Lay Summary

The social environment can affect an individual’s wellbeing. This is true for both humans and animals. Here we show that even survival depends on social integration. Wild Barbary macaques were more likely to survive an extremely harsh winter when they were part of close affiliative social groups. However, the best predictor for survival was integration in the aggression network – individuals that interacted aggressively with more but less connected partners had the best chances of survival.

The effects of social network position on the survival of wild Barbary macaques, *Macaca sylvanus*

Running header: Sociality and survival in macaques

Abstract

It has long been shown that the social environment of individuals can have strong effects on health, wellbeing and longevity in a wide range of species. Several recent studies found that an individual's number of affiliative partners positively relates to its probability of survival. Here we build on these previous results to test how both affiliation and aggression networks predict Barbary macaque (*Macaca sylvanus*) survival in a 'natural experiment'. Thirty out of 47 wild Barbary macaques, living in two groups, died during an exceptionally cold winter in the Middle Atlas Mountains, Morocco. We analyzed the affiliation and aggression networks of both groups in the six months before the occurrences of these deaths, to assess which aspects of their social relationships enhanced individual survivorship. Using only the affiliation network we found that network clustering was highly predictive of individual survival probability. Using only the aggression network we found that individual survival probability increased with a higher number of aggression partners and lower clustering coefficient. Interestingly, when both affiliation and aggression networks were considered together, only parameters from the aggression network were included into the best model predicting individual survival. Aggressive relationships might serve to stabilize affiliative social relationships, thereby positively impacting on individual survival during times of extreme weather conditions. Overall, our findings support the view that aggressive social interactions are extremely important for individual wellbeing and fitness.

Keywords: *network clustering, primates, fitness, aggression, affiliation*

Introduction

In recent decades, evidence has accumulated to suggest that social integration affords fitness benefits in both human and animal societies. Social integration is often described as the number or strength of social relationships an individual shares with their conspecific group members, although the use of social network analysis has provided a variety of additional measures to quantify how individuals are embedded into their groups. In humans, social integration can have far reaching health and wellbeing consequences (Berkman and Glass, 2000; Smith and Christakis, 2008). For example, being strongly embedded into a network of close friends can enhance psychological wellbeing (Fiori et al., 2006) and lower mortality risk in humans (Holt-Lunstad et al., 2010). Whilst most studies to date have focused on humans in this respect, social network analysis has also been employed to examine the social networks of animal societies (Croft et al., 2004; Lehmann and Dunbar, 2009; Lusseau and Newman, 2004; Sade and Dow, 1994; Whitehead and Lusseau, 2012). Similar to the results reported in humans, better social integration has also been found to increase animal health, fitness and survival (e.g. McFarland and Majolo, 2013; Schuelke et al., 2010; Silk et al., 2003)

An increasing number of animal studies have demonstrated that the degree to which an animal is integrated into their social group can affect their reproductive success. For example, juvenile male house finches (*Carpodacus mexicanus*) with greater inter-group movements (as captured by network betweenness) can increase their relative attractiveness to females in the mating context (Oh and Badyaev 2010), and male long-tailed manakins (*Chiroxiphia linearis*) are more likely to succeed in reaching high-ranking positions when they are highly connected and central to their social network as juveniles (McDonald, 2007). In great tits (*Parus major*), territory acquisition is modulated by social network structure (Farine and Sheldon, 2015) and having more stable neighbors results in higher fledgling success (Royle et al., 2012). Associating with other calving females increases reproductive success in dolphins (*Tursiops sp*) (Frère et al., 2010) and in feral horses (*Equus sp.*), individuals that are better integrated into their social networks have increased foal survival (Cameron et al., 2009). In baboons (*Papio cynocephalus*), females that have strong and consistent social bonds within their group have improved infant survival (Silk et al., 2003; Silk et al., 2009), while strong social bonds in male Assamese macaques (*Macaca assamensis*) increase their reproductive success by enhancing their competitive abilities (Schuelke et al., 2010).

Social networks also provide immediate survival consequences in a variety of species. For example, in dolphins (*Tursiops sp*) juvenile male social integration is negatively linked to survival (Stanton and Mann, 2012) while in foals (*Equuus caballus*) the number of close associates predict their survival after a catastrophic event (Nuñez et al., 2015). In rock hyrax (*Procavia capensis*) longevity of females increases when there is little variation in network centrality (Barocas et al., 2011), while in female baboons (*Papio cynocephalus*) good social integration enhances longevity (Silk et al., 2010).

The mechanisms by which social integration is linked to survival, health and reproductive success are not entirely clear, although several hypotheses have been suggested. In groups with differentiated social relationships, individuals that are more socially integrated tend to cope better with both environmental and social stressors (Crockford et al., 2008; Wittig et al., 2008). For example in rhesus macaques (*Macaca mulatta*) high social capital (i.e., an individuals’ access to social support) in the form of small, focused networks was found to reduce physiological stress levels (Brent et al., 2011; Crockford et al., 2008); these studies may provide a physiological mechanism that underpins the previously reported relationships between sociability, reproductive success and survival (Sapolsky, 2004, 2005). Social integration may also lead to direct health benefits, for example, through social immunity, as seen in social insects (Cremer et al., 2007), or by improving thermal efficiency, as seen in primates (McFarland et al., 2015). In addition, a predictable and stable social environment, as achieved by good social integration, may improve an individual’s wellbeing (Brent et al., 2011). Finally, the establishment of strong and consistent social bonds with some individuals of the social group may have direct benefits for an individual through better access to resources via social tolerance, reduced exposure to danger (Berghänel et al., 2011; Silk et al., 2009) and increased availability of valuable coalition partners in times of need (Berghänel et al., 2011).

The vast majority of the studies linking social integration to fitness and survival have focused on socio-positive, affiliative behaviors, while far fewer studies have looked at agonistic relationships. Agonistic relationships are an integral part of the social environment of many group living species and aggression networks are often very different from affiliation networks (Lehmann and Ross, 2011). Moreover, some aspects of agonistic relationships are captured by social dominance rank which has previously been shown to have strong effects on individual health and thus fitness and survival (Sapolsky, 2004, 2005). However, even in species with clear dominance hierarchies, the aggression network can be unpredictable and complex, with no clear correlation between aggression given and received (Crofoot et al., 2011), showing that rank does not capture the same as social position in an aggression network or social integration *per se*. Aggressive interactions can also involve coalitions. Gilby et al. (2013) found that coalitionary aggression in chimpanzees (*Pan troglodytes*) affects male reproductive success in the short- as well as in the long-term: Individuals with high centrality in the coalitionary aggression network had a higher chance to sire offspring and subsequently to increase their rank position (Gilby et al., 2013). Furthermore, aggressive tendencies in rhesus macaques (*Macaca mulatta*) are heritable and linked to individual fitness (Brent et al., 2013). Similarly, in yellow-bellied marmots (*Marmota flaviventris*) victimization (i.e., receiving of aggression) was heritable and agonistic relationships positively influenced fitness (Lea et al., 2010). In dolphins, harassment by juveniles may decrease survival rates (Stanton and Mann, 2012). Collectively, these studies highlight the importance of agonistic relationships for our understanding of the link between sociality and fitness.

