

1 Lay Summary

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

8

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

10 *Macaca sylvanus*

11

12 **Running header: Sociality and survival in macaques**

13

14 *Abstract*

15 It has long been shown that the social environment of individuals can have strong

16 effects on health, wellbeing and longevity in a wide range of species. Several recent

17 studies found that an individual's number of affiliative partners positively relates to its

18 probability of survival. Here we build on these previous results to test how both

19 affiliation and aggression networks predict Barbary macaque (*Macaca sylvanus*)

20 survival in a 'natural experiment'. Thirty out of 47 wild Barbary macaques, living in

21 two groups, died during an exceptionally cold winter in the Middle Atlas Mountains,

22 Morocco. We analyzed the affiliation and aggression networks of both groups in the

23 six months before the occurrences of these deaths, to assess which aspects of their

24 social relationships enhanced individual survivorship. Using only the affiliation

25 network we found that network clustering was highly predictive of individual survival

26 probability. Using only the aggression network we found that individual survival

27 probability increased with a higher number of aggression partners and lower clustering

28 coefficient. Interestingly, when both affiliation and aggression networks were

29 considered together, only parameters from the aggression network were included into

30 the best model predicting individual survival. Aggressive relationships might serve to

31 stabilize affiliative social relationships, thereby positively impacting on individual

32 survival during times of extreme weather conditions. Overall, our findings support the  
33 view that aggressive social interactions are extremely important for individual  
34 wellbeing and fitness.

35

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

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38

39 **Introduction**

40           In recent decades, evidence has accumulated to suggest that social integration  
41 affords fitness benefits in both human and animal societies. Social integration is often  
42 described as the number or strength of social relationships an individual shares with  
43 their conspecific group members, although the use of social network analysis has  
44 provided a variety of additional measures to quantify how individuals are embedded  
45 into their groups. In humans, social integration can have far reaching health and  
46 wellbeing consequences (Berkman and Glass, 2000; Smith and Christakis, 2008). For  
47 example, being strongly embedded into a network of close friends can enhance  
48 psychological wellbeing (Fiori et al., 2006) and lower mortality risk in humans (Holt-  
49 Lunstad et al., 2010). Whilst most studies to date have focused on humans in this  
50 respect, social network analysis has also been employed to examine the social  
51 networks of animal societies (Croft et al., 2004; Lehmann et al., 2010; Lusseau and  
52 Newman, 2004; Sade and Dow, 1994; Whitehead and Lusseau, 2012; Barrett et al.,  
53 2012). Similar to the results reported in humans, better social integration has also been  
54 found to increase animal health, fitness and survival (e.g. Silk et al., 2003; Schuelke et  
55 al., 2010; McFarland & Majolo, 2013).

56           An increasing number of animal studies have demonstrated that the degree to  
57 which an animal is integrated into their social group can affect their reproductive  
58 success. For example, juvenile male house finches (*Carpodacus mexicanus*) with  
59 greater inter-group movements (as captured by network betweenness) can increase  
60 their relative attractiveness to females in the mating context (Oh and Badyaev 2010),  
61 and male long-tailed manakins (*Chiroxiphia linearis*) are more likely to succeed in

62 reaching high-ranking positions when they are highly connected and central to their  
63 social network as juveniles (McDonald, 2007). In great tits (*Parus major*), territory  
64 acquisition is modulated by social network structure (Farine & Sheldon 2015) and  
65 having more stable neighbors results in higher fledgling success (Royle et al., 2012).  
66 Adult affiliative social integration affects reproductive success in dolphins (*Tursiops*  
67 *sp*) (Frère et al., 2010) and in feral horses (*Equus sp.*), individuals that are better  
68 integrated into their social networks have increased foal survival (Cameron et al.,  
69 2009). In baboons (*Papio cynocephalus*), females that have strong and consistent social  
70 bonds within their group have improved infant survival (Silk et al., 2003; 2009), while  
71 strong social bonds in male Assamese macaques (*Macaca assamensis*) increase their  
72 reproductive success by enhancing their competitive abilities (Schuelke et al., 2010).

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

80 The mechanisms by which social integration is linked to survival, health and  
81 reproductive success are not entirely clear, although several hypotheses have been  
82 suggested. In groups with differentiated social relationships, individuals that are more  
83 socially integrated tend to cope better with both environmental and social stressors  
84 (Crockford et al., 2008; Wittig et al., 2008; Young et al., 2014; McFarland et al., 2015).

85 For example in rhesus macaques (*Macaca mulatta*) social capital (i.e., an individuals'  
86 access to social support) in the form of small, focused networks was found to reduce  
87 stress levels (Crockford et al., 2008; Brent et al., 2011); these studies may provide a  
88 physiological mechanism that underpins the previously reported relationships between  
89 sociability, reproductive success and survival (Sapolsky 2004, 2005). Social integration  
90 may also lead to direct health benefits, for example, through social immunity, as seen  
91 in social insects (Cremer et al., 2007), or by improving thermal efficiency, as seen in  
92 primates (McFarland et al., 2015). In addition, a predictable and stable social  
93 environment, as achieved by good social integration, may improve an individual's  
94 wellbeing (Brent et al., 2011). Finally, the establishment of strong and consistent social  
95 bonds with some individuals of the social group may have direct benefits for an  
96 individual through better access to resources via social tolerance, reduced exposure to  
97 danger (Berghänel et al., 2011; Silk et al., 2009) and increased availability of valuable  
98 coalition partners in times of need (Berghänel et al., 2011).

