximity. Proximity, however, has been studied in other cercopithecine species including other macaque species. Kinship plays an important role in certain macaque species, such as Japanese macaques, where individuals have been shown to preferentially visit food patches with matrilineal relatives (Maruhashi, 1986). Since females are philopatric, it can then be expected that kinship between females is much higher than kinship between males. Females remain in their natal group and so form strong affiliative relationships with other females. Males, by virtue of them being the dispersing sex, and as a result of the female-biased sex ratio in the groups, may be spread further from other males. Males may also remain on the peripheries of the group to better monitor other groups and police within their own group, a common behaviour in non-human primates which involves controlling group in-fighting through impartial intervention (Beisner and McCowan, 2013). However, kinship has also been shown to have less of an effect on the social interactions in more 'egalitarian' societies of macaques, such as the Moor and Sulawesi macaques, so kinship may also play a minor role in proximity (Matsumura and Okamoto, 1997; Thierry, 1990).

Another important factor that may affect proximity in Barbary macaques is seasonal variation. Barbary macaques are known as seasonal breeders, with their mating season during the winter months (Taub, 1980). It is therefore expected for males to be more spread than females during the winter months, since they may stay on the peripheries of their home-ranges and roam more, visiting other groups and hoping to gain opportunities to mate with females from these groups. This is made possible by the fact that the macaque groups have overlapping home ranges.

Grooming may also influence proximity: it is an important reciprocal behaviour which can be used to maintain close social relationships, reduce physiological stress, and act as a market commodity to gain other benefits such as coalitionary support from individuals during agonistic encounters (Gust et al, 1993; Henzi and Barrett, 1999; Schino et al, 2001; Roubová et al, 2015). In this study, we are most interested in it as a measure of the strength of a dyad's affiliative relationship. It is expected, then, that an individual's proximity to another individual should be related to the grooming that has occurred between these two individuals. We are also expecting there to be reciprocity in the grooming between individuals, so that grooming given and grooming received may have a similar impact on the proximity of individuals. If there is association in this direction, we also expect that closer proximity between individuals will result in more grooming between those individuals.

There have been studies on grooming about the Gibraltar Barbary macaques. Schutt et al (2007) investigated how grooming may reduce physiological stress in the Middle Hill troop, finding that giving grooming is associated with lower stress levels in the macaques. Roubovà et al (2015) tested whether grooming was related to rank, kinship and friendship in the females of the Apes Den group, finding that grooming was reciprocally exchanged between individuals and that it was usually directed up the hierarchy. Sonnweber et al (2015) have also investigated the factors affecting post-copulatory grooming on the Apes Den group and Prince Philip's Arch group. None of these studies have of yet focussed on how grooming may influence the inter-individual distances of these macaques.

The papers on rank difference, again, have not considered yet its association with proximity. Papers previously published on rank difference in Gibraltar have focussed on whether it impacts reproductive success, finding no evidence that higher rank significantly improves reproductive success in males or females (Shutt et al, 2007; Modolo and Martin, 2008). Groups of primates are often organised into dominance hierarchies where the higher-ranked individuals have first access to resources such as food and mates (Swedell, 2012). Higher-ranked individuals are also usually found in a more central position than low-ranking individuals, reflecting their priority of access, and to avoid predation in species where predation risk is high (Sueuer et al, 2011; Heesen et al, 2014; Amici et al, 2021). The Barbary macaques have no predators on Gibraltar, but it is expected that dyads within which there is a smaller rank difference will be in closer proximity than dyads who have a greater difference in rank, reflecting conflict avoidance and the priority of access.

Many of these studies have thus far focussed on only one or two of the groups living on Gibraltar, but since this human-primate interface is so unique, it may be more representative to include more than just one or two groups in a study. The importance of the anthropogenic environment cannot be underestimated. It is a unique interface where the study of non-human primates is facilitated by the fact that most of the groups are habituated to humans. All the groups have different exposure to tourists and this has altered their behaviour. The Apes Den group has been said to experience up to 100 interactions per hour at peak times during the summer months and 13.2% of their day is spent interacting with humans (O'Leary and Fa, 1993). Their diurnal activities have even adapted to the tourist visitation patterns, meaning they spend 41.9% of their day inactive, waiting for buses to arrive. This is a study from the early 90s, when there were less troops and touristic attractions, so this exposure may have altered with the growth of the tourist industry. Other groups, like the O'Hara group, experience lower levels of tourism since the taxi and buses do not take their tours up to O'Hara's battery, a historical artillery battery which is no longer in use but can be visited by foot. There may then be much variation in the behaviour between groups, making it important to include multiple groups in studies. There are already different cultural traits emerging between them: for example, two groups that are more exposed to high levels of tourism have learnt to unzip bags, giving them the ability access even more tourist-derived food (S. Lemoine, pers. comm.). The other groups with less tourist exposure do not exhibit this cultural trait. More frequent human-macaque interactions have been shown to shorten grooming and resting times in Rhesus and Bonnet macaques living in urban and semi-urban areas (Kaburu et al, 2018; Kaburu et al 2019; Balasubramaniam et al, 2020).The anthropogenic environment in which the macaques live must be considered since this may alter and add to the macaques behavioural repertoire (Sawchuk and Tripp, 2019).

In this study, variation in inter-individual proximity was investigated in five of the eight groups of Barbary macaques in Gibraltar. The aims of this paper are to test the assumptions that males have greater inter-individual distance between them than females, that grooming positively influences proximity within dyads, that proximity variation positively influences grooming and that individuals that are closer in rank will be closer in proximity.

Materials and Methods

Study Site and Population

The study population was five out of the eight stable neighbouring groups of Barbary macaques living in the Upper Rock Nature Reserve of Gibraltar (36°8'N, 5°21'E; Figure 1). Established in 1993, it stretches from North to South covering 2.5-3 km of the middle and upper slopes of a Jurassic limestone uplift named the Rock of Gibraltar (Fuentes et al, 2007). The reserve's highest peak is 424m above sea level, and the terrain includes cliff faces, fire breakers, high maquis and other habitats (Fa, 1984). Human infrastructures cover the rock, with extensive roads, trails, restaurants, a cable car, landscape and monkey viewing points, and tourist attractions including gun batteries, tunnels and a cave.

The groups studied were Apes Den (AD), Cable Car (CC), O'Hara (OH), Prince Philip's Arch (PPA) and Royal Anglian Way (RAW), all of whom have overlapping home-ranges (Figure 2). The population consists of about 230 macaques and has split into eight stable groups living in different areas on the rock. AD is the longest-standing group, having been established in the 19th century, giving rise of the Middle Hill group in the 1960s, and has been visited by tourists consistently since the 1930s (Fa, 1984; Shaw and Cortes, 2006; Fuentes et al, 2007). The other groups are the result of group fissioning because of population increases that culminated in six stable groups around 2004 (Fuentes et al, 2004). PPA then split to form CC, and split into OH more recently. AD is usually found at Queen's Gate and spread up the stairs towards Prince Philips Arch. CC is located around the cable car and down towards Prince Philips's Arch. PPA frequents the Skywalk, a panoramic viewing platform, and Prince Philip's Arch when CC is not there. OH is located around O'Hara's Battery. RAW is found around St. Michael's Cave, a popular tourist attraction with a café. AD and RAW locations can be accessed by bus, taxi and on foot. CC and PPA are accessed by the cable car, taxi and on foot. OH is usually only visited by people on foot since the bus and taxi tours do not journey up there. As a result, each group experiences varying degrees of touristic pressure.

Only adult and subadult individuals in the groups were included in the analysis. Infants and juveniles were excluded since it is much harder to differentiate between them as they were still growing over the study period. The largest group was CC with a mean group size of 33 individuals over the study period and the smallest was OH with 12 individuals (Table 1). Group size stayed quite stable over the study period, only varying by 2 individuals at most. The variation was caused either by the deaths of individuals or the migration of males between groups.

Table 1. Table of the mean number of adults and subadults overall, mean number of females and mean number of males in each group during the study period.

Group	All Adults and Subadults		Males		Females	
	Mean	Standard Deviation	Mean	Standard Deviation	Mean	Standard Deviation
Apes Den AD	24	1	6	1	18	0
Cable Car CC	33	1	10	1	23	0
O'Hara OH	12	2	5	1	7	1
Prince Philip's Arch PPA	18	1	4	1	14	1
Royal Anglian Way RAW	21	1	8	1	14	1

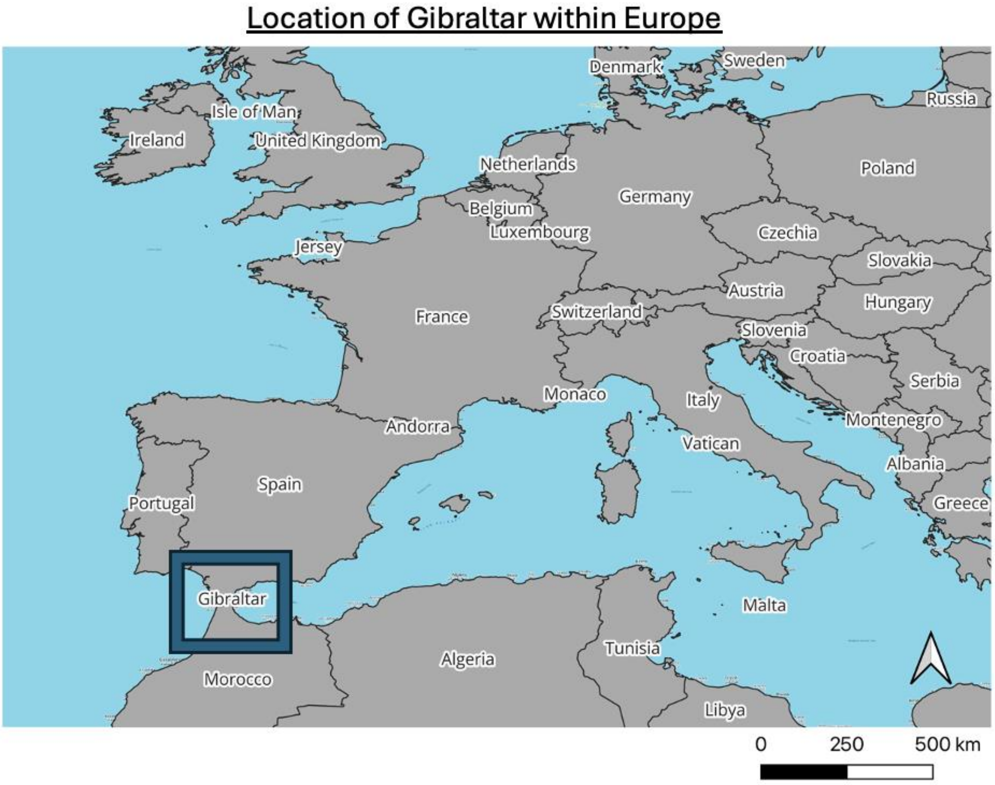

Figure 1. Map showing the location of Gibraltar in Europe.

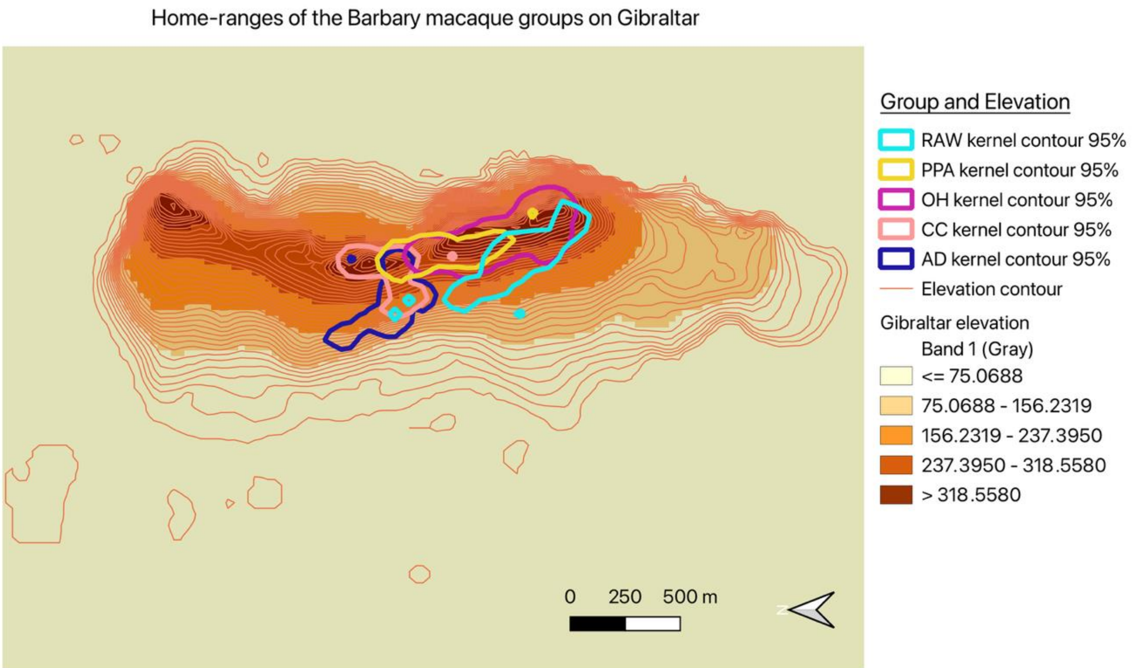

Figure 2. Map showing the overlapping home-ranges of the Barbary macaques. The home-ranges are produced using kernel contour 95% defines the home-range where the macaques spend 95% of their time.

Data collection

Data was collected for this project over a one-year period, from August 2023 to August 2024. The data was collected in seasons with data available for Summer 2023 (15/08/2023 to 14/09/2023), Winter 2023/24 (06/12/2023 to 17/01/2024) and Summer 2024 (07/08/2024 to 14/08/2024). We pooled the data from the two summers into one summer dataset to be compared with the winter dataset. I was involved in the data collection that occurred in the Summer of 2024. Observation sessions lasted 7 to 8 hours and alternated between groups each day. All observational data was non-invasive collected in accordance with the guidelines established by the International Union for Conservation of Nature. Data collection protocols have been approved by the Ethics Review Board of the Archaeology Department, University of Cambridge.

The data collection protocol consists of 1h focal follows and group scan sampling (Altmann, 1974), alternating across the day. In this study, inter-individual distances were extracted from group scan data. The scan data was taken by recording a GPS location of each visible individual in a target group, noting the individuals age class and activity. Individuals were identified, and if necessary, photographs were taken. The groups were followed on alternating days, with these scans being taken multiple times per day. Focal follow data consisted of one hour-long observations on a single adult or subadult individual with GPS tracking recorded every 30 seconds. During the hour, the following information was recorded every minute: activity of the target individual, the substrate used, whether the target was in the shade or the sun, the proximity of humans to the target, which direction the target faced, and the number of conspecifics visible to the target. A distance of at least 2 metres was maintained between us and the target so as not to stress the individual. Data was recorded on tablets and iPhones using CyberTracker software. GPS tracking and waypoints were recorded using handheld Garmin GPSs.

Building the Social Networks

The following network terms will be used in the description below (following Kasper and Voelkl, 2009; Zhang et al, 2012; Farine and Whitehead, 2015). A node, in this case, represents an individual macaque and the edges in the networks represent how these macaques relate to each other. All edges in the networks used in this analysis were weighted, possessing a numeric value indicating the strength of the relationship between the two nodes they connect. The networks used in this analysis are weighted. Edges can also be either undirected (e.g. A is in proximity to B) or directed (e.g. A gives grooming to B).

For each scan and each group, we used the coordinates and elevation measurements to make matrices which contained inter-individual distances between each dyad. Given the nature of the landscape where individuals can be located across the rock's slopes, the longitude, latitude and elevation recorded from the GPS were considered to reconstruct the exact locations of individuals. Although 95% of adults in the population have been identified, identification of all individuals was not possible in some of the group scans. We chose to include scans where at least half of the adult and subadult females had been identified. This was to ensure that multiple distance measurements for each dyad combination in each group could be used to create the social networks so that distances were representative, as spatial proximity can vary substantially. If the total number of adult or subadult females in the scan was an odd number but almost half of these females had been identified (for example 3 out of 7), we included the scan in the analysis. Adult and subadult males are easier to identify than females since there are fewer in each group, given that these macaques have a female-biased sex ratio. The mean number of usable scans per group was 24 and the mean number of usable scans per group per season was 8 (see Table 2 for the number of usable scans per group). The mean proportion of adults and subadults identified in each scan per group was 0.81 or 81%.