Both affiliation and aggression network positions are therefore likely to play a role in predicting the survival of individuals during times of hardship. McFarland & Majolo (2013) have previously shown that the probability of surviving an extremely hard winter in Barbary macaques was most strongly predicted by feeding time and the number of social partners an animal had. In other words, macaques were more likely to survive if they had spent more time feeding in the preceding months and if they had more grooming partners, while the strength of those relationships was not found to affect survival. Here, we analyzed the same dataset (McFarland and Majolo, 2013), but we examined whether the position an individual held in their social network could be used to predict their survival across the extremely cold winter. We expanded on the previously reported results by analyzing a number of other social properties that have previously been shown to be important for individual survival and fitness. To do so, we constructed two social networks – one based on affiliative behavior and one based on aggressive behavior – and calculated a variety of commonly used network measures to capture how individuals were embedded in their social environment. We then used these measures to assess which social variables have the potential to enhance the survival of wild Barbary macaques.

Methods:

Data collection

We collected data from two groups (groups F: June – December 2008; group L: September to December 2008) of wild Barbary macaques living in the Middle Atlas Mountains of Morocco. At the beginning of the study group F consisted of 19 (11 males and 8 females) and group L consisted of 29 (19 males and 10 females) adult/sub-adult individuals (>4 years old). These groups were fully habituated and fed on a completely natural diet. An adult female from group F died at the beginning of the study and was therefore excluded from the current analyses. Thirty of our 47 study animals died during the exceptionally cold and snowy winter between December 2008 and January 2009 (McFarland and Majolo, 2013).

We collected data using continuous focal and instantaneous scan sample techniques (Altmann, 1974). The order of focal observations was randomized and each subject was only sampled once per day. In total 661hrs of focal data (mean ± SD = 14 ± 9h/subject) and 9536 scans (mean ± SD = 198 ± 125scans/subject) were collected from our study animals.

During continuous 20 min focal sessions we recorded all occurrences of aggressive behavior (i.e., bite, charge, chase, displace, grab, lunge or slap) exchanged between (i.e. irrespective of the direction) our focal animal and all other group members. During focal sessions we also collected instantaneous scan samples from the focal subject every five minutes to record data on their activity: i) Feeding: consuming food, ii) Foraging: searching for food but not consuming it, iii) Socializing: allo-grooming or body contact, iv) Moving: locomotion without foraging, v) Resting: without feeding or socializing, vi) Other: e.g. mating or vigilance. The identities of all aggressive and social partners were recorded. Data on dyadic aggressive and submissive exchanges, collected both *ad libitum* and during focal sessions, were used to calculate the relative dominance rank of our subjects. For this, all dyadic occurrences of decided aggression (i.e., aggression followed by submission) were entered into a giver/receiver matrix. We then analyzed these data using MatMan 1.0 Software (de Vries et al., 1993) following (de Vries, 1995) I&SI method to determine rank order consistent with a linear hierarchy. Based on the analysis of 1520 dyadic interactions (group F = 905, group L = 615), MatMan revealed that the dominance hierarchies for both groups were significantly linear (P<0.001). Ranks ranged from one (highest) to N, where N is the total size of each group.

Social network analysis

For each group, two different social networks were constructed: one affiliation network and one aggression network. Because our focus is on overall social integration, we used a symmetric (undirected) data structure, which maximizes network densities and minimizes the number of (often correlated) parameters to be included into the models (avoiding the differentiation into in/out for some of the network variables). Dyadic affiliative behavior was measured as the proportion of scans the two members of the dyad were in social contact (i.e., grooming or body contact). Dyadic aggressive behavior was measured as the rate of aggression per hour the two members of the dyad exchanged during focal observations. From these undirected and symmetric matrices, we created social networks and calculated the following commonly used network parameters to quantify individual social integration (Opsahl, 2009): binary and weighted degree (strength), weighted betweenness, eigenvector centrality and individual clustering coefficient. In order to differentiate between the quantity and strength of social relationships, we used two degree measures: binary degree, which reflects the number of interaction partners over the entire period, and strength, which reflects the tie strength between partners, i.e. the frequency (mean number of interactions per unit of time) with which the interactions take place. Thus, a high binary degree value suggests that an individual is interacting with many partners while a high strength value indicates that an individual is frequently involved in interactions. Betweenness was calculated in order to assess the importance of individuals in overall network cohesion. The weighted betweenness measures how often an individual is situated on the shortest path between all others, taking into account the number and strength of these ties in equal proportions (alpha = 0.5) (Opsahl, 2009). A high weighted betweenness value indicates that an individual plays an important role in connecting other dyads and as such is considered central to its network. Eigenvector centrality is a measure of both direct and indirect network ties, reflecting the strength and quantity of social partners; individuals with high eigenvector centrality have many social partners who themselves also have many partners. Finally, clustering coefficient was used to assess to what extent individual survival depended on subgroup membership. The clustering coefficient indicates how well an individual is embedded into its local neighborhood, i.e. how well the individual's interaction partners are connected among themselves; the weighted version used here includes weights as based on interaction frequencies, using the arithmetic mean. A high value indicates strong local clustering (sub-grouping), whereby an individual's partners are well connected among themselves. Two individuals in the affiliation network (Spike and Jack; Figure 1) and one individual in the aggression network (Tony) were very peripheral, and due to their position the clustering coefficient could not be calculated. Thus, these individuals were not included into the respective analysis (see below), reducing the sample size to N=45 (affiliation), N=46 (aggression) and N=44 (all variables together) respectively. All these network variables have been demonstrated to be important predictors of various aspects of animal behavior, survival and physiology. For example, binary degree centrality was found to predict survival in Barbary macaques (McFarland & Majolo, 2013) and foals (Nuñez et al., 2015), while Aplin et al. (2012) found that food patch discovery rate in birds was linked to eigenvector and betweenness centrality (see also Oh and Badyaev, 2010). Stanton and Mann (2012) found that dolphin survival could be predicted by eigenvector centrality. Betweenness centrality was also found to be important in predicting coalitionary aggression in chimpanzees (Gilby et al., 2013) and clustering coefficient has been shown to have implications for cooperation and disease transmission (Aplin et al., 2012; Gilby et al., 2013; Kurvers et al., 2014; Oh and Badyaev, 2010).

Statistics

In order to avoid different scaling ratios for the network parameters derived from groups of different sizes, we first scaled all network variables by subtracting the mean from each individual value and dividing this by the standard deviation. This enabled us to run the analysis for both groups combined, eliminating potential effects of group size on the network variables (e.g. individuals in a larger network can have, by definition, more interaction partners). We analyzed the data using a binary logistic regression model, with survivorship as dependent variable and individual network parameters as well as group, sex and rank as predictors. In order to minimize the problem of collinearity, we first ran a correlation analysis on all network parameters. Variables that were highly correlated (Spearman $r>0.8$) were not entered together into the model to avoid problems with collinearity. Instead, we ran the model multiple times, substituting variables, and selected the ones for which the final model had the lowest AIC values. In addition, we calculated variance inflation factors (VIF) for the network variables and excluded all network variables with VIFs>10 (Stanton and

Mann, 2012). VIFs in the final models were all below 10, indicating low collinearity in our models. Because no previous assumptions regarding the importance of the network parameters could be made, we used an information-theoretical approach, whereby we tested all possible models using the weighted AIC to select the best model to predict of individual survival. Because the percentage of feeding time has been shown to significantly predict macaque survival (McFarland and Majolo, 2013), we also included this variable in all our analyses in order to control for possible effects of network position on access to food. Including this variable also allowed us to assess if any of the network parameters were better predictors of macaque survival than feeding time alone.

We ran three separate logistic regression analyses: first we expanded on the analysis of McFarland & Majolo (2013) assessing the predictive effect of affiliation network position on survival. Secondly, we assessed in a separate analysis the predictive power of aggression network position on survival. Finally, in order to assess whether affiliation or aggression were stronger predictors of survival, we ran the analysis on all predictors simultaneously (affiliation and aggression) to obtain our final model. Regressions were run separately for two reasons: firstly, we wanted to expand on the original findings of McFarland & Majolo (2013), by further analyzing what properties of affiliation contribute to macaque survival. Secondly, as many studies only use affiliation networks, we were interested in finding out the predictive power of aggression network position on survival. Finally, running separate models in addition to the combined analysis helped overcome issues related to over-parameterization. Because individual social network measures are not independent for the members of one group, p-values from the logistic regression analyses might be anti-conservative. To address this issue we used node-permutations (n=999 permutations) in order to compare the observed relationships between network variables and survival to those from randomized networks. Although node permutations may be more susceptible to type I or type II errors (Farine, 2014), there is no established method for performing permutations at the level of the data when using focal observations. We did this separately for all three best models described above. All analyses were run using R (R Development Core Team, 2008); network parameters were calculated using tnet (Opsahl, 2009), VIF calculations were done using the VIF function in the car package(Fox and Weisberg, 2011), binary logistic regressions were run using the step function in the nlme package (Pinheiro et al., 2015), and model selection was carried out based on Akaike Information Criterion (AIC) using the MuMIn package (Bartoń, 2013).

Results

The networks for the two groups are depicted in Figure 1a (affiliation) and 1b (aggression). Although network densities differed between groups, density across network type was remarkably consistent within groups (group L aggression: 0.36, affiliation: 0.32; group F aggression: 0.79, affiliation: 0.73). In order to illustrate how survivors and non-survivors differed in the parameters included into our models we used boxplots indicating the median values for all survivors and non-survivors on the respective variables (Figure 2).

Affiliation and survival

Affiliation network parameters were largely uncorrelated with one another: of the five network parameters (binary degree and strength, betweenness, clustering coefficient and eigenvector centrality) only strength correlated above r_s=0.8 with eigenvector centrality (Table 1S). In addition strength and eigenvector had VIFs above 10. Thus, we excluded strength from the analysis, as it correlated highly with binary degree and eigenvector centrality. Following this, all VIFs were below 3. In order to assess if strength was a better predictor of survival than degree, we re-ran the model with strength instead of binary degree, and found that the AIC of the full model increased; thus, for further analyses binary degree was maintained. In the full model (AIC=60.02) only binary degree was significant (β= -1.51, z=-2.22, p=0.03) while percentage feeding (β= 0.12, z=-1.80, p<0.08) was close to significance (see Table 2S for full results). The best fit model (AIC=50.83; Δ AIC to next best model = 1.69, see Table 3S) was one containing binary degree and percentage time feeding, both of which were also significant (Table 1; VIFs<2). Node-permutations confirmed that both parameter coefficients, as well as the p-values, were significantly different from randomized values (Table 2). Overall, this model correctly predicted the survival of macaques in 76.6% of cases. Thus, individuals with more affiliative partners and a higher percentage of feeding time were more likely to survive the exceptionally harsh winter (Figures 2), initially confirming the previously published results (McFarland & Majolo, 2013). None of the other variables in the model were maintained during model selection.

Aggression and survival

From the network variables, strength and binary degree were strongly correlated with each other (Table 4S) and their VIFs were > 10. Thus, we only included one of the two variables in the model and subsequently maintained binary degree, as the AIC of the full model containing degree was lower compared to the model using strength ($AIC_{degree} = 47.58$ vs $AIC_{strength} = 50.48$; Table 5S). In addition, eigenvector centrality was strongly correlated with several other network parameters and had a high VIF value. Thus, we excluded eigenvector centrality from the analysis. After this, all remaining VIFs were below 5. In the full model, none of the variables reached significance, although clustering coefficient ($\beta= 1.72$, $z=1.9$, $p<0.07$) and binary degree ($\beta= -3.03$, $z=-1.78$, $p<0.08$) were close to significance (see Table 5S for full results). The best model (AIC=32.88; Δ AIC to next best model = 2.02, see Table 6S), identified by the model selection procedure contained binary degree and clustering coefficient, both of which were also significant (see Table 1, VIFs<2). Node-permutations confirmed that both parameter coefficients as well as p-values were significantly different from randomized values (Table 2). This final model achieved an overall correct classification of macaques as survivors/non-survivors of 87%. Macaques that had aggressive interactions with many partners were more likely to survive (Fig. 3a), while those that had a high local clustering coefficient, i.e. those who had partners who themselves were strongly connected via aggression, had a lower chance of survival (Fig. 3b).

Combined predictors of survival

Although some of the affiliation network variables were significantly correlated with aggression network variables, none of these correlations were found to be above $r_s=0.6$ (Table 7S) and all VIFs were <8. In the full model, containing all eleven variables simultaneously (i.e. combining affiliation and aggression network parameters while maintaining feeding time, group, sex and rank), only clustering coefficient of the aggression network reach significance ($\beta= 2.67$, $z=2.19$, $p=0.03$) while binary degree of the aggression network ($\beta= -4.32$, $z=-1.78$, $p<0.09$) and clustering coefficient of the affiliation network ($\beta= -2.13$, $z=-1.68$, $p<0.1$) were close to significance (see Table 8S for full results). When running the model selection process on, the best fit model (AIC=38.86; Δ AICc to next best model = 0.02, see Table 9S) was identical to the aggression model described above: only binary degree of the aggression network and clustering coefficient of the aggression network were maintained in the model, both of which were also significant (Table 3). An alternative model with a very similar AIC value (AIC=38.45) contained in addition to binary degree and clustering coefficient of the aggression network also the clustering coefficient of the affiliation network, however, this variable did not reach significance (Table 3). The next best model (containing the non-significant variable rank) had Δ AIC value = 1.34; see Table 9S). Thus, compared to non-survivors, survivors in both groups of macaques had aggressive interactions with more partners (high binary degree) who themselves showed less of a tendency to interact aggressively (low clustering coefficient). The results suggest that overall aggressive relationships are better predictors of macaque survival than affiliative relationships.

Discussion

We expanded on a previous study (McFarland and Majolo, 2013) by assessing whether social network position can help to predict the survival of wild Barbary macaques during an extremely hard winter in which 63% of the individuals under observation died. When looking at affiliative relationships only, our results supported previous findings (McFarland and Majolo, 2013), suggesting that feeding time and the number of affiliative interaction partners were indeed the best predictors of macaque survival. None of the additional variables assessing network integration improved the model fit. In contrast, when we included network properties of the aggression as well as of the affiliation network, we found that the best model to predict macaque survival consisted entirely of those network parameters obtained from the aggression network, while the variables obtained from the affiliation network were not included.

Although a variety of network measures were used to assess social integration as well as quantitative aspects of sociality, we found that binary measures such as number of interaction partners were better predictors of macaque survival than variables including relationship strength. This was surprising, because it has previously been argued that relationship strength, and not the number of these relationships, is the most important component of primate social networks (Dunbar and Shultz, 2010; Fraser et al., 2008; Silk et al., 2009). Weighted network measures are expected to capture some aspects of the strength of social relationships, while binary measures capture the quantity. In our study, individuals that had more interaction partners in general had a survival advantage, suggesting that under these extreme conditions it is the quantity but not the ‘quality’ of these social relationships that is important, confirming previous findings from McFarland & Majolo (2013). Similarly, a recent study on foal (*Equus caballus*) survival also found that binary degree was an important predictor for survival (Nuñez et al., 2015). In some aspects, these results demonstrate the importance of weak links (i.e., infrequent social interactions) within the social network (Granovetter, 1973), as they appear to enhance survival while the strength of the link appears to be less important. The significant correlation between affiliative degree and aggression degree (Table 7S) indicates that individuals with many aggressive partners also had many affiliative partners, suggesting that these individuals might in general be socially more integrated (Schino et al., 2005).