We used the matrices from the scans to build undirected proximity social networks for each season and an average network across all seasons for each group. We used the median of the inter-individual distances for these networks since these distances were quite variable – the mean maximum distance of 413.248 metres between individuals per group. The median, by contrast, is less sensitive to extreme values. We constructed weighted networks for proximity: one node represented one individual in the group, and the edges connecting them represented how close the individuals were to each other, weighted by a normalised proximity score between 0 and 1. We calculated the reciprocal of the median distance between each dyad to invert the measurements (1/median distance) and then normalised the values using the minimum-maximum scaling for each group. This meant that the closer a dyad's score was to 1, the closer the individuals were to each other. Some individuals were never observed together in group scans so distance measurements for certain dyads were not recorded. Inverting the data allowed these cases to be assigned a proximity score of 0, implying that they were very far apart. All social networks were produced using the R-package 'igraph' (v. 2.1.4).

Figure 3. The first photo shows of one adult female giving grooming and another receiving grooming while sleeping. The second photo shows an adult female sleeping with her infant while being groomed by another adult female.

Group scan data may inflate correlations between proximity and grooming, since individuals in close proximity who are grooming are more likely to be recorded. We therefore also included grooming data from focal follows in the matrices. We built grooming networks, where one node represented one individual, and the edges were weighted by the number of grooming occurrences that occurred between named individuals observed over the study period per group (see Figure 3 for examples of grooming). The networks were directed from the individual giving to the individual receiving the grooming. A 0 represented that no observed grooming interaction within the dyad had been observed. We transposed the networks so that there was both a grooming given and grooming received directed network (henceforth, GRG and GRR).

To investigate whether there was a significant relationship between the proximity and grooming networks, we used the multiple regression quadratic assignment procedure (MR-QAP), an extension of the quadratic assignment procedure developed to allow the inclusion of multiple matrices as covariates (Krackhardt, 1988). This is a permutation-based approach to hypothesis testing, which accounts for the non-independence of network data– by randomly shuffling the rows and columns of the tested matrices multiple times (van der Waal et al, 2014). We used the R-package 'asnipe' (v. 1.1.17) and the R function *mrqap.dsp* to compute the results using the double semi-partialling method (DSP) and 5000 permutations (Dekker et al, 2007). DSP randomises the residuals, regressed from each independent variable, to calculate a p-value (Dekker et al, 2007). DSP works by removing the influence of all other predictor matrices from the predictor of interest and the dependent variable, then testing the association between the residuals. The p-value obtained reflects the proportion of permuted datasets in which the semi-partial correlation between the residualised predictor and the outcome is as large (or larger) than the observed correlation. This provides a non-parametric test of significance, accounting for dyadic dependence and thus providing accurate statistical inference.

We first used the proximity matrix created from the full social network for the study period as the response matrix, testing it against the GRG and GRR matrices (model 1P) to assess whether grooming interactions could explain proximity. Since these had more individuals than the data available for the grooming matrices, proximity matrices had to be cut down to match the number of individuals in the grooming networks. The grooming matrix for CC reduced the most, from 32 to 20 individuals. We created binary dummy matrices to test whether the sex match or no sex match between individuals was associated with proximity (model 2P), and ran a test with only them as covariates: the sex match matrix had a 1 if the dyad was male-male and a 0 if not, and the no sex match matrix had a 1 if the dyad was male-female or female-male and a 0 if not. Female-female dyads were the reference level for these matrices. We then ran models which included the grooming matrices and sex matrices to see if the associations changed when all the matrices were included (model 3P). We also ran two models using GRG and GRR as the dependent matrix in each model respectively (model GRG and model GRR), and the proximity matrix and the sex matrices as the independent variables, to see if proximity would influence grooming direction when controlling for sex pairing within a dyad. We repeated this for each group. We defined marginal significance as $p < 0.10$ and a value as significant if $p < 0.05$.

Table 2. Table of number of usable scans per group. AD refers to adult individuals and SAD refers to subadult individuals.

Group	Total number of usable scans	Mean number of usable scans per season (SD)	Mean proportion of AD and SAD identified in scans
Apes Den	24	8 (3)	0.77
Cable Car	15	5 (1)	0.80
O'Hara	23	8 (1)	0.77
Prince Philip's Arch	25	8 (4)	0.84
Royal Anglian Way	34	11 (8)	0.85

Rank Difference Statistical Analyses

We wanted to test whether rank difference influenced inter-individual proximity within the groups, assuming that individuals close in rank should be close in proximity. We used GLMMs (generalised linear mixed models) instead of social network analysis since the interaction data was too sparse to create comparable social networks. We used David's Scores (DS) (David, 1987, 1988) to calculate hierarchies within the groups. This is a measure of an individual's success which considers the outcome of agonistic interactions within dyads in a group. It is based on the sum of unweighted and weighted proportions of an individual's losses subtracted from the sum of unweighted and weighted proportions of an individual's wins in agonistic interactions, where the weighted values are the individual's summed win or loss proportions weighted by the summed win or loss proportions of its interaction partners (David, 1978, 1988; de Vries et al, 2006). Defeating a high-ranking individual is valued greater than defeating a low-ranking individual. We used the group scan and focal follow data to gain frequencies of wins and losses within the dyads in the groups. Overall, a total number of 138 interactions were observed over the study period. The mean number of agonistic interactions per group was 16 for females and 14 for males. We used these to calculate the DSs for each individual, splitting these calculations by sex, since macaques are organised into matrilineal dominance hierarchies and male and female dominance ranks should be considered separately (Kapsalis, 2004). Since there were low numbers of interactions available, we could not use a more dynamic measure of the hierarchies so the assumption was that the ranks remained stable over the year. The DSs were used to give each individual an ordinal rank in their group, which were then standardised into a proportional relative rank within each group, ranging 1 and 0. The difference between these scores was used to calculate the rank difference between all same-sex dyadic pairs in each group.

We fitted 16 GLMMs with a Gaussian error structure to analyse how distance within dyads was influenced by different within-group factors. The main model (model 1) used the full dataset, using data from all groups and both sexes. In OH, agonistic interaction data was only available for females, so only females from OH were included in the models. The test predictors included rank difference within dyads, group and sex. These were included as the model's fixed effects. Rank difference was z-transformed to normalise the variable before being used in the models (to a mean of 0 and a standard deviation of 1). We included random effects of the combination of the date and scan number, and the dyad identity. To keep type 1 error rates at the nominal level of 5%, random intercepts for dyad, and random intercepts and slopes for rank difference, group and sex across the different unique combinations of date and scan number were incorporated to account for repeated observations for each dyad on the same day.

We then split the dataset by sex and ran two different models with the same fixed and random effects, one on only females (model 1F) and one on only males (model 1M), but excluding sex as a fixed and random effect. We then split the dataset by group and ran separate models for each of the groups, using the same fixed and random effects as the main model (model 1) but excluding group as a fixed and random effect. We split these datasets by sex into female-only and male-only, running similar models without the effect of sex. We split the models by sex and group since the hierarchical set-up and social interactions may differ between groups and sexes. We wanted to investigate the effect of rank difference and group on social proximity with each sex separately. OH only had a model including females (model OHF) since male rank data was not available for the group. Details of model structures and their respective sample sizes can be found in Table 3. All models were fitted in R using the function *lmer* of the R-package 'lme4' (v. 1.1-37) (Bates et al, 2015).

We checked the assumptions of the models and tested for model stability. These tests did not return any major issues and globally model assumptions were fulfilled. We used likelihood ratio tests (R function *anova,* argument test set to 'Chisq') to check the significance of the full models as compared to the null models (comprising only random effects, intercepts and slopes) (Dobson and Barnett, 2008). The models were fitted using maximum likelihood, rather than restricted maximum likelihood, to allow for the likelihood ratio test. R function *drop1* was used to obtain *p*-values for the individual effects which were based on these likelihood ratio tests. For the models which included group as a test predictor (models 1, 1F, 1M), *post-hoc* Tukey Honest Significant Difference (HSD) were run to investigate any pair-wise differences between groups (R-package *emeans* (v. 1.10.6), argument adjust set to 'tukey').

Table 3. Table of GLMM model names, the data used for each model and each model's sample size.

Model Name	Model Contents	Sample Size

1	Full dataset, all groups, both sexes	2093
1F	Full dataset, all groups, only females	1689
1M	Full dataset, all groups, only males	404
1AD	Full dataset, AD, both sexes	614
1ADF	Full dataset, AD, only females	513
1ADM	Full dataset, AD, only males	101
1CC	Full dataset, CC, both sexes	493
1CCF	Full dataset, CC, only females	327
1CCM	Full dataset, CC, only males	121
1PPA	Full dataset, PPA, both sexes	290
1PPAF	Full dataset, PPA, only females	237
1PPAM	Full dataset, PPA, only males	53
1RAW	Full dataset, RAW, both sexes	594
1RAWF	Full dataset, RAW, only females	465
1RAWM	Full dataset, RAW, only males	129
1OHF	Full dataset, OH, only females	102

Results

Seasonal Variation in Proximity Social Networks

We compared the summer and winter networks of each season by extracting the summary statistics for the inter-individual distances within dyads of different combinations of sex.

For AD, the summer network had 25 nodes and 247 edges, and the winter network had 21 nodes and 187 edges (Figure 4). Male-male dyads (MM dyads), female-female dyads (FF dyads) and mixed-sex dyads were all more distant from each other during winter than summer (Table 4; Figure 5). However, inter-individual distance in summer was more variable, as shown by the higher standard deviations and the larger whiskers on the boxplot (Table 4;

Figure 5). Interestingly, MM dyads had lower maximum and median inter-individual distance than female-female dyads in winter, which does not align with the hypothesis that males would be more spread than females during the mating season (median: MM dyads = 64.556m, FF dyads = 72.211m; Table 4).

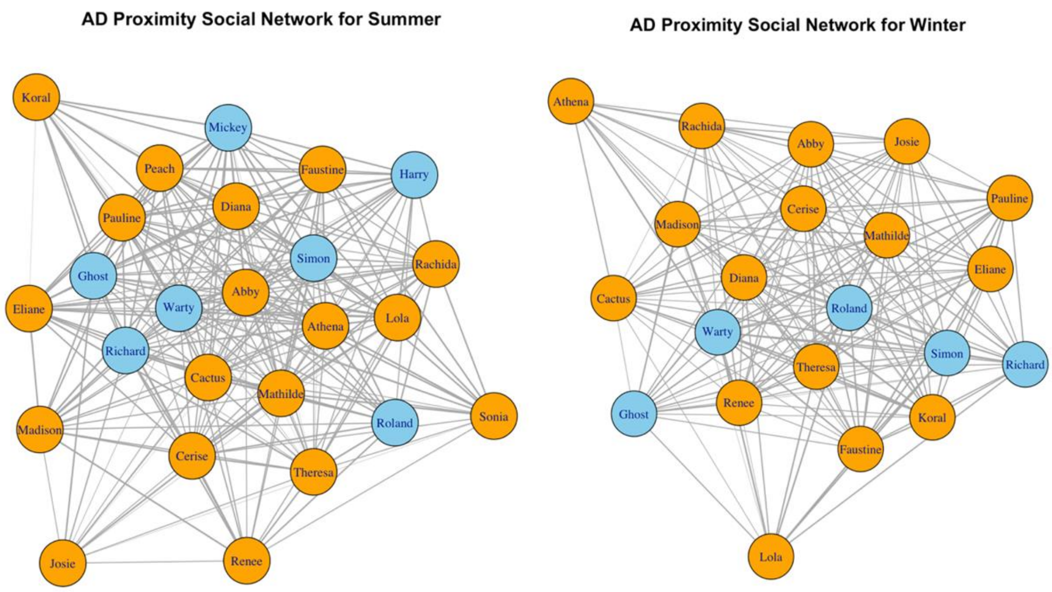

Figure 4. The first plot shows the AD proximity social network for Summer. The second plot shows the AD proximity social network for Winter. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. Orange individuals are females, blue individuals are males.

Table 4. Table comparing AD Summer and AD Winter Inter-individual distances in metres within dyads of different sex combinations. FF = female-female, M-M = male-male, Mixed = male-female. SD = Standard Deviation.

Season	Sex Pair Type	Mean	Median	SD	Minimum	Maximum
Summer	FF	67.938	43.289	61.184	0.000	273.541
	MM	58.894	32.571	61.108	0.000	216.841
	Mixed	64.618	38.243	62.372	0.000	267.638
Winter	FF	80.572	72.211	44.556	8.201	214.897
	MM	78.813	64.556	41.849	39.748	160.192
	Mixed	77.364	73.583	52.094	0.000	276.197

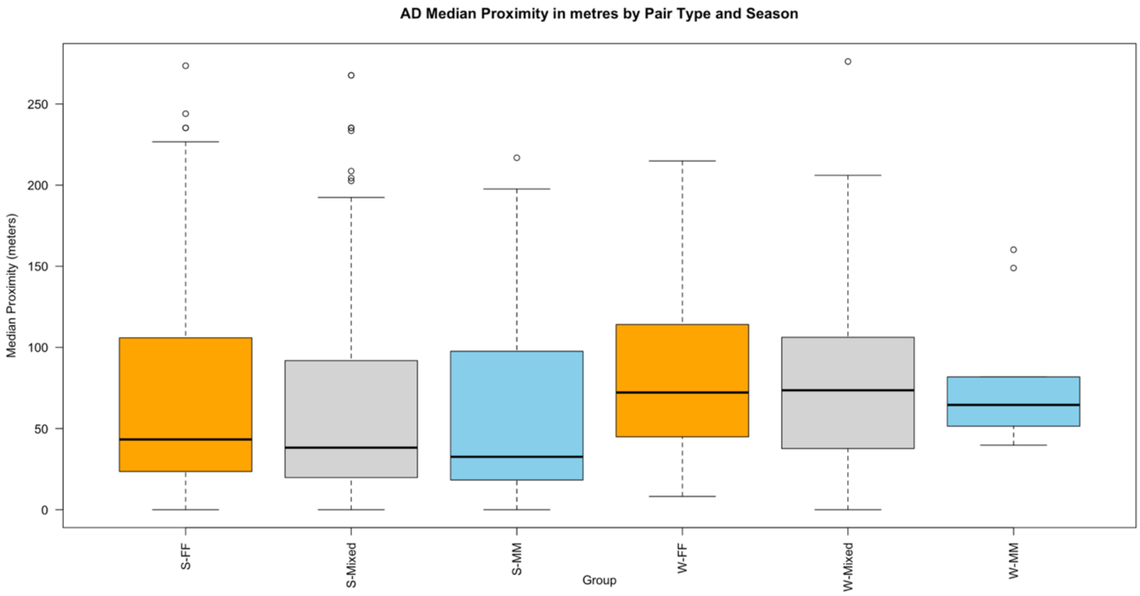

Figure 5. Boxplot comparing AD median inter-individual distances between the summer and winter grouped by sex pair type. S-FF = Summer distances within female-female dyads, S-Mixed = Summer distances within mixed dyads, S-MM = Summer distances within male-male dyads. W-FF = Winter distances within female-female dyads, W-Mixed = Winter distances within mixed dyads, W-MM = Winter distances within male-male dyads.

For CC, the summer network had 32 nodes and 391 edges, and the winter network had 26 nodes and 192 edges (Figure 6). The winter median inter-individual distance between dyads were greater than the summer median inter-individual distances as was expected (Summer: MM = 24.391m, FF = 28.955m; Winter: MM = 40.087, FF = 33.568m; Table 5; Figure 7). MM dyads had greater median inter-individual distance in winter compared to summer, and greater median inter-individual distance in winter than FF dyads. FF dyads, again, had a greater maximum distance within dyads than MM dyads in both summer and winter at 258.485m and 136.973m compared to 215.127m and 100.132m which is logical since there are more females than males in the group, so probability to have longer maximum distances between females is higher. The maximum inter-individual distances were greater in summer than in winter but these are likely outliers (Figure 7). However, the whiskers of the boxplots all overlapped, suggesting that the data from both seasons was similar in range.