Interestingly, when we combined the network parameters from the two behavioral networks the best predictors for Barbary macaque survival came from the aggression and not the affiliation network. Lea et al. (2010) reported evidence that agonistic relationships may positively influence fitness in yellow-bellied marmots and our results on Barbary macaques are in line with this. Similarly, Wey and Blumstein (2012) showed that affiliative bonds in marmots have a negative association with fitness while agonistic relationships, at least for males, positively affect fitness. In Barbary macaques we found that the number of aggressive interaction partners for an individual is positively linked to survival. Although here we did not distinguish between the amount of aggression each individual gave or received as we used the overall number of agonistic interactions each dyad was involved in (i.e. the data were not directional), the fact that rank was not maintained in the model suggests that the aggression network does not simply reflect rank. Rank was not included into any of the best models and there is no indication that higher ranking individuals had a survival advantage. This finding is intriguing, as it is often assumed that rank increases nutritional status (Soumah and Yokota, 1991; Vogel, 2005) which in turn should increase survival during periods of low food availability.

Affiliation and aggression are, however, not necessarily mutually exclusive dimensions of a social relationship. For example, McFarland and Majolo (2011) have shown that aggression in Barbary macaques is used to coerce grooming from subordinates. Barrett et al. (2012) make the point that in baboons dominance serves to regulate affiliative interactions between group members by stabilizing the social network. These authors found that the aggression network produced the biggest compensatory changes in the spatial and grooming network of baboons, suggesting that the aggression (i.e. dominance) network is the means by which the social niche is structured (Barrett et al., 2012). That is, it is not necessarily that aggression is more important than affiliation at predicting survival in Barbary macaques (as affiliation parameters also predicted survival), rather that the complex association (beyond mere correlations) between the aggressive and affiliative nature of social relationships is best represented – and primarily dictated – by aggressive interactions.

One of the strengths of social network analysis is that it can quantify not only direct interaction patterns but also indirect ones, such as clustering and betweenness. In our study, only clustering coefficient in the agonistic network was maintained in the best model, where it significantly predicted macaque survival. Figure 3 suggests that low local clustering is beneficial for survival in the context of aggression. Low local clustering indicates that the aggression partners of an individual are not particularly aggressive amongst themselves, thus, they do not form aggressive clusters. This suggests that being involved in aggressive interactions with a high number of partners is beneficial but only if these partners are not aggressive amongst themselves. Clustering coefficient was also negatively correlated with feeding time as well as with rank (Table 7S), suggesting that higher ranking individuals tend to have highly clustered aggression networks. Clustering emerges as an increasingly important variable in animal social networks; e.g. clustering can aid or hinder the spread of diseases (Turner et al., 2008), personality will drive local network clustering in sticklebacks (Pike et al., 2008) and clustering coefficient in an association network was found to be negatively related with reproductive fitness in forked fungus beetles (Formica et al., 2012). The direction of the effect is the same as in our analysis, i.e. individuals in more cliquish environments appear to have a fitness disadvantage, at least in the context of aggression. However, other studies have shown that focused affiliation networks might convey an advantage in terms of e.g. stress relief (Wittig et al., 2008).

Together, the finding that the overall number of agonistic interaction partners, but not rank, predicted survival, suggests that having a larger aggression network provides a selection advantage, in the absence of any rank-related benefit. This may in part be explained by the fact that Barbary macaques are a relatively tolerant species, which may result in a more dispersed distribution of rank-related benefits among groups (Thierry, 2000). Variables like number of interaction partners, rank and feeding time are expected to be linked – if not statistically so, at least conceptually. Here, we found that both rank and feeding time were significantly correlated with network variables in the aggression context but not in the affiliative context. Rank is assumed to give priority of access to food sources to individuals (Barton and Whiten, 1993; Bercovitch and Strum, 1993 but see Majolo et al., 2012), which in turn can influence feeding time. Rank is often (but not always) linked to (or based on) aggressive interactions and their outcomes (Bernstein, 1976). In addition, many affiliative interaction partners can improve foraging efficiency due to the increased feeding tolerance (Barrett et al., 1999; Marshall et al., 2012; McFarland and Majolo, 2013). Therefore, both the affiliative (i.e., feeding tolerance) and aggressive (i.e., priority of access) nature of social relationships – as well as their interaction – are likely to impact the amount of time an individual needs to spend feeding to fulfil their energetic requirements in the cold. Furthermore, rank can be difficult to measure and ranking individuals is often hampered by missing dyadic interactions (de Vries, 1995; Klass and Cords, 2011). As such, the methods currently used to assess rank might not always be suited to capture the dynamics and multidimensionality of dominance interactions in group living animals, especially when some dyads interact rarely or fail to do so all together. Recently, social network analysis, and especially a triad census, has been suggested as a potentially more powerful way of assessing dominance relationships in animals, especially when there is large proportion of dyads with no interaction data (e.g. Shizuka and McDonald, 2012). In addition, rank-related benefits can be very variable, and tend to lack cross-species consistency (Majolo et al., 2012). Indeed, some network measures of social integration might prove better predictors of individual fitness than rank (Gilby et al., 2013). Our findings of network parameters being stronger predictors of survival in wild Barbary macaques than rank reflect this view.

Conclusion

In this study we add to the existing evidence that quantitative measures of social integration are important predictors of survival. Furthermore we show that the aggression network provided the strongest predictor of Barbary macaque survival in a hard winter. Our findings thus highlight the multi-dimensional social space in which individuals' act, as neither rank nor feeding time was maintained in the final model. These findings add to existing evidence that an individual's integration in their social networks can have strong fitness consequences.

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Figure Legends

Figure 1. Affiliation (A) and aggression (B) network for the two groups of Barbary macaques; black=survivors, grey: non-survivors; triangles = females, circles = males; line thickness = tie strength; node size = binary degree.

Figure 2. Illustrative boxplots indicating the median values and percentiles of the variables entered into the full model using affiliative network parameters: non-normalized binary degree, clustering coefficient, betweenness, eigenvector, feeding time and rank. Values are depicted for survivors and non-survivors in Barbary macaques for group F (N=18) and group L (N=29). Circles and asterisk represent outliers. Sex was also entered into the model but is not displayed graphically. ‘variable maintained’ indicates variables that were included into the best model using only affiliation network variables.

Figure 3. Illustrative boxplots indicating the median values and percentiles of the variables entered into the full model using aggressive network parameters of the non-normalized binary degree, local clustering coefficient and betweenness. Values are depicted for survivors and non-survivors in Barbary macaques for group F (N=18) and group L (N=29). Circles and asterisk represent outliers. Sex was also entered into the model but is not displayed graphically. The effects of rank and feeding time are displayed in Figure 2. ‘variable maintained’ indicates variables that were included into the best model using only aggression network variables.

Table 1. Best models predicting macaque survival resulting from the model selection procedure using affiliation and aggression network variables separately.