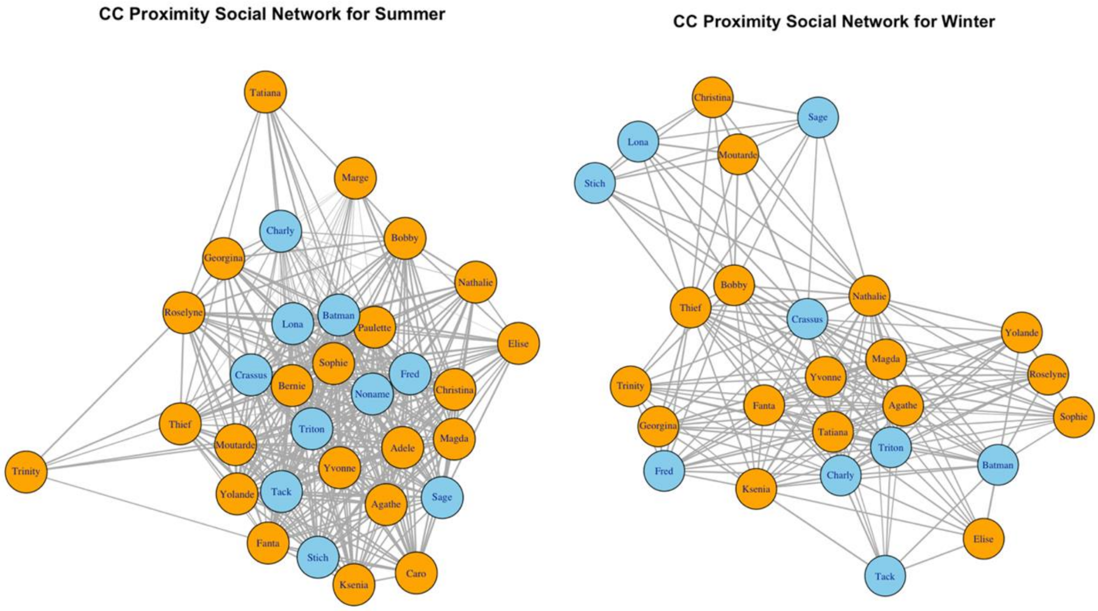

Figure 6. The first plot shows the CC proximity social network for Summer. The second plot shows the CC proximity social network for Winter. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. Orange individuals are females, blue individuals are males.

Table 5. Table comparing CC Summer and CC Winter Inter-individual distances in metres within dyads of different sex combinations. FF = female-female, M-M = male-male, Mixed = male-female. SD = Standard Deviation.

Season	Sex Pair Type	Mean	Median	SD	Minimum	Maximum
Summer	FF	52.822	28.955	58.341	0.000	258.485
	MM	56.097	24.391	64.748	1.793	215.127
	Mixed	49.344	26.673	56.176	0.000	268.590
Winter	FF	39.160	33.568	25.314	0.000	136.973
	MM	44.775	40.087	26.054	5.794	100.132
	Mixed	39.031	36.615	23.470	0.000	100.132

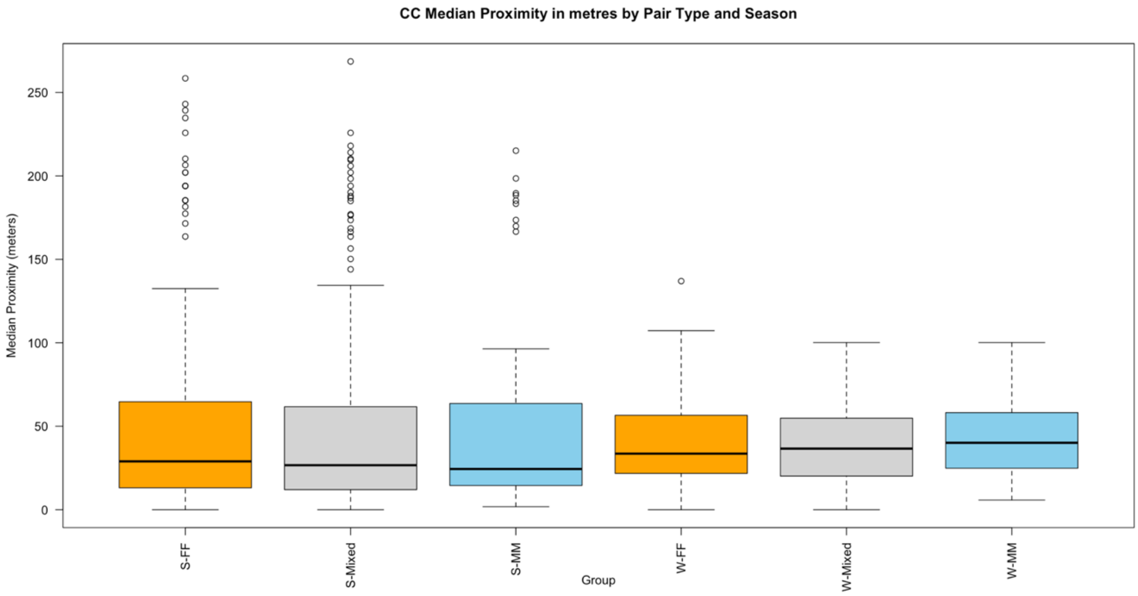

Figure 7. Boxplot comparing CC median inter-individual distances between the summer and winter grouped by sex pair type. S-FF = Summer distances within female-female dyads, S-Mixed = Summer distances within mixed dyads, S-MM = Summer distances within male-male dyads. W-FF = Winter distances within female-female dyads, W-Mixed = Winter distances within mixed dyads, W-MM = Winter distances within male-male dyads.

For OH, the summer network had 12 nodes and 48 edges, and the winter network had 10 nodes and 41 edges (Figure 8). The winter median inter-individual distance within MM dyads was over three times higher than the median inter-individual distance within FF dyads (Winter: MM = 184.436m, FF = 52.414; Summer: MM = 48.565, FF = 30.841; Table 6; Figure 9), and within the MM dyads for summer (Table 6). The maximum inter-individual distance for winter was highest within MM dyads at 263.890m but the maximum FF dyad inter-individual distance was highest in summer at 390.156m. This is likely an outlier in the distribution of the data (see Figure 9).

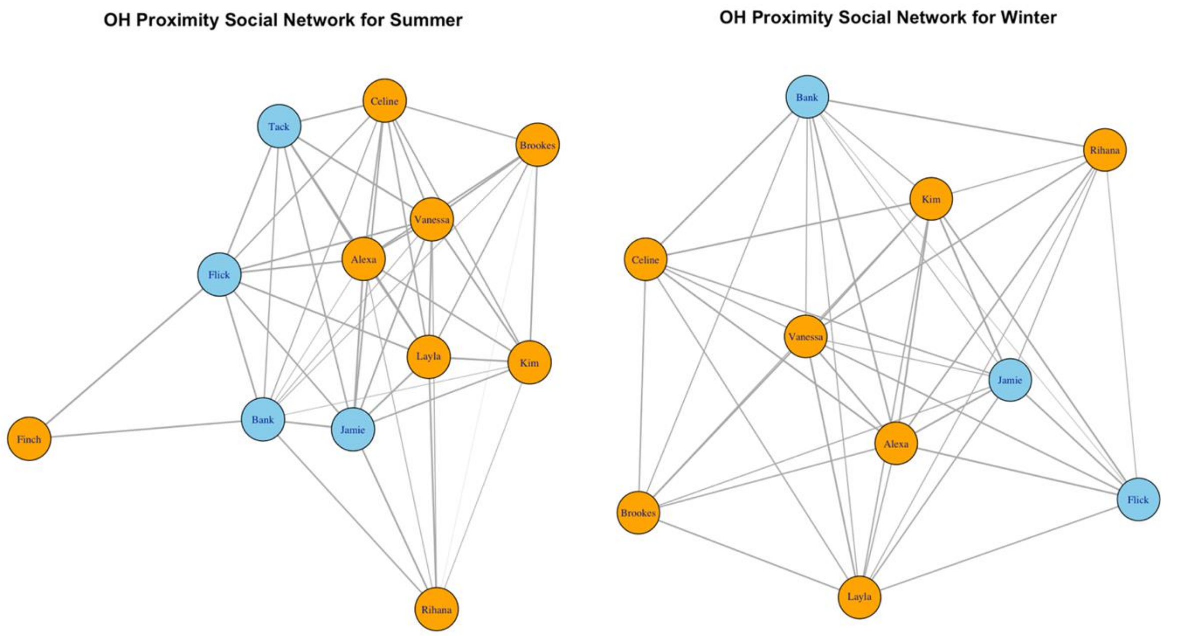

Figure 8. The first plot shows the OH proximity social network for Summer. The second plot shows the OH proximity social network for Winter. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. Orange individuals are females, blue individuals are males.

Table 6. Table comparing OH Summer and OH Winter Inter-individual distances in metres within dyads of different sex combination.

Season	Sex Pair Type	Mean	Median	SD	Minimum	Maximum
Summer	FF	78.928	30.841	108.224	1.638	390.156
	MM	53.980	48.565	32.434	13.156	110.802
	Mixed	72.838	37.675	37.675	0.000	249.302
Winter	FF	71.327	52.414	50.939	12.446	170.948
	MM	160.817	184.436	116.690	34.124	263.890
	Mixed	84.763	82.837	63.019	0.000	192.481

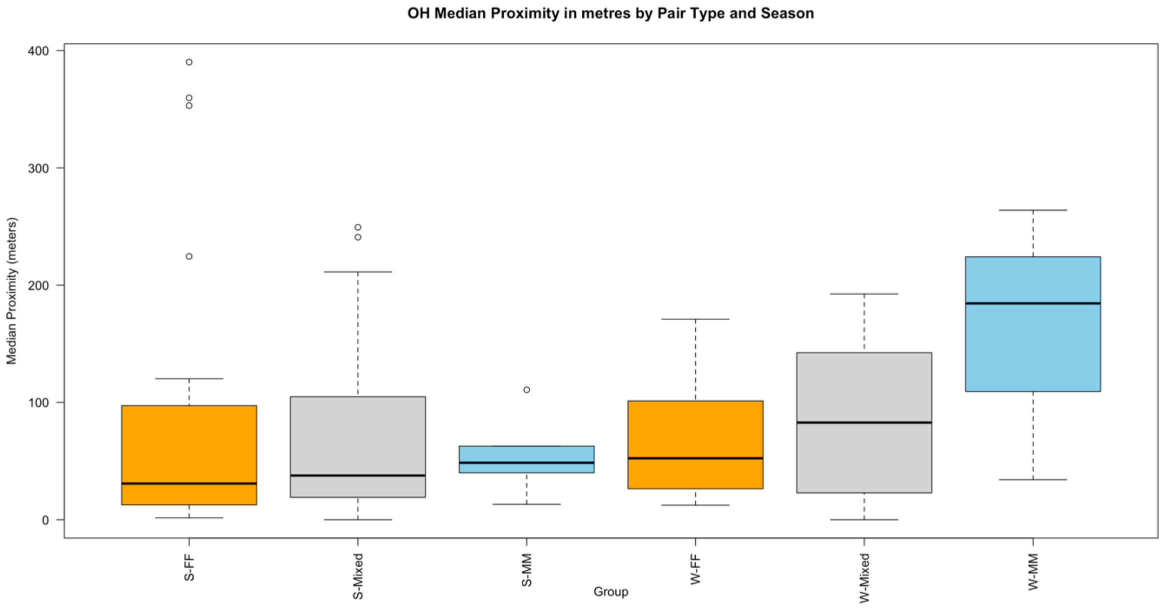

Figure 9. Boxplot comparing OH median inter-individual distances between the summer and winter grouped by sex pair type. S-FF = Summer distances within female-female dyads, S-Mixed = Summer distances within mixed dyads, S-MM = Summer distances within male-male dyads. W-FF = Winter distances within female-female dyads, W-Mixed = Winter distances within mixed dyads, W-MM = Winter distances within male-male dyads.

For PPA, the summer network had 17 nodes and 121 edges, and the winter network had 15 nodes and 100 edges (Figure 10). The median inter-individual distance within MM dyads was much higher in summer at 80.791m compared to winter at 25.234m (Table 7). This is not in line with the expectation that males will be more spread during the winter mating season. MM dyadic median distances were greater than FF median dyadic distances in summer and winter (Summer: FF median = 36.556m; Winter: FF median = 20.698m; Table 7). The boxplot showed that the inter-quartile ranges (IQR) in winter were much smaller than those in summer in all pair types, the most obvious difference being between summer and winter inter-individual distance within the MM dyads (Figure 11). This showed that 50% of the MM dyadic inter-individual distance in summer was greater than the MM dyadic inter-individual distance in winter. The maximum inter-individual distances were greater within MM dyads in summer but within FF dyads in winter (Table 7). Again, this may be due to outliers.

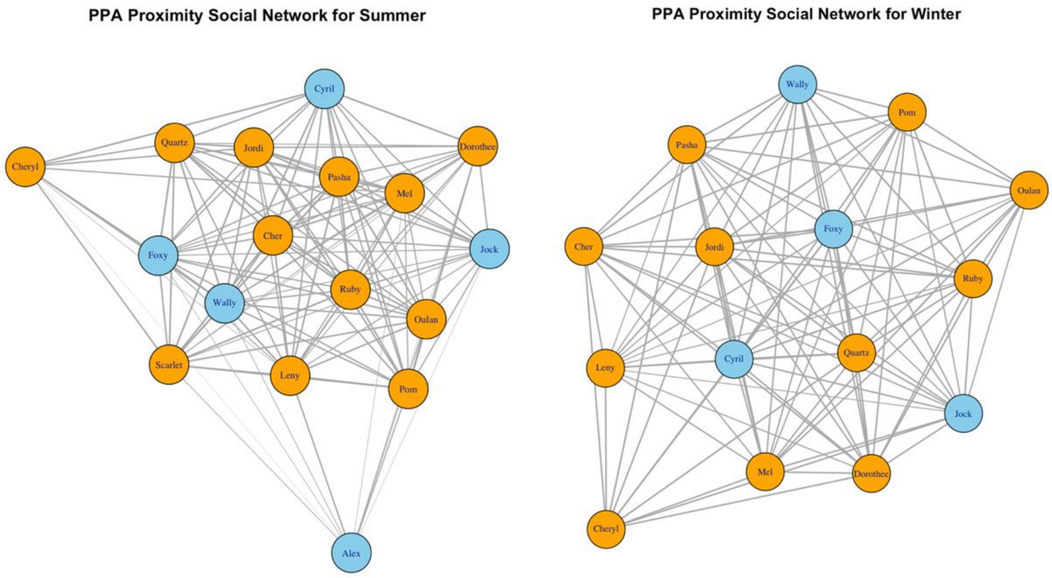

Figure 10. The first plot shows the PPA proximity social network for Summer. The second plot shows the PPA proximity social network for Winter. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. Orange individuals are females, blue individuals are males.

Table 7. Table comparing PPA Summer and PPA Winter Inter-individual distances in metres within dyads of different sex combinations. FF = female-female, M-M = male-male, Mixed = male-female. SD = Standard Deviation.

Season	Sex Pair Type	Mean	Median	SD	Minimum	Maximum
Summer	FF	54.534	36.556	58.259	0.000	223.767
	MM	111.088	80.791	81.933	6.663	250.623
	Mixed	71.645	54.330	76.016	0.000	328.119
Winter	FF	29.321	20.698	28.318	0.000	117.020
	MM	24.664	25.243	10.130	10.300	39.071
	Mixed	29.718	21.768	25.881	0.000	134.100

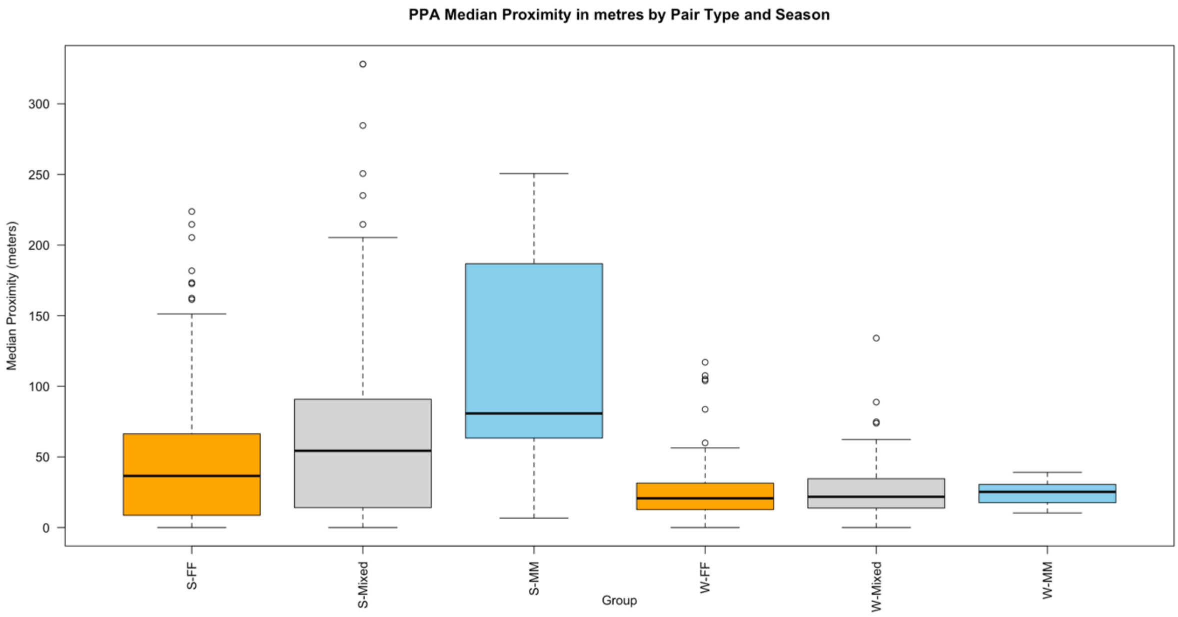

Figure 11. Boxplot comparing PPA median inter-individual distances between the summer and winter grouped by sex pair type. S-FF = Summer distances within female-female dyads, S-Mixed = Summer distances within mixed dyads, S-MM = Summer distances within male-male dyads. W-FF = Winter distances within female-female dyads, W-Mixed = Winter distances within mixed dyads, W-MM = Winter distances within male-male dyads.

For RAW, the summer network had 21 nodes and 184 edges, and the winter network had 22 nodes and 210 edges (Figure 12). The median inter-individual distances within MM dyads was higher than within FF dyads in winter and summer (Summer: MM = 115.100m, FF = 92.640m; Winter: MM = 97.805m, FF = 58.639; Table 8; Figure 13). The median distance within MM dyads was slightly higher in summer, with a greater maximum distance of 350.845m compared with 308.335m in winter. This was quite a minor difference so no real difference between the seasons (Table 8). This, again, was not in line with the hypothesis that males are more spread in winter during mating season.

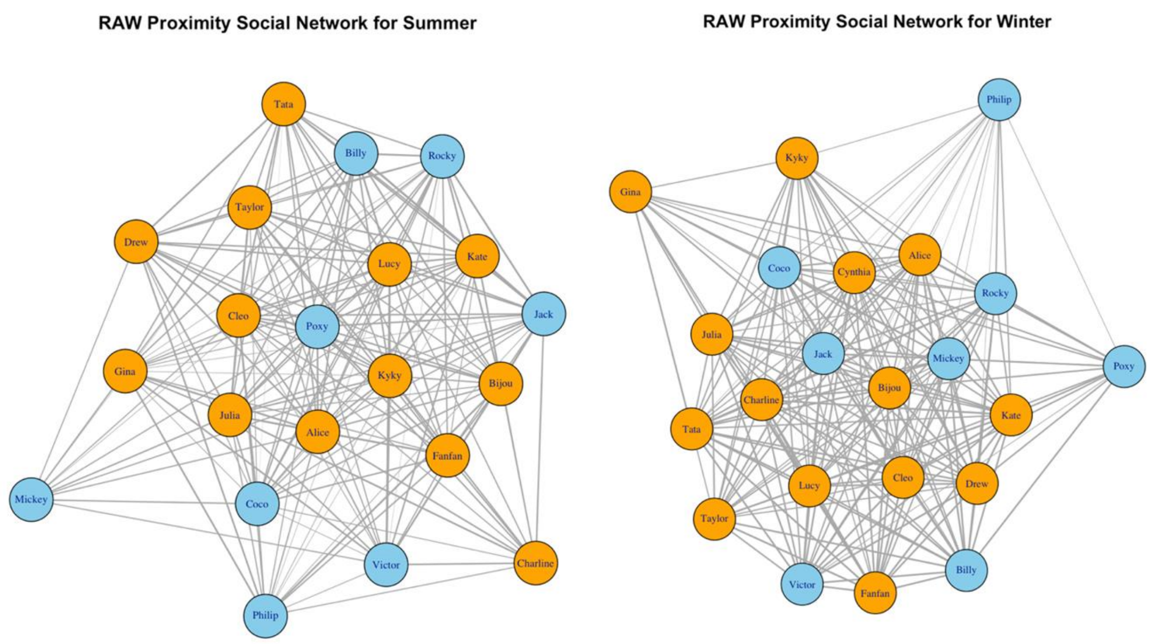

Figure 12. The first plot shows the RAW proximity social network for Summer. The second plot shows the RAW proximity social network for Winter. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. Orange individuals are females, blue individuals are males.

Table 8. Table comparing RAW Summer and RAW Winter Inter-individual distances in metres within dyads of different sex combinations. FF = female-female, M-M = male-male, Mixed = male-female. SD = Standard Deviation.

Season	Sex Pair Type	Mean	Median	SD	Minimum	Maximum
Summer	FF	101.155	92.640	63.730	9.253	297.550
	MM	133.820	115.100	105.066	0.000	350.845
	Mixed	115.142	94.037	89.278	0.000	397.318
Winter	FF	55.999	58.639	58.639	0.000	261.854
	MM	90.782	97.805	97.805	0.000	308.335
	Mixed	63.820	85.275	85.275	0.000	429.963

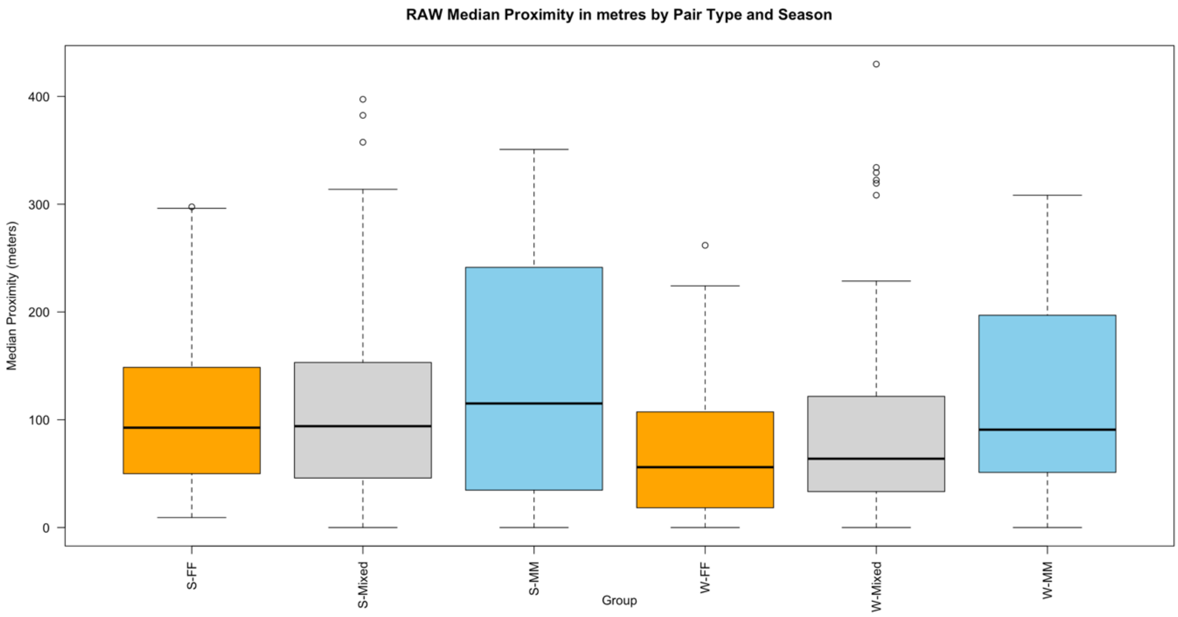

Figure 13. Boxplot comparing RAW median inter-individual distances between the summer and winter grouped by sex pair type. S-FF = Summer distances within female-female dyads, S-Mixed = Summer distances within mixed dyads, S-MM = Summer distances within male-male dyads. W-FF = Winter distances within female-female dyads, W-Mixed = Winter distances within mixed dyads, W-MM = Winter distances within male-male dyads.

Proximity and Grooming Social Networks

Table 9. Table of the variables used in each MR-QAP model. These models were repeated for each group. GRG = grooming given, GRR = grooming received, Sex match = if the dyad is male-male, Sex mixed = if the dyad is male-female.

Model	Response	Covariates
1P	Proximity	GRG, GRR
2P	Proximity	Sex Match, Sex Mixed
3P	Proximity	GRG, GRR, Sex Match, Sex Mixed
GRG	GRG	Proximity, Sex Match, Sex Mixed
GRR	GRR	Proximity, Sex Match, Sex Mixed

We ran the same models on each group to test whether the proximity matrix was significantly predicted by the GRG or GRR matrices while controlling for the sex match and sex mixed matrices (model 1P, 2P and 3P; Table 9). We ran models with the grooming and sex matrices separate first to see how the bivariate associations functioned and whether these changed when they were included in the same model. We then ran the same two models on each group to test whether either the GRG or GRR matrices were significantly predicted by the proximity matrix while controlling for the sex match and sex mixed matrix (model GRG and GRR;

Table 9). The networks are presented below (Figure 14; Figure 15; Figure 16; Figure 17; Figure 18).

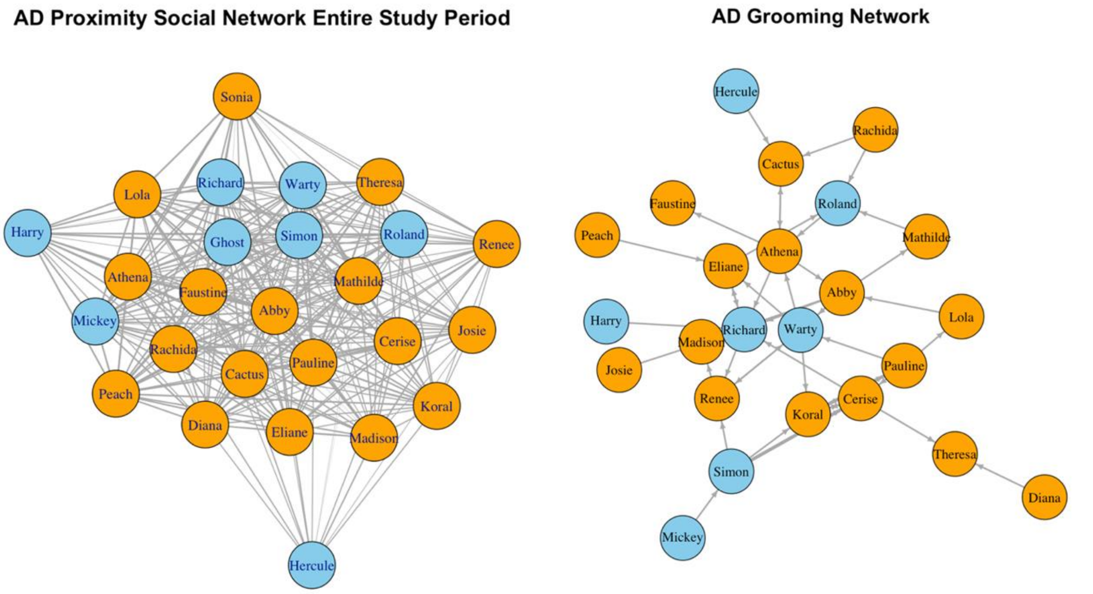

Figure 14. The first plot shows the AD proximity social network for the entire study period. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. The second plot shows the AD grooming network. Arrows are directed in the direction of grooming given and weighted by frequency of grooming given. Orange individuals are females, blue individuals are males.

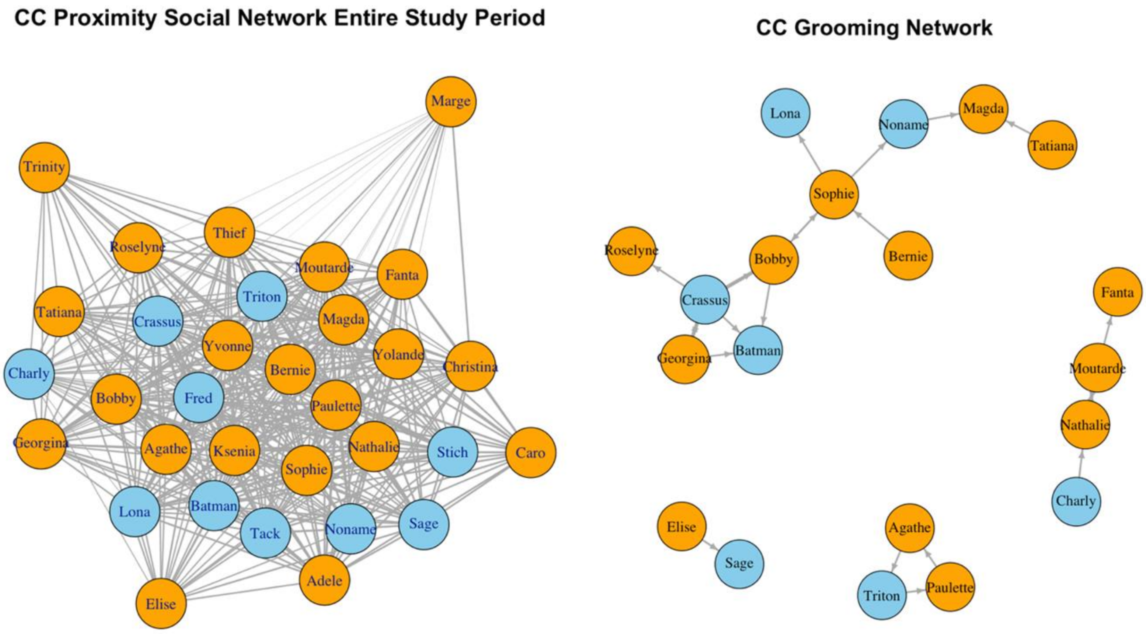

Figure 15. The first plot shows the CC proximity social network for the entire study period. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. The second

plot shows the CC grooming network. Arrows are directed in the direction of grooming given and weighted by frequency of grooming given. Orange individuals are females, blue individuals are males.

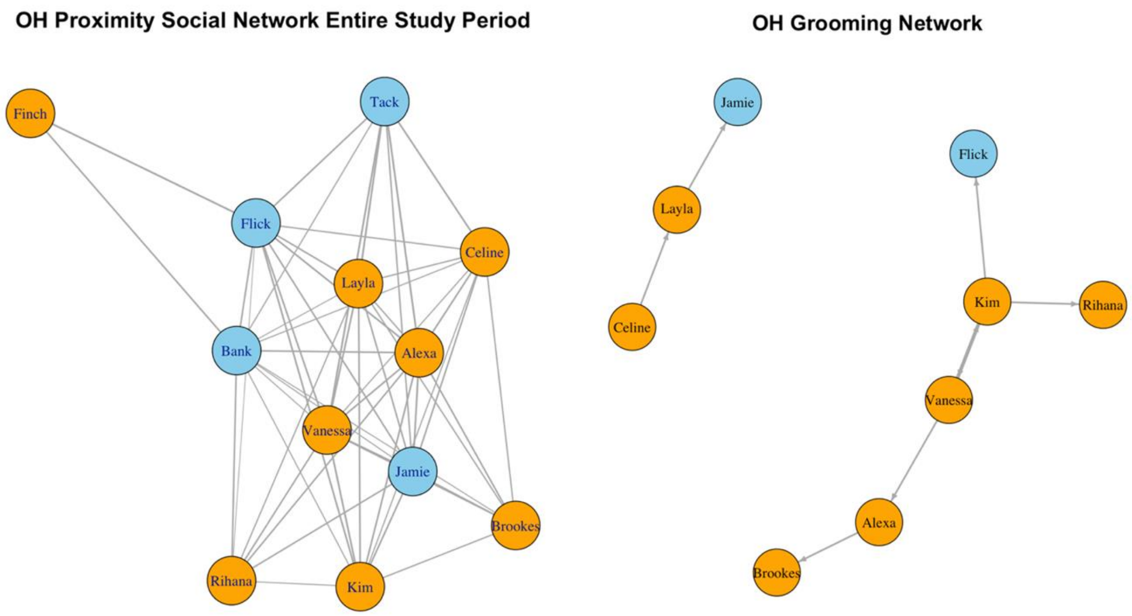

Figure 16. The first plot shows the OH proximity social network for the entire study period. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. The second plot shows the OH grooming network. Arrows are directed in the direction of grooming given and weighted by frequency of grooming given. Orange individuals are females, blue individuals are males.