	B±SE	**Wald z**	**P**	**AIC**
Affiliation (N=45)				
Constant	5.90 ± 2.13	2.77	0.006	
Feed	-0.11 ± 0.04	-2.54	0.011	
Binary degree	-1.26 ± 0.52	-2.44	0.015	
Model overall				50.83 (60.02)
76.6% correct				
Aggression (N=46)				
Constant	1.53 ± 0.65	2.37	0.018	
Binary degree	-2.04 ± 0.78	-2.60	0.009	
Clustering	1.61 ± 0.78	2.07	0.038	
Model overall				32.88 (47.58)
87.0% correct				

AIC – value in () represents value of the full model, including all predictors

Table 2: Permutation results for variable coefficients and p-values of the best models (affiliation, aggression and combined).

	Proportion observed B < randomized B	**Proportion observed p > randomized p**
Best model affiliation		
Binary degree$_{\text{Aff}}$	0.996	0.026
Feed	0.998	0.002
Best model aggression		
Binary degree$_{\text{Agg}}$	0.998	0.009
Clustering$_{\text{Agg}}$	0.017	0.039
Best model combined		
Binary degree$_{\text{Agg}}$	1	0.005
Clustering$_{\text{Agg}}$	0.002	0.03

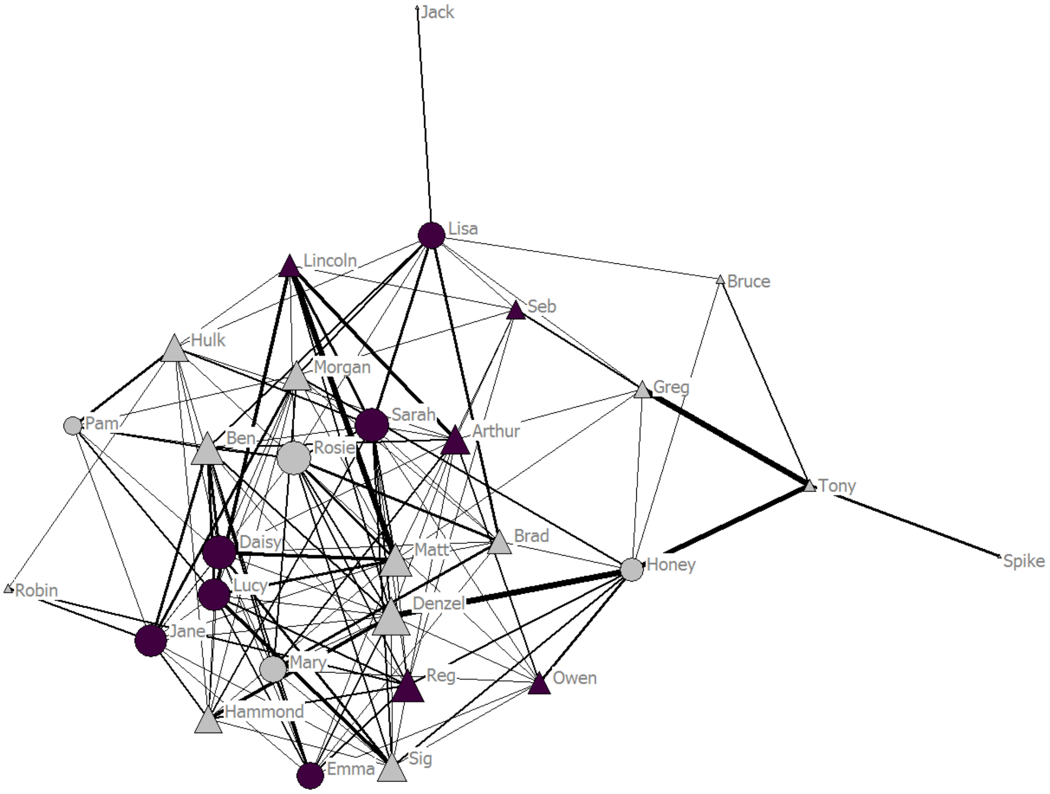
Subscript Agg = aggression network, Aff = affiliation network; note the best model overall is identical to the aggression model

Table 3: The two best models predicting macaque survival resulting from the model selection procedure combining the affiliation and aggression network variables. N=44

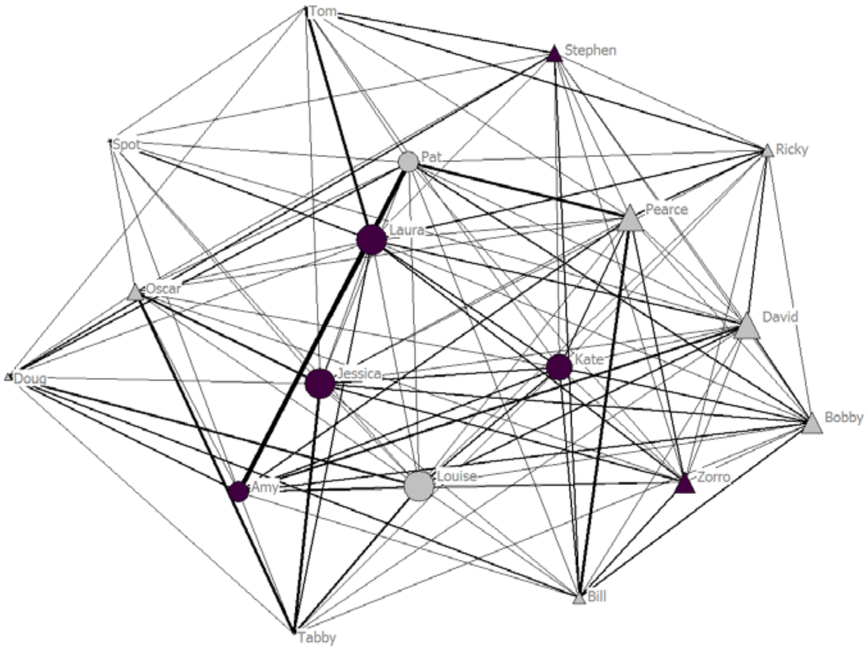
	B±SE	**Wald z**	**P**	**AIC**
Best model				
Constant	1.52 ± 0.65	2.34	0.019	
Binary degree$_{\text{Agg}}$	-2.03 ± 0.79	-2.58	0.01	
Clustering$_{\text{Agg}}$	1.60 ± 0.78	2.05	0.041	
Model overall				38.85(49.6)
2nd best model				
Constant	1.81 ± 0.75	2.42	0.016	
Binary degree$_{\text{Agg}}$	-2.17 ± 0.85	-2.58	0.01	
Clustering$_{\text{Agg}}$	1.89 ± 0.80	2.36	0.019	
Clustering$_{\text{Aff}}$	-0.84 ± 0.63	-1.34	0.18	
Model overall				38.45 (49.6)