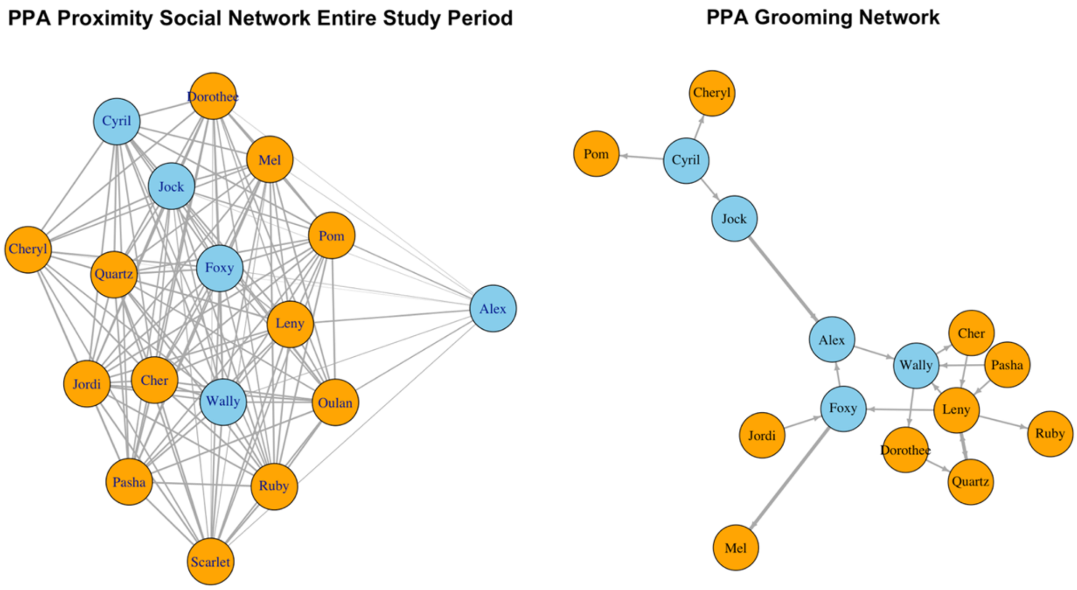

Figure 17. The first plot shows the PPA proximity social network for the entire study period. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. The second plot shows the PPA grooming network. Arrows are directed in the direction of grooming given and weighted by frequency of grooming given. Orange individuals are females, blue individuals are males.

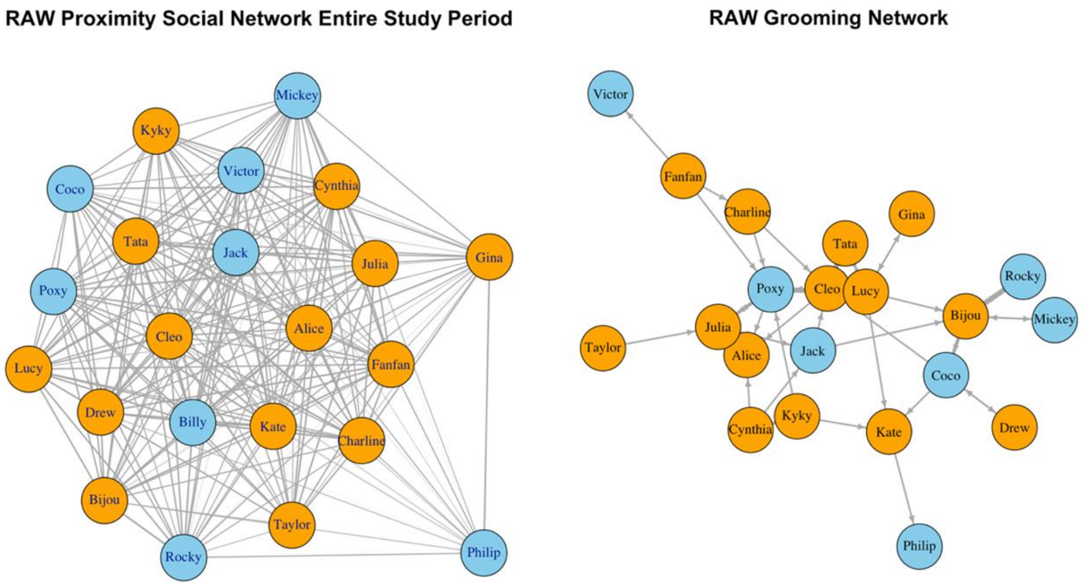

Figure 18. The first plot shows the RAW proximity social network for the entire study period. Edges are weighted by proximity, so thicker edges denote dyads in closer proximity with each other. The second plot shows the RAW grooming network. Arrows are directed in the direction of grooming given and weighted by frequency of grooming given. Orange individuals are females, blue individuals are males.

MR-QAP Models with Proximity as the response matrix

Model 1P for AD (see Table 9) indicated that both grooming given and grooming received were positively correlated with how close individuals were to each other (GRG matrix: coefficient = 0.116, p = 0.038, GRR matrix: coefficient = 0.122, p = 0.045; Table 10). Grooming explained only 3.2% of the variance in proximity (adjusted R^2 = 0.032; Table 10), which is to be expected since other factors such as rank difference, kinship, recent agonistic interactions and sex likely have an impact. Model 1P for CC, OH and PPA did not return any significant results (Table 12; Table 13; Table 14). For RAW, the GRG matrix had a significant positive association with proximity (coefficient = 0.090, p = 0.006; Table 14), indicating that individuals that give grooming to certain individuals were more likely to be closer to those individuals. This was in line with the expected hypothesis that individuals who groom each other are more likely to be in closer proximity with each other.

In Model 2P for AD (see Table 9), there was a trend for the sex match matrix being negatively correlated with the proximity matrix (coefficient = -0.184, p = 0.085; Table 10), suggesting that male-male dyads were less likely to be in closer proximity with one another than female-female dyads. Sex match between dyads explained 2.5% of proximity within dyads (adjusted R^2 = 0.025; Table 10). Model 2P for CC, OH and PPA did not return any significant results (Table 11; Table 12; Table 13). For RAW, a negative association between proximity and the sex match matrix approached significance (coefficient = -0.167, p = 0.077; Table 14) , suggesting a trend towards male-male dyads being more spread than female-female dyads. Females being the philopatric sex in macaque socities could explain this, since they may have more kin in their group than the males. The sex mixed matrix was not significantly correlated with proximity for any of the groups.

When including all the predictors in model 3P for AD (see Table 9), giving grooming showed a significant positive association with proximity (coefficient = 0.119, p = 0.031; Table 10), and receiving grooming approached significance, showing a trend for being positively associated with proximity (coefficient = 0.115, p = 0.056; Table 10). Sex match showed a trend for male-male dyads to be in less proximity than female-female dyads (coefficient = -0.178, p = 0.081; Table 10) and sex mixed was not significant, suggesting that female-female dyads are most likely to be in proximity with each other. Including all the matrices altered only the significant positive association of grooming received. This showed a trend instead of significance when the sex matrices were added, suggesting that sex-based differences explained some of the proximity associated with grooming received between dyads. Model 3P for CC, OH and PPA did not return any significant results (Table 12; Table 13; Table 14).

Model 3P for RAW no longer showed a trend towards a negative association between proximity and the sex match matrix when the other matrices were controlled for (coefficient = -0.155, p = 0.116; Table 14). This lack of effect was inconsistent with the findings in the models for AD. Including the sex mixed and sex match matrices for RAW in model 3P did improve model fit (model 1P: adjusted R^2 = 0.029, model 3P: adjusted R^2 = 0.068; Table 14) suggesting adding these matrices meant that more variance was explained by model structure. The GRR matrix was not significantly associated with proximity in either model 1P or 3P where proximity was the response, which was also was not in line with the expected hypothesis (model 1P: coefficient = 0.029, p = 0.485; model 3P: coefficient = 0.020, p = 0.617; Table 14).

Table 10. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for AD investigating whether proximity is associated with the independent matrices. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model 1P	Model 2P	Model 3P
GRG	0.116 (0.038*)		0.119 (0.031*)
GRR	0.122 (0.045*)		0.115 (*0.056*)
Sex match		-0.184 (*0.085*)	-0.178 (*0.081*)
Sex mixed		-0.033 (0.550)	-0.039 (0.451)
Adjusted R^2	0.032	0.025	0.057

Table 11. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for CC investigating whether proximity is associated with the independent matrices. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model 1P	Model 2P	Model 3P
GRG	0.066 (0.312)		0.065 (0.318)
GRR	0.087 (0.185)		0.077 (0.275)
Sex match		-0.098 (0.344)	-0.093 (0.362)
Sex mixed		-0.018 (0.716)	-0.015 (0.813)
Adjusted R^2	0.008	0.009	0.014

Table 12. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for OH investigating whether proximity is associated with the independent matrices. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model 1P	Model 2P	Model 3P
GRG	0.140 (0.459)		0.160 (0.420)
GRR	0.064 (0.553)		0.068 (0.515)
Sex match		0.133 (0.576)	0.165 (0.439)
Sex mixed		0.024 (0.881)	0.045 (0.740)
Adjusted R^2	-0.017	-0.052	-0.065

Table 13. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for PPA investigating whether proximity is associated with the independent matrices. The p-values with an asterisk

(*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model 1P	Model 2P	Model 3P
GRG	-0.033 (0.674)		0.017 (0.768)
GRR	0.062 (0.531)		0.052 (0.622)
Sex match		-0.235 (0.204)	-0.241 (0.204)
Sex mixed		-0.106 (0.313)	-0.105 (0.323)
Adjusted R^2	-0.013	0.050	0.035

Table 14. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for RAW investigating whether proximity is associated with the independent matrices. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model 1P	Model 2P	Model 3P
GRG	0.090 (0.006*)		0.089 (0.005*)
GRR	0.029 (0.485)		0.020 (0.617)
Sex match		-0.167 (<u>*0.077*</u>)	-0.155 (0.110)
Sex mixed		-0.062 (0.241)	-0.067 (0.191)
Adjusted R^2	0.029	0.042	0.068

MR-QAP Models with Grooming as the response matrix

In model GRG for AD, only proximity was significantly associated with grooming given by individuals (coefficient = 0.168, p = 0.002; Table 15), suggesting individuals were more likely to give grooming to individuals in closer proximity to them. In model GRR proximity was significantly associated with grooming received by individuals (coefficient = 0.168, p = 0.003; Table 15), so individuals were more likely to receive grooming from individuals which were closer to them. This was in line with expectation that individuals in closer proximity will groom more. In both models, sex match and sex mixed showed no significant association with grooming. Proximity explained only 2.1% of grooming given and received in both models (adjusted R^2 = 0.021; Table 15), highlighting that this grooming network is likely affected, like proximity, by many other factors such as exchanging grooming for market commodities like support in agonistic interactions and lower-ranked individuals preferably grooming for grooming individuals higher-up in the hierarchy (Schino, 2001).

In model GRG and model GRR for CC, there was a trend indicating that individuals in closer proximity were more likely to give grooming to each other (model GRG: coefficient = 0.114, p-value = 0.063; Table 16) or receive grooming from each other (model GRR: coefficient = 0.114, p-value = 0.076; Table 16). Model GRG and model GRR did not return any significant results for OH (Table 17). For PPA, the sex match matrix almost had a significant positive association with grooming given (model GRG: coefficient = 0.185, p = 0.057; Table 18) and grooming received (model GRR: coefficient = 0.185, p = 0.058; Table 18), suggesting a trend towards grooming more likely occurring within male-male dyads compared with female-female dyads. This was not consistent with the results from AD and surprising since females, who are more related in the group were expected to be more likely to groom.

In model GRG for RAW, grooming given was significantly associated with the proximity matrix (coefficient = 0.263, p = 0.018; Table 19), indicating that individuals that were in closer proximity to each other were more likely to give each other grooming. In model GRR for RAW, there was also significant positive association between grooming received and the proximity matrix (coefficient = 0.263, p = 0.016; Table 19), suggesting individuals in closer proximity are more likely they are to receive grooming from each other individual.

Table 15. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for AD investigating whether grooming given or grooming received is associated with the independent matrices. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model GRG	Model GRR
Proximity	0.168 (0.002*)	0.168 (0.003*)
Sex match	0.009 (0.878)	0.009 (0.879)
Sex mixed	0.032 (0.286)	0.032 (0.281)
Adjusted R^2	0.021	0.021

Table 16. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for CC investigating whether grooming given or grooming received is associated with the independent matrices. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model GRG	Model GRR
Proximity	0.114 (<u>*0.063*</u>)	0.114 (<u>*0.076*</u>)
Sex match	-0.023 (0.668)	0.023 (0.672)
Sex mixed	0.023 (0.501)	0.023 (0.477)
Adjusted R^2	0.007	0.007

Table 17. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for OH investigating whether grooming given or grooming received is associated with the independent matrices. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model GRG	Model GRR
Proximity	0.246 (0.148)	0.246 (0.158)
Sex match	-0.199 (0.290)	-0.199 (0.286)
Sex mixed	-0.101 (0.284)	-0.101 (0.273)
Adjusted R^2	0.005	0.005

Table 18. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for PPA investigating whether grooming given or grooming received is associated with the independent

matrices. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model GRG	Model GRR
Proximity	0.056 (0.504)	0.056 (0.513)
Sex match	0.185 (*0.057*)	0.185 (*0.058*)
Sex mixed	0.028 (0.635)	0.028 (0.632)
Adjusted R^2	0.007	0.007

Table 19. Estimated coefficients and their p-values (in brackets) returned by a MR-QAP for Royal Anglian Way investigating whether grooming given or grooming received is associated with the independent matrices. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised p-values indicate trends at a threshold of p <0.10.

Matrix	Model GRG	Model GRR
Proximity	0.263 (0.018*)	0.263 (0.016*)
Sex match	-0.072 (0.427)	-0.071 (0.419)
Sex mixed	0.049 (0.336)	0.049 (0.358)
Adjusted R^2	0.023	0.023

Rank difference and Proximity

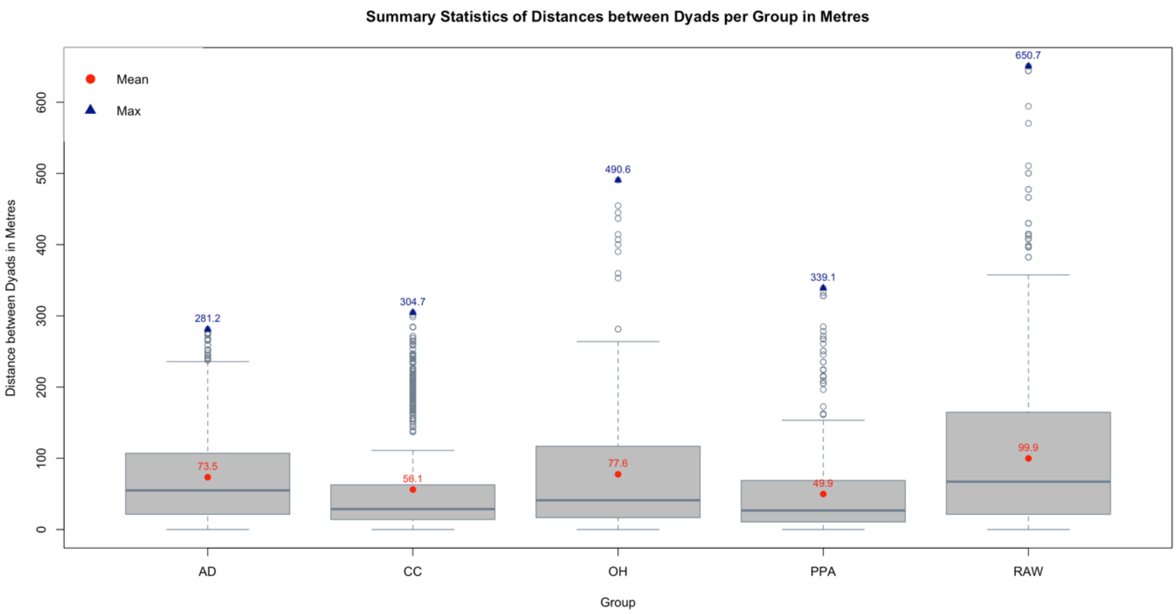

Figure 19. Boxplot of distances between dyads in metres per group. The mean and maximum distance between individuals has been added as points on the plot.