AIC – value in () represents value of the full model, including all predictors

Figure 1 A: Group L

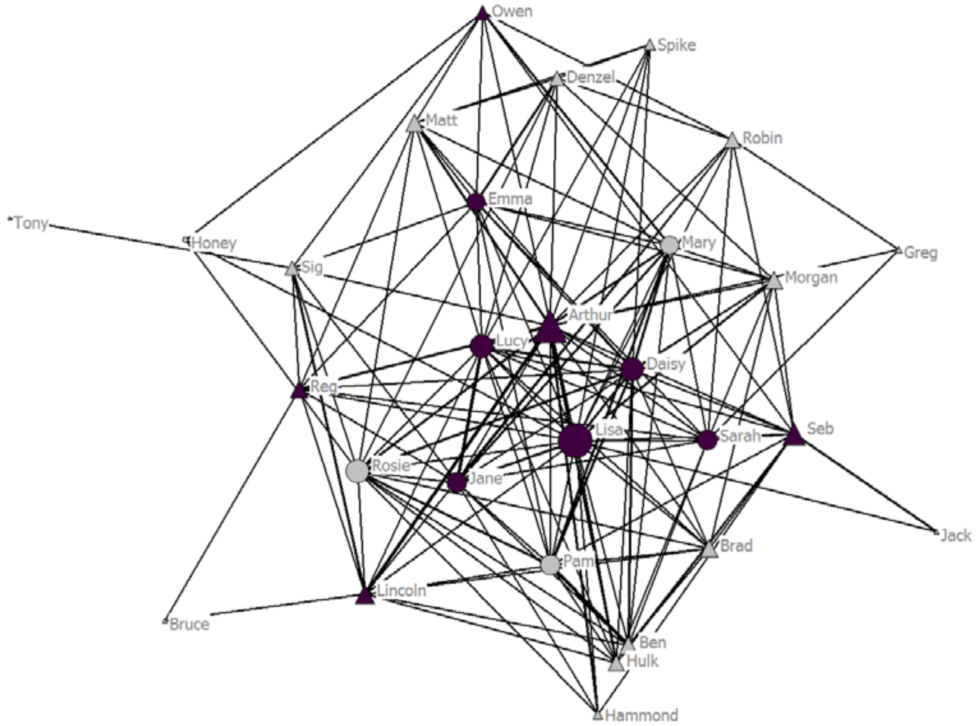


Group F



B

Group L



Group F

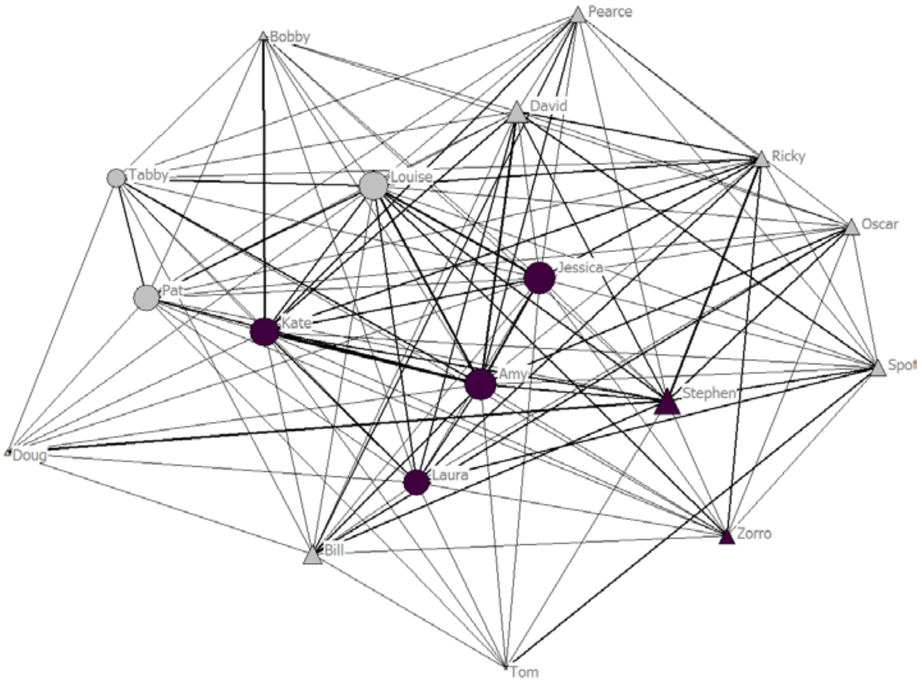
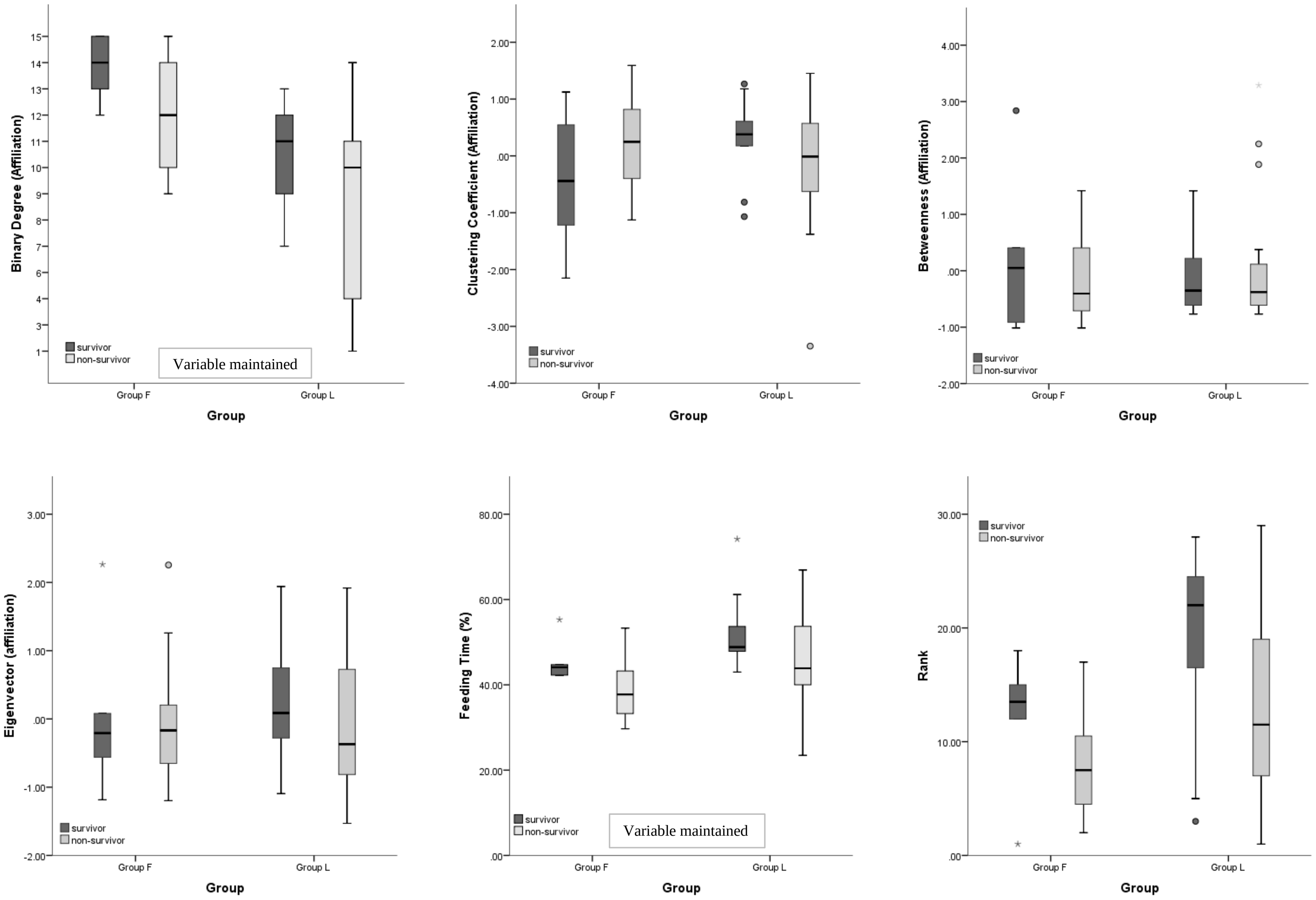
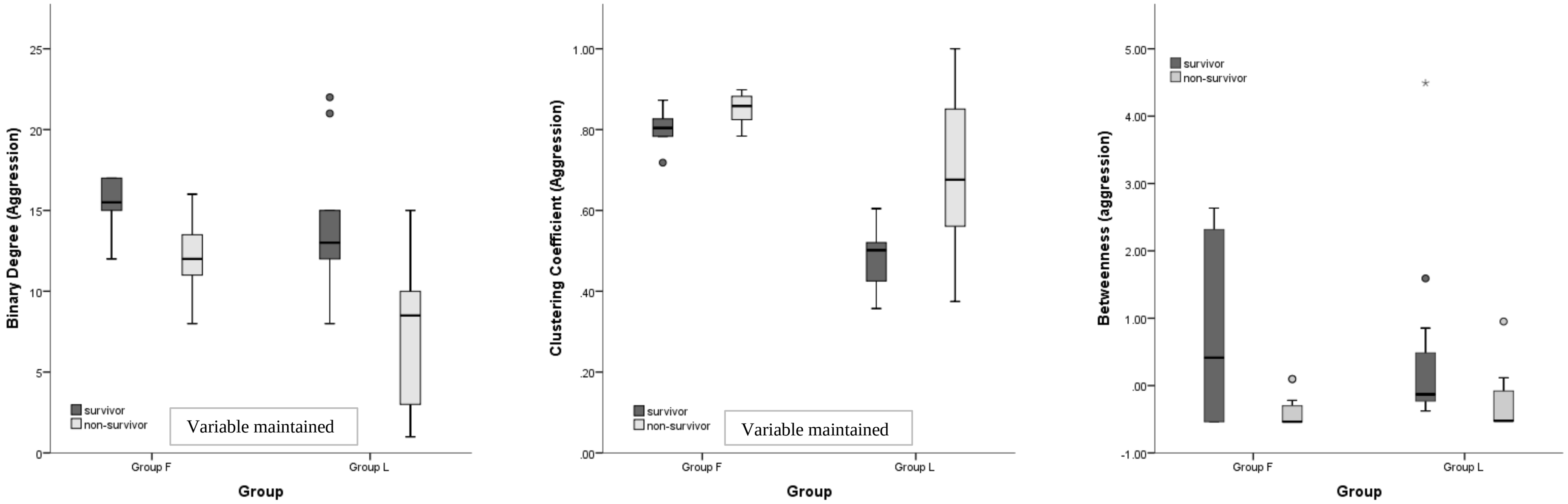