Full null-model comparisons for model 1 (n = 2093) showed that distances within dyads were significantly affected by the test predictors (Likelihood ratio test (LRT): $\chi^2(6) = 50.896$, p = <0.001). Rank difference had no significant effect on dyadic distance (estimate ± SE = 0.007

± 2.048, $p = 0.997$; Table 20) but group did have a significant effect ($p < 0.001$; Table 20). *Post-hoc* Tukey HSD comparisons showed that there were significant pair-wise differences in spread between the groups (Table 21): AD was significantly less spread than RAW (mean difference = -41.340, $p < 0.001$), as was CC (mean difference = -50.280, $p = 0.015$) and PPA (mean difference = -53.850, $p < 0.001$). The difference between OH and RAW was almost significant (mean difference = -28.970, $p = 0.053$; Table 21), suggesting a trend towards OH being less spread than RAW. RAW has the highest mean and maximum distance between dyads, the mean being 99.852 metres, the maximum being 650.673 metres, suggesting their home-range is larger than the other groups, consistent with the result above (Figure 19). There was also a trend indicating that males were more spread out than females, but the effect of sex was not statistically significant overall (estimate ± SE = 11.915 ± 6.934, $p = 0.088$; Table 20).

Table 20. Model 1: Effect of Rank difference, Group and Sex on Inter-individual Distance within dyads (Full dataset, all data, all groups, both sexes). SE = Standard Error, χ^2 = Chi-square, d.f. = degrees of freedom, CI = Confidence Interval. SexM indicates that female is being used as the reference level for the categorical variable. Group AD is also not present, as it is being used as the reference level for the other groups. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised values indicate trends at a threshold of p <0.10. Marginal R^2 = 0.116 and conditional R^2 = 0.195.

Fixed effect	Estimate	SE	χ^2	d.f.	95% CI	*p*-value
Intercept	59.227	7.481			44.102; 73.933	
Rank difference[a,b]	0.007	2.048	<0.001	1	-4.113; 4.074	0.997
Group CC[a]	-8.936	13.661	47.161	4	-39.588; 18.368	<0.001*
Group OH[a]	12.373	11.511	47.161	4	-10.268; 35.271	<0.001*
Group PPA[a]	-12.510	9.312	47.161	4	-30.833; 6.068	<0.001*
Group RAW[a]	41.341	9.194	47.161	4	23.274; 59.780	<0.001*
SexM[a]	11.915	6.934	2.911	1	-1.806; 25.738	<u>*0.088*</u>

[a]Test predictor

[b]z-transformed, mean and s.d. of the original values were 0.257 and 0.199, respectively

Table 21. Tukey HSD Results for Model 1. Estimate = mean pair-wise difference estimate, SE = standard error. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised values indicate trends at a threshold of p <0.10.

Group 1	Group 2	Estimate	SE	*p*-value
AD	CC	8.940	14.600	0.972
AD	OH	-12.370	11.700	0.830
AD	PPA	12.510	9.550	0.685

AD	RAW	-41.340	9.430	<0.001*
CC	OH	-21.310	15.900	0.671
CC	PPA	3.570	14.300	0.999
CC	RAW	-50.280	14.400	0.015*
OH	PPA	24.880	10.500	0.128
OH	RAW	-28.970	10.700	*0.053*
PPA	RAW	-53.850	8.280	<0.001*

Full null model comparisons for model 1F (n = 1689) showed that distances within female-only dyads were significantly affected by the test predictors (LRT: χ^2 (5)= 54.523, p <0.001). Rank difference did not have a significant effect on distance within female dyads (estimate ± SE = 1.133 ± 1.960, p = 0.567; Table 22) but group did have a significant effect (p <0.001; Table 22). *Post-hoc* Tukey HSD tests on the groups showed that females were significantly more spread in RAW than in the other groups: AD was significantly less spread (mean difference = -39.450, p <0.001), as was CC (mean difference = -51.120, p = 0.016), OH (mean difference = -33.950, p = 0.001) and PPA (mean difference = -60.870, p<0.001) (Table 23). RAW has the highest mean distance between female dyads at 88.914 metres, and the second highest maximum distance of 414.880 metres, with OH having the greatest maximum distance at 436.690 metres. OH showed a trend towards females being more spread than PPA females (mean difference = 26.910, p = 0.062; Table 23). OH's mean distance between females dyads is 68.387 metres compared to PPA at 44.428 metres.

Table 22. Model 1F: Effect of Rank difference and Group on Inter-individual Distances within female-only dyads (Full dataset, all data, all groups, only females). SE = Standard Error, χ^2 = Chi-square, d.f. = degrees of freedom, CI = Confidence interval. Group AD is also not present, as it is being used as the reference level for the other groups. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Marginal R^2 = 0.129 and conditional R^2 = 0.18..

Fixed effect	Estimate	SE	χ^2	d.f.	95% CI	*p*-value
Intercept	62.247	7.471			47.138; 76.940	
Rank difference[a,b]	1.133	1.960	0.327	1	-2.718; 5.342	0.567
Group CC[a]	-11.662	13. 927	53.272	4	-42.032; 16.175	<0.001*
Group OH[a]	5.499	11.143	53.272	4	-16.439; 27.708	<0.001*
Group PPA[a]	-21.414	9.382	53.272	4	-39.854; -2.804	<0.001*
Group RAW[a]	39.453	9.451	53.272	4	20.814; 58.575	<0.001*

[a]Test predictor

[b]z-transformed, mean and s.d. of the original values were 0.251 and 0.195, respectively

Table 23. Tukey HSD Results for Model 1F. Estimate = mean pair-wise difference estimate, SE = standard error. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised values indicate trends at a threshold of p <0.10.

Group 1	Group 2	Estimate	SE	*p*-value
AD	CC	11.660	14.900	0.933
AD	OH	-5.500	11.400	0.989
AD	PPA	21.410	9.630	0.173
AD	RAW	-39.450	9.700	<0.001*
CC	OH	-17.160	15.900	0.815
CC	PPA	9.750	14.600	0.961
CC	RAW	-51.120	14.800	0.016*
OH	PPA	26.910	10.100	<u>*0.062*</u>
OH	RAW	-33.950	10.400	0.001*
PPA	RAW	-60.870	8.550	<0.001*

Full null model comparisons for model 1M (*n* = 404) showed that distances within male-only dyads were significantly affected by the test predictors (LRT: $\chi^2(4) = 11.325$, d.f. = 4, *p* = 0.023). Rank difference again did not have a significant effect on inter-individual distance between males (estimate ± SE = -7.776 ± 6.298, *p* = 0.220; Table 24) but group did have a significant effect (*p* = 0.012, Table 24). *Post-hoc* Tukey HSD tests revealed that AD males were significantly less spread than RAW males (mean difference = -59.400, *p* = 0.032; Table 25). The mean distance between male dyads for RAW was 111.880 metres, with a maximum of 510.701 metres, while the mean for AD was 72.582 metres with a maximum of 276.197 metres. Males from the other groups were not shown to be significantly less spread than males from RAW.

Table 24. Model 1M: Effect of Rank difference and Group on Inter-individual Distances within male-only dyads (Full dataset, all data, all groups, only males). SE = Standard Error, χ^2 = Chi-square, d.f. = degrees of freedom, CI = Confidence interval. Group AD is also not present, as it is being used as the reference level for the other groups. Group OH is not present as no data was available for males. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Marginal R^2 = 0.069, conditional R^2 = 0.478.

Fixed effect	Estimate	SE	χ^2	d.f.	95% CI	*p*-value
Intercept	54.384	14.372			25.297; 82.665	
Rank difference[a,b]	-7.776	6.298	1.508	1	-20.497; 4.757	0.220
Group CC[a]	12.980	18.580	10.977	3	-23.572; 51.740	0.012*
Group PPA[a]	41.370	22.619	10.977	3	-3.508; 87.723	0.012*
Group RAW[a]	59.441	18.446	10.977	3	23.082; 96.343	0.012*

[a]Test predictor

[b]z-transformed, mean and s.d. of the original values were 0.278 and 0.212, respectively

Table 25. Tukey HSD Results for Model 1M. Estimate = mean pair-wise difference estimate, SE = standard error. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05.

Group 1	Group 2	Estimate	SE	*p*-value
AD	CC	-13.000	23.700	0.945
AD	PPA	-41.400	25.400	0.367
AD	RAW	-59.400	21.200	0.032*
CC	PPA	-28.400	24.200	0.648
CC	RAW	-46.500	21.000	0.148
PPA	RAW	-18.100	21.400	0.834

Full null model comparisons for models 1AD showed no significant effect of the test predictors, rank difference and sex, on distances within dyads (LRT: $\chi^2(2) = 1.747$, $p = 0.418$), and models 1ADF and 1ADM (models split by sex) showed that rank difference had no effect inter-individual distance within dyads (model 1ADF: LRT: $\chi^2(1) = 0.473$, $p = 0.492$; model 1ADM: LRT: $\chi^2(1) = 0.633$, $p = 0.426$). Full null model comparisons for models 1CC, 1CCF and 1CCM (CC models) also showed no significant effect of the rank difference and sex on distances within dyads, regardless of whether the dyads were male or female (model 1CC: LRT: $\chi^2(2) = 3.855$, $p = 0.146$; model 1CCF: LRT: $\chi^2(1) = 2.399$, $p = 0.121$; model 1CCM: LRT: $\chi^2(1) = 1.241$, $p = 0.265$). Similarly, full null model comparisons for models 1RAW, 1RAWF and 1RAWM (RAW models) showed no significant effect of the test rank difference on distances within dyads, regardless of whether the dyads were male or female (model 1RAW: LRT: $\chi^2(2) = 2.820$, $p = 0.244$; model 1RAWF: LRT: $\chi^2(1) = 0.000$, $p = 0.999$; model 1RAWM: LRT: $\chi^2(1) = 1.744$, $p = 0.187$).

However, full null model comparisons for model 1PPA ($n = 290$) showed that the test predictors had a significant effect on dyadic distance within PPA (LRT: $\chi^2(2) = 6.003$, $p = 0.050$). The effect of rank difference on dyad proximity was however not significant (estimate $\pm$ SE = 6.195 $\pm$ 4.557, $p = 0.180$; Table 26) but there was a trend for the effect of sex indicating that male individuals were more spread than female individuals (estimate $\pm$ SE = 18.664 $\pm$ 10.401, $p = 0.086$; Table 26). The mean distance within male dyads in PPA was 64.194 metres, with a maximum of 332.605 metres compared to the mean distance within female dyads which was 44.428 with a maximum of 267.382 metres.

Table 26. Model 1PPA: Effect of Rank difference and Sex on Inter-individual Distances within dyads in PPA (Full dataset, PPA, both sexes). SE = Standard Error, χ^2 = Chi-square, d.f. = degrees of freedom, CI = Confidence interval. SexM indicates that female is being used as the reference level for the categorical variable. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised values indicate trends at a threshold of p <0.10. Marginal R^2 = 0.057, conditional R^2 = 0.107.

Fixed effect	Estimate	SE	χ^2	d.f.	95% CI	*p*-value
Intercept	41.394	8.075			24.694; 57.571	

Rank difference[a,b]	6.195	4.557	1.795	1	-3.059; 15.698	0.180
SexM[a]	18.664	10.401	2.943	1	-2.906; 40.782	<u>*0.086*</u>

[a]Test predictor

[b]z-transformed, mean and s.d. of the original values were 0.266 and 0.186, respectively

Full null model comparisons for model 1PPAF (n = 237) showed that the distances within female dyads were significantly affected by the test predictor in PPA (LRT: $\chi^2(1) = 5.078$, p = 0.024). There was a positive significant effect of rank difference on female proximity within dyads (estimate ± SE = 10.022 ± 4.247, p = 0.024; Table 27) indicating that the females who had a greater difference in rank were farther apart from each other in the group. This is in line with what was expected from the hypothesis that individuals who are more closely ranked in the dominance hierarchy are likely to be closer together than those who have a greater disparity in rank between them.

Table 27. Model 1PPAF: Effect of Rank difference on inter-individual distances within female-only dyads in PPA (Full dataset, PPA, only females). SE = Standard Error, χ^2 = Chi-square, d.f. = degrees of freedom, CI = Confidence interval. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Marginal R^2 = 0.052, conditional R^2= 0.163

Fixed effect	Estimate	SE	χ^2	d.f.	95% CI	*p*-value
Intercept	42.396	7.278			27.309; 57.092	
Rank difference[a,b]	10.022	4.247	5.078	1	1.418; 19.029	0.024*

[a]Test predictor

[b]z-transformed, mean and s.d. of the original values were 0.228 and 0.146, respectively

Full null model comparison for model 1PPAM was not significant indicating that there was no significant effect of rank difference on distance within male dyads (LRT: $\chi^2(1) = 1.064$, p = 0.302)

The full null model comparison for model OH1F (n = 102) approached significance (LRT: $\chi^2(1) = 3.411$, p = 0.065) indicating a trend towards rank difference influencing female dyad proximity. Rank difference showed a trend towards females that were further apart in rank being closer in proximity to one another (estimate ± SE = -18.236 ± 9.369, p = 0.065; Table 28). This is the opposite of what was expected from the hypothesis.

Table 28. Model 1OHF: Effect of Rank difference on Inter-individual distances within female-only dyads in OH (Full dataset, OH, only females). SE = Standard Error, χ^2 = Chi-square, d.f. = degrees of freedom, CI = Confidence interval. The p-values with an asterisk (*) indicate a statistically significant effect at a threshold of p <0.05. Underlined and italicised values indicate trends at a threshold of p <0.10. Marginal R^2 = 0.059, conditional R^2 = 0.166.

Fixed effect	Estimate	SE	χ^2	d.f.	95% CI	*p*-value
Intercept	64.172	14.432			33.732; 94.451	
Rank difference[a,b]	-18.236	9.369	3.411	1	-39.516; 1.297	<u>*0.065*</u>

[a]Test predictor

[b]z-transformed, mean and s.d. of the original values were 0.327 and 0.189, respectively

Discussion

Seasonal Variation in Networks

The seasonal comparisons showed much variation in inter-individual distances between groups. AD, CC and OH had a greater median inter-individual distance within male-male dyads in winter compared to summer, in line with the hypothesis that males would be more spread out in winter than in summer because of the seasonality of the mating season. Males from these groups may stay on the peripheries of their home-ranges or cross into other groups to compete for access to mates. This difference was particularly extreme for OH, which could reflect the large home-range they inhabit. Males are competing for access to less females in OH, so they may need to spread further than other groups to gain access to extra-group females (mean number of females = 7 versus males = 9).

AD, CC and OH females were more spread from each other in winter than summer. This could be due to increased mating competition in the group, leading to females spreading to avoid conflicts.

PPA had higher median inter-individual distances within male-male dyads in summer compared to in winter, which was not consistent with the results from other groups. PPA males may stretch to more shaded areas in summer compared to winter, avoiding condensing around Skywalk out. RAW male-male dyads were at similar proximity in both seasons, inconsistent with what was expected. This similarity may be because their home-range has a more constant flux of tourists compared to other groups: while the cable car and Skywalk are more exposed and are often closed off in winter due to bad weather, St Michael's Cave is further down the rock so is sheltered from harsher conditions. This may reduce the impact of the mating season on male roaming since there are always tourists in the area condensing the macaques to specific areas. RAW also has comparatively more males and a larger home-range than other groups so males may spread themselves out year-round. There are many sterile females at RAW, meaning mating competition may be reduced and males may spread out less, although a few males have been recorded visiting other groups, with one male, Mickey, permanently moving to AD.

PPA and RAW females were also more spread, perhaps reflecting the thermoregulation and high touristic pressure in these areas as above.

Most of the groups showed higher inter-individual distances within male-male dyads than within female-female dyads. In line with expectations, males move around more while females tend to concentrate around food resources . However, AD and CC showed lower inter-individual distances within male-male dyads than female-female dyads in winter. AD has few males in the group compared to other groups, so the males may not move around so much over winter as they already have less competition for females in their group. CC's females may distribute themselves between the two feeding sites in their home-range, so may be more spread than the males. CC, like PPA, may be less subject to the effects of the mating season since they are constantly condensed in highly touristic areas. Other groups, like OH, have larger home range and more flexibility in where to roam so may be more spread.

These results are only descriptive so their statistical significance is unclear. The GLMMs below shed more light on the differences in spread between groups.

Proximity and Grooming

The results from models using proximity as the response variable revealed significant associations between proximity, and grooming given and received in AD, and associations between proximity and grooming given in RAW. This was in line with the expected hypothesis that individuals who groom each other more frequently would be in closer proximity with each other. However, grooming was not significantly associated with proximity in CC, OH and PPA in these models. The grooming networks for AD and RAW are much more interconnected compared to CC, OH and PPA. This lack of association may reflect bias in the data. CC is a large group and requires more observations to gain a representative grooming network. 22 grooming interactions were recorded between 20 individuals in CC, whose mean size was 33 individuals over the study period. This may be the case for PPA, although its grooming network was slightly more interconnected with 19 grooming interactions recorded between 15 individuals out of a mean group size of 18. OH's network may reflect lack of data since there were only 8 grooming interactions recorded for the 9 individuals with a mean group size of 12, but it could also reflect the linearity of the dominance hierarchies.

The results from models with grooming as the response variable for AD showed that proximity was significantly associated with grooming given and received indicating individuals in closer proximity were more likely to groom each other, in line with the expected hypothesis and previous result. In the models for CC, there was a trend indicating that individuals in closer proximity were more likely to give or receive grooming from each other. It is then surprising that in the proximity models for CC, grooming was not significantly associated with proximity; a bidirectional association between these behaviours was expected. As mentioned above, this lack of association may be due to CC's grooming networks being unrepresentative. The popularity of locations in CC's home-range for tourists may also have had an influence: tourists access this location by taking the cable car up the rock, driving up the rock by taxi tour or walking up the stairs from Queen's Gate. This constant flow of tourists through the group may disrupt association patterns, resulting in individuals who groom more being further from each other. When these individuals are in close proximity, they will groom, as suggested by the trend in the models where grooming was the response variable. In highly touristic areas, disruptions in grooming behaviour of both rhesus and bonnet macaques have been observed and times of greater interactions with humans have been linked to shortened bouts of grooming in these primates (Kaburu et al, 2018; Balasubramaniam et al, 2020).

If this lack of association can be explained by touristic disruption, it is strange that proximity is significantly associated with grooming and vice versa in AD (Table 10, Table 15). Queen's Gate, where AD lives, is a high-density tourist area where macaque-human interactions can be as high as 100/hour at peak times (O'Leary and Fa, 1993). However, Queen's gate allows a larger area for interaction: AD's interactions with humans occur in an area of about 10 by 50 metres whereas CC's interactions with humans are concentrated in areas like Prince Philip's Arch, a small ~10 by 5 metres interaction area (Fuentes et al, 2007). This means that AD can avoid interactions with humans much easier than CC, who choose between the Cable car, Prince Philip's Arch or the road and feeding sites between them where much human interaction still occurs. Association patterns in AD could then be less disrupted than those in CC.

Proximity was not significantly associated with grooming for OH and PPA in these models. This is likely due to less available data for these groups or unique linear patterns of grooming in OH, as stated above. The lack of correlation between proximity and grooming in PPA may also be due to disruptions in their association patterns, as in CC. PPA is more condensed in space than CC, with their home-range including the road along which taxi-drivers must drive to reach Prince Philip's Arch and the cable car. This consistent flow of taxis and people through their home-range may result in individuals in PPA being further from their grooming partners than in other groups.

For RAW, while grooming given was associated with proximity in the models with proximity as the response variable and with grooming as the response, grooming received was not. This could be due to grooming being directed up the hierarchy, with higher-ranked individuals receiving more and giving less grooming. Grooming has been observed previously going up the hierarchy in AD, and low-ranking individuals have been shown to preferentially groom high-ranking individuals (Roubová et al, 2015; Schino, 2001). High-ranking individuals may be more likely to associate or be in closer proximity with each other than low-ranking individuals, and are often more central in the group (Amici et al, 2021). Grooming received would then not be correlated with proximity.

Male-male dyads in AD were less likely to be in close proximity than female-female dyads. This is likely because females are the philopatric sex in Barbary macaques, staying in their natal group their entire lives, enabling them to build long-lasting affiliations with other females in the group, many of whom are their kin (Paul and Kuester, 1985). Male macaques may lack such close social associations by virtue of being the dispersing sex and having fewer relatives in the group. If they remain in their natal group, they will also not be related to other males that may have migrated to the group, so will not have such close associations with other males as compared to the kin-based associations of females. For AD specifically, it may also be a question of number: AD has few males compared to females in the group, and these males may prefer to stay on the outskirts of the group to better monitor other groups and police their own group. As mentioned, policing is a common behaviour in primates which involves the impartial intervention in group conflicts (Beisner and McGowan, 2013). The specific configuration of AD may add to this distance between males since to be on the peripheries of the group, the males must stretch along the long flight of stairs up to Prince Philip's Arch from Queen's Gate.

Models for CC and OH showed no significant associations of sex differences of dyads on grooming or proximity. This, again, may be due to the lack of grooming data available for these groups. For PPA, there was a trend towards male-male dyads grooming more than female-female dyads. This was inconsistent with the results from AD and unexpected since the more related females were expected to groom more in the group. There are also less males in this group at 6 with some turnover within the group, with males moving between CC, PPA and OH. This may impact associations between the males since males may spend less time with the same set of males so are less affiliated. However, this movement between groups could also result in greater association between the males. These groups all splintered from one group, so some of the males in these groups may be kin. Macaques will often groom individuals more who are related matrilineally to them (Bernstein, 1988; Roubová et al, 2015). This could result in greater affiliative associations between the PPA males. This trend may also be the result of less grooming interactions recorded in this group, so the grooming network may not be representative.

There was initially a trend for male-male dyads being further apart in RAW in the models with proximity as the response variable and only the sex matrices, but this trend disappeared when all the matrices were included in the model. This was inconsistent with the results from AD. RAW has more males and a sex ratio which is relatively more balanced than the other groups with a mean number of 8 males and 14 females, so proximity between the sexes may be more similar. Based on their tattoos, some of the males come from CC so may be related, and therefore could have built stronger associations resulting in them being in closer proximity. The group is also often concentrated around St Michael's Cave which could reduce the differences in proximity between the sexes.

The coefficients and *p*-values returned by MR-QAP are correlations and not causal effects. They are still informative about what behaviours are related to proximity in the different groups. All the models that returned significant results had very small effect sizes, indicating that other factors not included in these models must be influencing the structure of the models. These may include kinship and changes in activity for proximity. Barbary macaques are egalitarian so are expected to show less bias in affiliative behaviour towards kin (Paul and

Kuester, 1987). In this study, there does however seem to be some impact on kin, based on the assumption that females are more related than males. In Assamese macaques, individuals were further from their neighbours when group feeding was occurring than when the group was resting or moving (Heesen et al, 2015). Grooming networks may also be influenced by infants: in Japanese and Long-tailed macaques, individuals may groom mothers with infants more in exchange for the handling of their infant (Gumert, 2007; Sekizawa and Kutsukake, 2023). Including infants in the study may then have increased these effect sizes.

Proximity and Rank difference

Most of the models showed that rank difference had no significant effect on proximity within dyads. However, in the model on PPA females, rank difference had a significant effect on proximity, with dyads which had greater differences in rank being further from each other. This may reflect stricter matrilines in PPA because there is more competition for food within the group. As mentioned, PPA is restricted in movement and often has a consistent flow of tourists through it. Macaques are more condensed within the group and share both feeding sites they use, one at Prince Philip's Arch where there is competition for food with CC and occasionally AD, and one with OH nearer O'Hara's Battery**.** Increased competition between groups for access to these feeding sites means access to human food is much more important for PPA than for other groups, especially from the taxi drivers that take tours to the Cable Car and stop at the Skywalk where PPA often spend time. This increases feeding competition within PPA. The distance between females may then follow the hierarchy in PPA more than in other groups since being at more strategic locations along the road where they can access human food from these drivers is more relevant; higher-ranking females may occupy these locations more. PPA may be made up of 2 or 3 matrilines that compete more with each other for these resources. Barbary macaques experience both scramble and contest competition, and when contest competition is high and food is clumped, even in egalitarian species like Bonnet macaques access to food depends on their rank in the group and aggressive behaviours may increase (Boccia et al, 1988; Thierry, 2004). While Barbary macaques are tolerant, stricter social hierarchies can emerge especially when within-group competition is high and food is concentrated in one area, as is the case for PPA.

A similar stricter hierarchy could be expected CC since they experience high flows of tourists around the cable car and Prince Philip's Arch. However, if a group is at Prince Philip's Arch, they will get food either from the feeding platform, to which CC has priority of access, or from people. Taxi drivers stop for extended periods of time at the arch for tourists to take photos with the macaques. They have learnt to jump on peoples shoulders as the taxi drivers will feed them peanuts. Skywalk is more random in terms of food acquisition for the macaques, since it is visited more as a viewing platform to view the eastern side of the rock. PPA will avoid Prince Philip's Arch if CC is there, so food competition is likely increased in PPA. CC is a larger group with a greater number of individuals (mean group size over the study period = 33 compared to PPA = 18) so maintaining distance between females that are further in rank may be more difficult than in PPA. Rank differences may not be as accurate for CC as they are for PPA. Agonistic interactions between lots of different females was lacking in CC, while for PPA almost all of the females had been observed in at least 2 interactions. CC has more adult and subadult females than PPA (mean number of females = 23 compared to PPA = 14) and less agonistic interaction data, so rank differences may be inaccurate.

The model on OH females showed a trend towards females further in rank being closer together. This is the opposite of what was expected from the hypothesis. This could be because OH is a much smaller group than the other groups with a mean number of only 7 females. Since the group has less individuals, there may be less need to follow the hierarchy as within-group food competition is much lower than in the larger groups. It is also likely, that the females in OH may be part of the same matriline, being the most recent splinter group from PPA. Kinship between the females and the lower number of individuals may have reduced within-group food competition enough that it may not be necessary to enforce the strictness of the hierarchy. Proximity may then not be so affected by rank difference. However, although the agonistic interactions recorded included 6 out of the 7 females in the group, it is possible that the calculated rank differences between the females is not an accurate representation of the hierarchy since only four interactions were available.

The models returned more significant results relating to group and sex differences on proximity. Distance within female dyads was significantly less than distance within male dyads in most of the groups, indicating that males were more spread than females. As mentioned, this could be explained by females macaques being philopatric while males disperse, so females are more likely to have close kin in the group and may spend more time in closer proximity with these females than males do with other males.

In many of the models, RAW was found to be significantly more spread than the other groups. RAW has a large home-range two separate sleeping sites and two feeding sites which are quite distant from each other compared to the other groups so it is logical that RAW was found to be significantly more spread. Individuals in the group may prefer to spread out to these separate feeding sites since this reduces competition for food at these sites.

Another interesting result was that OH showed a trend towards being more spread than PPA. This is surprising since OH is a smaller group, so does not need to spread out so much to avoid within-group feeding competition. The highly touristic area PPA inhabits and being condensed between OH and CC could limit the within dyad inter-individual distances since the macaques are more condensed in space. The groups avoid mixing with one another, except for the males roaming other groups during mating season for access to females or males switching groups entirely (Majolo and Maréchal, 2021). Therefore, the restricted home-range of the individuals in PPA could explain why there is a trend that OH is more spread. OH's home-range, though not formally tested, may also be larger, stretching from the O'Hara's battery to the Skywalk. They have access to only one feeding station at the bottom of the road leading to the battery, so they may be more spread to forage and feed on natural foods.

Limitations

The main limitations of this study are the lack of data on grooming and agonistic behaviours, and the lack of an acute measure of the differences in human pressure the different groups experience at different locations.

Observational data comes with its own set of limitations: data cannot be collected from every group every day, and some individuals may not be visible on certain days so it is hard to take complete group scans. Averages may then be skewed by data variability. For some groups, there were few grooming interactions available so the lack of association between proximity and grooming found in these groups may have been because the grooming networks were not representative. Two of the grooming networks were much interconnected, which made the lack of data for some groups clear. Some groups did not have agonistic interactions between lots of different individuals available for calculating the David's scores for rank difference, and this may have made the hierarchies less reliable; missing data meant some relationships between individuals were unknown, and these individuals were placed in the middle of the rank order with similar scores (Neumann et al, 2011). A more dynamic score like an Elo rating which considers the timing of events would have been a better measure, but there was not enough data.

A way of quantifying differences in anthropogenic pressure experienced by each group and at each location would have been useful. This would have supported the claims made above about the levels of tourism the different groups experience, but for now these are just observational. Future studies should include a more standardised measure of this like a count of the number of people per day at each group or a measure of the number of human-macaque interactions per group per day.

Conclusion

There is considerable variation in inter-individual proximity between groups. Grooming and proximity were associated in most of the groups, suggesting that dyads which groomed each other were more likely to be in closer proximity and dyads in closer proximity were more likely to groom. Where there was no association, disruption of grooming in groups exposed to high levels of tourism and the incomplete nature of the grooming networks may have caused this. Future studies could focus on the directionality of these behaviours and which has a stronger effect on the other. Male-male dyads in certain groups showed greater inter-individual distances in the mating season compared to in summer, but these results were unclear and require further investigation. In most groups, male-male dyads were more spread than female-female dyads, reflecting the greater kinship between the philopatric females. Rank difference was not shown to have a significant effect, except in the females of PPA, suggesting the important impact that the location and geographical set-up of each group may have in how it is organised by rank and sex. This was reiterated by the fact that the main finding of group differences was that spread reflects home-range: it is not related to group size but rather to areas of high tourist concentrations. Future research is needed to confirm this, but it seems likely because of the uniqueness of the habitat and differing levels of exposure to humans that each group face because of the human-primate interface on Gibraltar.

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Appendices

R Script

All code was repeated for each group. Most of the code below is from code ran only on AD.