Figure 2



Binary Degree (Affiliation)
15
14
13
12
11
10
9
8
7
6
4
3
1
■ survivor
□ non-survivor
Variable maintained
Group F
Group L
Group
Clustering Coefficient (Affiliation)
2.00
1.00
.00
-1.00
-2.00
-3.00
-4.00
■ survivor
□ non-survivor
Group F
Group L
Group
Betweenness (Affiliation)
4.00
3.00
2.00
1.00
.00
-1.00
-2.00
■ survivor
□ non-survivor
Group F
Group L
Group
Eigenvector (affiliation)
3.00
2.00
1.00
.00
-1.00
-2.00
■ survivor
□ non-survivor
Group F
Group L
Group
Feeding Time (%)
80.00
60.00
40.00
20.00
.00
■ survivor
□ non-survivor
Variable maintained
Group F
Group L
Group
Rank
30.00
20.00
10.00
.00
■ survivor
□ non-survivor
Group F
Group L
Group

Figure 3



Binary Degree (Aggression)
25
20
15
10
5
0
survivor
non-survivor
Variable maintained
Group F
Group L
Group
Clustering Coefficient (Aggression)
1.00
.80
.60
.40
.20
.00
survivor
non-survivor
Variable maintained
Group F
Group L
Group
Betweenness (aggression)
5.00
4.00
3.00
2.00
1.00
.00
-1.00
survivor
non-survivor
Group F
Group L
Group

Supplementary Data

Table 1S: Results of Spearman Rank correlation analysis between network parameters from the affiliation network (N=45 for Clustering coefficient, N=47 for all others); strength was subsequently excluded from the analysis due to the high correlation with the other metrics.

Affiliation network		Strength (weighted degree)	Betweenness (weighted)	Clustering Coefficient (weighted)	Eigenvector centrality
Degree (binary)	r_s	.638**	.455**	-.069	.671**
Strength (weighted degree)	r_s		.798**	.030	.929**
Betweenness (weighted)	r_s			-.289	.601**
Clustering Coef. (weighted)	r_s				.208

The asterisk indicate a significant correlation with p<0.01.

Table 2S: Logistic regression results predicting macaque survival based on the affiliation network (N=45), model 1 uses binary degree, model 2 uses strength instead.

Affiliation: Full model 1	**B**	**Wald z**	**P**	**AIC**
Constant	6.44	2.39	0.02	60.02
Group	1.22	1.18	0.24	
Sex	1.08	0.76	0.45	
Rank	-0.11	-1.27	0.20	
Binary degree	**-1.51**	**-2.22**	**0.03**	
Clustering	-0.34	-0.63	0.53	
Betweenness	0.06	0.11	0.91	
Eigenvector	0.06	0.12	0.91	
Feeding	*0.12*	*-1.80*	*0.07*	

Affiliation: Full model 2	**B**	**Wald z**	**P**	**AIC**
Constant	5.49	2.29	0.02	66.31
Group	0.92	0.93	0.35	
Sex	0.40	0.27	0.79	
Rank	-0.08	-1.01	0.31	
Strength	-1.50	-0.70	0.49	
Clustering	0.09	0.21	0.83	
Betweenness	0.52	0.66	0.51	
Eigenvector	0.77	0.47	0.64	
Feeding	*-0.10*	*-1.68*	*0.09*	

Significant variables are indicated in bold; variables nearing significance are indicated in italics. The coefficients for the two factors, sex and group, refer to group = group L and sex=female.

Table 3S

Model selection results (variable coefficients) for all models with an AIC difference of delta<3 to the best fit model containing only affiliation network parameters.

Inter-cept	Betweenness Aff	Clustering Aff	Degree Aff	Eigen-vector Aff	Feeding time	Group	Rank	Sex (fem)	df	Log Likelihood	AICc	Delta	weight
5.901			-1.263		-0.111				3	-22.417	51.4	0	0.322
5.731			-1.194		-0.096		-0.043		4	-22.055	53.1	1.69	0.138
6.118			-1.285		-0.121	+			4	-22.128	53.3	1.84	0.129
6.004		-0.183	-1.264		-0.113				4	-22.305	53.6	2.19	0.108
5.730	0.165		-1.330		-0.107				4	-22.346	53.7	2.27	0.103
5.771			-1.177		-0.106			+	4	-22.352	53.7	2.28	0.103
5.892			-1.267	0.0073	-0.111				4	-22.427	53.8	2.41	0.096

Aff = affiliation network, feeding time = percentage feeding time, AICc = Aikaikes Information Criterium with correction for finite sample size, Delta = difference of AICs to best model, weight = Aikaike weight, + indicates that these variables were selected in interaction with another variable.

Table 4S: Results of the Spearman Rank correlation analysis between network parameters from the aggression network (N=46 for clustering coefficient and N=47 for all others); strength (weighted degree) and eigenvector centrality were subsequently excluded from the analysis, due to the high correlation between these variables with the other network metrics.