Seasonal networks code

```
# Load libraries
library(igraph)
library(dplyr)
library(tidyr)

global_min_AD <- min(season_median_AD$MedianProximity, na.rm = TRUE)
global_max_AD <- max(season_median_AD$MedianProximity, na.rm = TRUE)

create_network_Normal <- function(season_df, node_ids, global_min, global_max) {
  g <- graph_from_data_frame(
    d = season_df,
    directed = FALSE,
    vertices = node_ids
  )
  normalized_weights <- 1 - (season_df$MedianProximity - global_min) /
    (global_max - global_min)
  E(g)$weight <- normalized_weights
    V(g)$color <- ifelse(V(g)$sex == "M", "skyblue", "orange")
  return(g)
}


season_networks_AD <- list()

for (season in unique(season_median_AD$Season)) {
  season_df_AD <- filter(season_median_AD, Season == season)
  season_df_AD$Season <- NULL  # Drop the Season column
```

```
  season_df_AD <- drop_na(season_df_AD, Indiv1, Indiv2, MedianProximity)
    season_networks_AD[[season]] <- create_network_Normal(
    season_df_AD,
    season_node_ids_AD,
    global_min_AD,
    global_max_AD
  )
}
summer_data_AD <- filter(season_median_AD, Season %in% c("Summer 2023", "Summer 2024"))
averaged_summer_data_AD  <- summer_data_AD %>%
  group_by(Indiv1, Indiv2) %>%
  summarise(MedianProximity = mean(MedianProximity, na.rm = TRUE))
averaged_summer_data_AD_clean <- drop_na(averaged_summer_data_AD, MedianProximity)

pooled_summer_network_AD <- create_network_Normal(
  season_df = averaged_summer_data_AD_clean,
  node_ids = node_ids_AD,
  global_min = global_min_AD,
  global_max = global_max_AD
)
winter_network_AD <- season_networks_AD[["Winter 2023/24"]]

vcount(winter_network_AD)
ecount(winter_network_AD)
vcount(pooled_summer_network_AD)
ecount(pooled_summer_network_AD)
```

Full network code

```
library(igraph)
# Create a results data frame
median_prox_AD_all <- data.frame(
```

```
  Indiv1 = AD_dyad_all[, 1],
  Indiv2 = AD_dyad_all[, 2],
  MedianProximity = NA_real_
)

for (i in seq_len(nrow(median_prox_AD_all))) {
  indiv1 <- median_prox_AD_all$Indiv1[i]
  indiv2 <- median_prox_AD_all$Indiv2[i]
  distances <- sapply(distance_matrices_3d_AD, function(mat) {
    if (indiv1 %in% rownames(mat) && indiv2 %in% colnames(mat)) {
      return(mat[indiv1, indiv2])
    } else if (indiv2 %in% rownames(mat) && indiv1 %in% colnames(mat)) {
      return(mat[indiv2, indiv1])
    } else {
      return(NA_real_)
    }
  })

  median_prox_AD_all$MedianProximity[i] <- median(distances, na.rm = TRUE)
}

write.csv(median_prox_AD_all, "median_prox_AD_all.csv", row.names = FALSE)

median_prox_AD_all <- read.csv("median_prox_AD_all.csv")

library(stringr)
median_prox_AD_all$Indiv1 <- str_trim(median_prox_AD_all$Indiv1)
median_prox_AD_all$Indiv2 <- str_trim(median_prox_AD_all$Indiv2)

create_full_network <- function(df, node_ids) {
  # Filter node list to only include present individuals
  present_ids <- unique(c(df$Indiv1, df$Indiv2))
```

```
  node_ids_filtered <- filter(node_ids, name %in% present_ids)

  g <- graph_from_data_frame(
    d = df,
    directed = FALSE,
    vertices = node_ids_filtered
  )



  prox_min <- min(df$MedianProximity, na.rm = TRUE)
  prox_max <- max(df$MedianProximity, na.rm = TRUE)

  similarity <- prox_max - df$MedianProximity
  similarity_std <- (similarity - min(similarity, na.rm = TRUE)) /
    (max(similarity, na.rm = TRUE) - min(similarity, na.rm = TRUE))

  E(g)$weight <- similarity_std



  V(g)$color <- ifelse(V(g)$sex == "M", "skyblue", "orange")

  return(g)
}

median_prox_AD_all <- na.omit(median_prox_AD_all)

full_prox_network_AD <- create_full_network(median_prox_AD_all, node_ids_AD)

groom_graph_AD <- graph_from_adjacency_matrix(
  grooming_matrix_AD,
  mode = "directed",
  weighted = TRUE,
```

```
  diag = FALSE
)
groom_node_ids_AD <- data.frame(name = V(groom_graph_AD)$name)
groom_node_ids_AD$name <- trimws(as.character(groom_node_ids_AD$name))

groom_node_ids_AD$sex <- hierarchy_AD$sex[match(groom_node_ids_AD$name,
hierarchy_AD$name)]
```

MR-QAP

```
## Make matrices for sex match and sex mixed
library(igraph)

GRR_matrix_AD <- t(grooming_matrix_AD)
inverted_prox_matrix_AD <- as.matrix(as_adjacency_matrix(full_prox_network_AD, attr = "weight",
sparse = FALSE))

common_nodes <- intersect(rownames(inverted_prox_matrix_AD), rownames(grooming_matrix_AD))
inverted_prox_matrix_AD <- inverted_prox_matrix_AD[common_nodes, common_nodes]
grooming_matrix_AD <- grooming_matrix_AD[common_nodes, common_nodes]

sexes <- node_ids_AD$sex
n <- length(sexes)

mm_matrix_AD <- matrix(0, nrow = n, ncol = n)
mixed_matrix_AD <- matrix(0, nrow = n, ncol = n)

rownames(mm_matrix_AD) <- node_ids_AD$name
colnames(mm_matrix_AD) <- node_ids_AD$name
rownames(mixed_matrix_AD) <- node_ids_AD$name
colnames(mixed_matrix_AD) <- node_ids_AD$name

for (i in 1:n) {
  for (j in 1:n) {
```

```
    if (sexes[i] == "M" & sexes[j] == "M") {
      mm_matrix_AD[i, j] <- 1
    }
    if ((sexes[i] == "M" & sexes[j] == "F") | (sexes[i] == "F" & sexes[j] == "M")) {
      mixed_matrix_AD[i, j] <- 1
    }
  }
}

print(mm_matrix_AD)
print(mixed_matrix_AD)

common_nodes <- intersect(rownames(grooming_matrix_AD), rownames(inverted_prox_matrix_AD))
mm_matrix_AD <- mm_matrix_AD[common_nodes, common_nodes]
mixed_matrix_AD <- mixed_matrix_AD[common_nodes, common_nodes]

## MR-QAP
install.packages("asnipe")
library(asnipe)
mrqap_sex_AD <- mrqap.dsp(inverted_prox_matrix_AD ~ mm_matrix_AD + mixed_matrix_AD,
                        directed = "undirected", randomisations = 5000)
mrqap_sex_AD

mrqap_groom_AD <- mrqap.dsp(inverted_prox_matrix_AD ~ grooming_matrix_AD + GRR_matrix_AD,
                         directed = "undirected", randomisations = 5000)
mrqap_groom_AD

mrqap_both_AD <- mrqap.dsp(inverted_prox_matrix_AD ~ grooming_matrix_AD + GRR_matrix_AD
                          + mm_matrix_AD + mixed_matrix_AD,
                          directed = "undirected", randomisations = 5000)
mrqap_both_AD
```

```
mrqap_groomgive_AD <- mrqap.dsp(grooming_matrix_AD ~ inverted_prox_matrix_AD
                    + mm_matrix_AD + mixed_matrix_AD,
                    directed = "directed", randomisations = 5000)
mrqap_groomgive_AD

mrqap_groomreceive_AD <- mrqap.dsp(GRR_matrix_AD ~ inverted_prox_matrix_AD
                       + mm_matrix_AD + mixed_matrix_AD,
                       directed = "directed", randomisations = 5000)
mrqap_groomreceive_AD

V(groom_graph_AD)$sex <- groom_node_ids_AD$sex
V(groom_graph_AD)$color <- ifelse(V(groom_graph_AD)$sex == "M", "skyblue", "orange")
```

David's Scores

```
install.packages("steepness")
library(steepness)
data3=read.table("table_interactions_AD_females.txt", header = TRUE, row.names = 1, sep = "\t", check.names = FALSE)

data3=as.matrix(data3)

install.packages("steepness")
library(steepness)

## AD females

individuals3 <-
c("Abby","Theresa","Madison","Cerise","Renee","Mathilde","Pauline","Diana","Eliane", "Josie", "Rachida", "Faustine", "Cactus", "Athena", "Sonia", "Lola", "Peach", "Koral")
```

```
res3 <- getNormDS(data3, names=individuals3,method="Dij")

res3



#### same for AD males


data4=read.table("table_interactions_AD_males.txt", header = TRUE, row.names = 1, sep =
"\t", check.names = FALSE)


data4=as.matrix(data4)


install.packages("steepness")

library(steepness)


individuals4 <-
c("Simon","Richard","Roland","Ghost","Warty","Hercule","Gaston","Harry","Mickey")

res4 <- getNormDS(data4, names=individuals4, method="Dij")

res4
```

GLMM code

The code for the GLMMs run on the full model is below. This was repeated with datasets split for sex and by group.

```
#### data all proximity both sexes


data1=read.table(file="hierarchy_proximity_both_sexes.txt", header=TRUE, sep="\t", fill = TRUE, quote
= "", row.names = NULL, stringsAsFactors = FALSE)


str(data1)   ## N = 2093
```

```
data1$Group=as.factor(data1$Group)
levels(data1$Group)

data1$ScanID=as.factor(data1$ScanID)
levels(data1$ScanID)

 data1$Sex=as.factor(data1$Sex)
levels(data1$Sex)

data1$Dyad=as.factor(data1$Dyad)
levels(data1$Dyad)

data1$Date=as.factor(data1$Date)

data1$combo_date_scan=paste(data1$Date, data1$ScanID, sep="_")
data1$combo_date_scan=as.factor(data1$combo_date_scan)

z.rankdiff1=as.vector(scale(data1$RankDiff)) ## z-transormation to normalize variable

mean(data1$RankDiff)

sd(mean(data1$RankDiff))



group.code=as.numeric(data1$Group==levels(data1$Group)[2]) ## to be included in random effects
group.code=group.code-mean(group.code)

sex.code=as.numeric(data1$Sex==levels(data1$Sex)[2]) ## to be included in random effects
sex.code=sex.code-mean(sex.code)



install.packages("lme4")
```

```
library(lme4)

contr=lmerControl(optCtrl=list(maxfun=100000)) ## in case

### main model - random effect of combination of date and scan number, random effect of dyad

mod1=lmer(Distance ~ z.rankdiff1 + Group + Sex + (1 + z.rankdiff1 + group.code + sex.code ||combo_date_scan) + (1 | Dyad), data=data1, REML=F, control=contr)

null1=lmer(Distance ~ 1 + (1 + z.rankdiff1 + group.code + sex.code ||combo_date_scan) + (1 |Dyad), data=data1, REML=F, control=contr)

## rank difference, group and sex as test variables

summary(mod1)

## to get p-values for coefficients

as.data.frame(drop1(mod1, test="Chisq"))

  ## post-hoc Tukey pairwise comparison of effect of group

install.packages("emmeans")

library(emmeans)

emmeans(mod1, pairwise ~ Group, adjust = "tukey")

### confidence intervals ###

confint(mod1)

## effect sizes

install.packages("performance")

library(performance)

r2(mod1)

?r2
```

```
source("diagnostic_fcns.r")
## model stability

source("glmm_stability.r")

m.stab=glmm.model.stab(model.res=mod1)

m.stab$detailed$warnings

m.stab$summary

diagnostics.plot(mod1)
ranef.diagn.plot(mod1)
```

Code for Network Plots

```
plot(winter_network_AD,
   vertex.size = 20,
   vertex.label.cex = 0.9,
   edge.width = E(winter_network_AD)$weight * 2.0)
title(main = "AD Proximity Social Network for Winter", cex.main = 1.3)

plot(pooled_summer_network_AD,
   vertex.size = 20,
   vertex.label.cex = 0.9,
   edge.width = E(pooled_summer_network_AD)$weight * 2.0)
title(main = "AD Proximity Social Network for Summer", cex.main = 1.3)
plot(full_prox_network_AD,
   vertex.size = 20,
   vertex.label.cex = 1.0,
   edge.width = E(full_prox_network_AD)$weight * 2.0)
title(main = "AD Proximity Social Network Entire Study Period", cex.main = 1.5)
```

```
plot(groom_graph_AD,
     vertex.size = 20,
     vertex.label.cex = 1,
     edge.width = E(groom_graph_AD)$weight*2,
     edge.arrow.size = 0.5,
     vertex.label.color = "black",
     vertex.color = V(groom_graph_AD)$color,
     layout = layout_nicer_AD)
title(main = "AD Grooming Network", cex.main = 1.5)
```

David's Score

Code for Boxplots

```
group_dists <- list(AD = distance_matrices_3d_AD, CC = distance_matrices_3d_CC, OH = distance_matrices_3d_OH,
                    PPA = distance_matrices_3d_PPA, RAW = distance_matrices_3d_RAW)
extract_all_distances <- function(group_list) {
  df <- data.frame(Group = character(), Spread = numeric(), stringsAsFactors = FALSE)

  for (group_name in names(group_list)) {
    matrices <- group_list[[group_name]]
    for (mat in matrices) {
      if (is.matrix(mat)) {
        dists <- mat[lower.tri(mat)]
        df <- rbind(df, data.frame(Group = group_name, Spread = dists))
      }
    }
  }
  return(df)
}

spread_df <- extract_all_distances(group_dists)
```

```
boxplot(Spread ~ Group, data = spread_df,
        main = "Spread Distribution by Group",
        xlab = "Group", ylab = "Spread",
        col = "gray")

means <- tapply(spread_df$Spread, spread_df$Group, mean)
max_values <- tapply(spread_df$Spread, spread_df$Group, max)

bp <- boxplot(Spread ~ Group, data = spread_df,
              main = "Summary Statistics of Distances between Dyads per Group in Metres",
              xlab = "Group", ylab = "Distance between Dyads in Metres",
              col = "gray",
              border = "slategray")

points(1:length(means), means, pch = 19, col = "red")
points(1:length(max_values), max_values, pch = 17, col = "darkblue")

text(1:length(means), means, labels = round(means, 1), pos = 3, cex = 0.8, col = "red")
text(1:length(max_values), max_values, labels = round(max_values, 1), pos = 3, cex = 0.8, col =
"darkblue")
legend("topleft",  # position of the legend
       legend = c("Mean", "Max"),  # text for each item in the legend
       col = c("red", "darkblue"),  # colors of the points
       pch = c(19, 17),  # point types (filled circle for mean, triangle for max)
       pt.cex = 1.5,  # size of the points
       box.lty = 0)  # remove the box around the legend

library(dplyr)

Summer_AD_data <- Summer_AD_data %>%
  mutate(PairType = case_when(
    Sex1 == "F" & Sex2 == "F" ~ "FF",
```

```
    Sex1 == "M" & Sex2 == "M" ~ "MM",
    TRUE ~ "Mixed"
  ))

summary_stats_SumAD <- Summer_AD_data %>%
  group_by(PairType) %>%
  summarise(
    mean_prox = mean(MedianProximity, na.rm = TRUE),
    median_prox = median(MedianProximity, na.rm = TRUE),
    sd_prox = sd(MedianProximity, na.rm = TRUE),
    min_prox = min(MedianProximity, na.rm = TRUE),
    max_prox = max(MedianProximity, na.rm = TRUE),
    count = n(),
    .groups = 'drop'
  )

print(summary_stats_SumAD)

Winter_AD_data <- Winter_AD_data %>%
  mutate(PairType = case_when(
    Sex1 == "F" & Sex2 == "F" ~ "FF",
    Sex1 == "M" & Sex2 == "M" ~ "MM",
    TRUE ~ "Mixed"
  ))

summary_stats_WinAD <- Winter_AD_data %>%
  group_by(PairType) %>%
  summarise(
    mean_prox = mean(MedianProximity, na.rm = TRUE),
    median_prox = median(MedianProximity, na.rm = TRUE),
    sd_prox = sd(MedianProximity, na.rm = TRUE),
    min_prox = min(MedianProximity, na.rm = TRUE),
```

```
    max_prox = max(MedianProximity, na.rm = TRUE),
    count = n(),
    .groups = 'drop'
  )

print(summary_stats_WinAD)

combined_data_AD <- rbind(Winter_AD_data, Summer_AD_data)

combined_data_AD$Group <- paste(combined_data_AD$Season, combined_data_AD$PairType, sep =
"_")

boxplot(MedianProximity ~ Group, data = combined_data_AD,
        col = c("orange", "lightgray", "skyblue"),
        las = 2,
        main = "AD Median Proximity in metres by Pair Type and Season",
        ylab = "Median Proximity (meters)",
        outline = TRUE,
        names = c("S-FF", "S-Mixed", "S-MM", "W-FF", "W-Mixed", "W-MM"))
```