Aggression network		Degree (weighted)	Betweenness (weighted)	Clustering Coefficient (weighted)	Eigenvector centrality
Degree (binary)	r_s	.921**	.561**	-.575**	.885**
Degree (weighted)	r_s		.746**	.553**	.970**
Betweenness (weighted)	r_s			-.571**	.666**
Clustering Coef. (weighted)	r_s				-.401**

The asterisks indicate a significant correlation with p<0.01.

Table 5S: Logistic regression results predicting macaque survival based on the aggression network (N=46); model 1 uses binary degree, model 2 uses strength instead.

Aggression: Full model 1	**B**	**Wald z**	**P**	**AIC**
Constant	1.23	0.48	0.63	47.58
Group	-1.09	-0.86	0.39	
Sex	0	0	1	
Rank	0.08	0.77	0.44	
Binary degree	-3.03	-1.78	0.07	
Clustering	1.72	1.90	0.06	
Betweenness	-0.11	-0.13	0.90	
Feeding	0.007	0.11	0.91	

Aggression: Full model 2	**B**	**Wald z**	**P**	**AIC**
Constant	0.41	0.18	0.86	50.48
Group	-0.39	-0.36	0.72	
Sex	-0.36	-0.24	0.81	
Rank	0.02	0.24	0.81	
Strength	-1.77	-1.39	0.16	
Clustering	**2.09**	**2.15**	**0.03**	
Betweenness	0.35	0.35	0.73	
Feeding	0.03	0.49	0.62	

Significant variables are indicated in bold; variables nearing significance are indicated in italics. The coefficients for the two factors, sex and group, refer to group = group L and sex=female.

Table 6S

Model selection results (variable coefficients) for all models with an AIC difference of delta<3 to the best fit model containing only aggression network parameters.

Intercept	Betweenness Agg	Clustering Agg	Degree Agg	Feeding time	Group	Rank	Sex (female)	df	Log Likelihood	AICc	Delta	weight
1.527		1.611	-2.042					3	-16.44	39.5	0	0.373
1.04		1.700	-2.528			0.04781		4	-16.25	41.5	2.02	0.136
1.943		1.594	-2.143		+			4	-16.28	41.5	2.07	0.132
1.346		1.607	-2.516				+	4	-16.32	41.6	2.16	0.127
1.455	-0.2699	1.527	-1.947					4	-16.38	41.7	2.28	0.119
1.52		1.612	-2.043	0.0002				4	-16.44	41.9	2.40	0.112

Agg = aggression network, feeding time = percentage feeding time, AICc = Aikaikes Information Criterium with correction for finite sample size, Delta = difference of AICc to best model, weight = Aikaike weight, +indicates that these variables were selected in interaction with another variable.

Table 7S: Spearman correlation coefficients between network parameters from the affiliation and the aggression network. Significant correlations are marked in bold.

Aggression network			Feeding time (%)	Degree (binary)	Degree (weighted)	Betweenness (weighted)	Clustering Coefficient (weighted)	Eigenvector centrality	Rank
Affiliation network	Feeding time (%)	r_s	-	**0.415**	**0.459**	**0.591**	**-0.469**	**0.370**	**0.496**
	Degree (binary)	r_s	-0.091	**0.592**	0.539	-0.277	0.159	**0.560**	0.122
	Degree (weighted)	r_s	-0.235	0.371	0.266	-0.161	0.055	0.281	0.180
	Betweenness (weighted)	r_s	-0.268	-0.042	0.048	0.181	0.024	0.054	0.113
	Clustering Coefficient (weighted)	r_s	0.009	0.227	0.094	-0.080	-0.094	0.115	-0.053
	Eigenvector centrality	r_s	-0.245	**0.378**	**0.303**	-0.166	0.101	**0.328**	0.161
	Rank	r_s	.496	**0.552**	**0.492**	**0.442**	**-0.280**	**0.436**	-

Table 8S: Logistic regression results predicting macaque survival based on all affiliation and aggression network parameters; N=44.

Combined Full model	B	Wald z	P	AIC
Constant	0.66	0.125	0.90	49.60
Rank	0.09	0.63	0.53	
Group	-0.50	-0.28	0.78	
Sex	1.03	0.39	0.70	
Binary degree$_{agg}$	-4.32	-1.78	*0.08*	
Clustering$_{agg}$	**2.67**	**2.19**	**0.03**	
Betweenness$_{agg}$	-0.09	-0.09	0.93	
Binary degree$_{aff}$	-1.18	-0.94	0.35	
Clustering$_{aff}$	-2.13	-1.68	*0.09*	
Betweenness$_{aff}$	-0.25	-0.25	0.80	
Eigenvector$_{aff}$	1.07	1.29	0.19	
Feeding	0.02	0.20	0.84	

Variables nearing significance are indicated in italics. The coefficients for the two factors, sex and group, refer to group = group L and sex=female.

Table 9S. Model selection results (variable coefficients) for all models with an AIC difference of delta<3 to the best fit model containing both, affiliation and aggression network parameters.

Intercept	Btwn Aff	Clust Aff	Deg Aff	EV Aff	Btwn Agg	Clust Agg	Deg Agg	Feed	Rank	df	Log Lik	AICc	Delta	weight
1.517						1.601	-2.033			3	-16.43	39.5	0	0.125
1.814		-0.840				1.895	-2.186		[+sex]	4	-15.23	39.5	0.02	0.124
1.031		-1.216				2.154	-3.382		0.099	5	-14.61	40.8	1.34	0.064
2.113		-1.072	-0.667			2.086	-1.938			5	-14.80	41.2	1.71	0.053
1.828		-0.971		0.429		1.938	-2.463			5	-14.85	41.3	1.82	0.05
1.634			-0.431			1.728	-1.790			4	-16.17	41.4	1.91	0.048
1.507		-0.947				1.902	-3.073			5	-14.91	41.4	1.93	0.048
1.041						1.694	-2.518		0.047	4	-16.24	41.5	2.05	0.045
1.932						1.582	-2.133	[+grp]		4	-16.26	41.6	2.09	0.044
1.339						1.598	-2.503		[+sex]	4	-16.31	41.6	2.19	0.042

1.553	0.219					1.591	-2.105			4	-16.35	41.7	2.27	0.04
1.5				0.174		1.591	-2.132			4	-16.35	41.7	2.27	0.04
1.444					-0.271	1.526	-1.936			4	-16.37	41.8	2.3	0.039
1.541						1.599	-2.032	-0.0005		4	-16.43	41.9	2.43	0.037
1.955		-0.794				1.878	-2.203	[+grp]		5	-15.20	42	2.52	0.036
1.823	-0.075	-0.876				1.911	-2.177			5	-15.22	42	2.56	0.035
1.633		-0.849				1.907	-2.196	0.004		5	-15.22	42	2.57	0.035
1.799		-0.834			-0.037	1.879	-2.171			5	-15.22	42	2.57	0.035
2.272		-1.487	-1.124	0.687		2.266	-2.192			6	-13.90	42.1	2.62	0.034
0.9356		-1.42		0.543		2.276	-3.955		0.115	6	-16.43	39.5	0	0.028

Aff = affiliation network, agg = aggression network, Btwn = betweenness, clust = clustering coefficient, deg = degree, EV = eigenvector, feed = percentage feeding time, Lik = likelihood, AICc = Aikaikes Information Criterium with correction for finite sample size, Delta = difference of AICs to best model, weight = Aikaike weight, [+grp] and [+sex] indicates that group/sex was selected in interaction with another variable.