99

100 The vast majority of the studies linking social integration to fitness and survival  
101 have focused on socio-positive, affiliative behaviors, while far fewer studies have  
102 looked at agonistic relationships. Agonistic relationships are an integral part of the  
103 social environment of many group living species and aggression networks are often  
104 very different from affiliation networks (Lehmann and Ross, 2011). Moreover, some  
105 aspects of agonistic relationships are captured by social dominance rank which has  
106 previously been shown to have strong effects on individual health and thus fitness and  
107 survival (Sapolsky 2004, 2005, other refs). However, even in species with clear

108 dominance hierarchies, the aggression network can be unpredictable and complex, with  
109 no clear correlation between aggression given and received (Crofoot et al., 2011),  
110 showing that rank does not capture the same as social position in an aggression  
111 network or social integration *per se*. Aggressive interactions can also involve  
112 coalitions. Gilby et al. (2013) found that coalitionary aggression in chimpanzees (*Pan*  
113 *trogodytes*) affects male reproductive success in the short- as well as in the long-term:  
114 Individuals with high centrality in the coalitionary aggression network had a higher  
115 chance to sire offspring and subsequently to increase their rank position (Gilby et al.,  
116 2013). Furthermore, aggressive tendencies in rhesus macaques (*Macaca mulatta*) are  
117 heritable and linked to individual fitness (Brent et al., 2013). Similarly, in yellow-  
118 bellied marmots (*Marmota flaviventris*) victimization (i.e., receiving of aggression)  
119 was heritable and agonistic relationships positively influenced fitness (Lea et al.,  
120 2010). In dolphins, harassment by juveniles may affect survival rates (Stanton and  
121 Mann, 2012). Collectively, these studies highlight the importance of agonistic  
122 relationships for our understanding of the link between sociality and fitness.

123         Both affiliation and aggression network positions are therefore likely to play a  
124 role in predicting the survival of individuals during times of hardship. McFarland &  
125 Majolo (2013) have previously shown that the probability of surviving an extremely  
126 hard winter in Barbary macaques was most strongly predicted by feeding time and the  
127 number of social partners an animal had. In other words, macaques were more likely to  
128 survive if they had spent more time feeding in the preceding months and if they had  
129 more grooming partners, while the strength of those relationships was not found to  
130 affect survival. Here, we analyzed the same dataset (McFarland and Majolo, 2013), but

131 we examined whether the position an individual held in their social network could be  
132 used to predict their survival across the extremely cold winter. We expanded on the  
133 previously reported results by analyzing a number of other social properties that have  
134 previously been shown to be important for individual survival and fitness. To do so, we  
135 constructed two social networks – one based on affiliative behavior and one based on  
136 aggressive behavior – and calculated a variety of commonly used network measures to  
137 capture how individuals were embedded in their social environment. We then used  
138 these measures to assess which social variables have the potential to enhance the  
139 survival of wild Barbary macaques.

140

141 **Methods:**

142 *Data collection*

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

152 We collected data using continuous focal and instantaneous scan sample  
153 techniques (Altmann, 1974). The order of focal observations was randomized and each



154 subject was only sampled once per day. In total 661hrs of focal data (mean  $\pm$  SD = 14  
155  $\pm$  9h/subject) and 9536 scans (mean  $\pm$  SD = 198  $\pm$  125scans/subject) were collected  
156 from our study animals.

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

174

175 *Social network analysis*

176 For each group, two different social networks were constructed: one affiliation  
177 network and one aggression network. Because our focus is on overall social  
178 integration, we used a symmetric (undirected) data structure, which maximizes  
179 network densities and minimizes the number of (often correlated) parameters to be  
180 included into the models (avoiding the differentiation into in/out for some of the  
181 network variables). Dyadic affiliative behavior was measured as the proportion of  
182 scans the two members of the dyad were in social contact (i.e., grooming or body  
183 contact). Dyadic aggressive behavior was measured as the rate of aggression per hour  
184 the two members of the dyad exchanged during focal observations. From these  
185 undirected and symmetric matrices, we created social networks and calculated the  
186 following commonly used network parameters to quantify individual social integration  
187 (Opsahl, 2009): binary and weighted degree (strength), weighted betweenness,  
188 eigenvector centrality and individual clustering coefficient. In order to differentiate  
189 between the quantity and strength of social relationships, we used two degree  
190 measures: binary degree, which reflects the number of interaction partners over the  
191 entire period, and strength, which reflects the tie strength between partners, i.e. the  
192 frequency (mean number of interactions per unit of time) with which the interactions  
193 take place. Thus, a high binary degree value suggests that an individual is interacting  
194 with many partners while a high strength value indicates that an individual is  
195 frequently involved in interactions. Betweenness was calculated in order to assess the  
196 importance of individuals in overall network cohesion. The weighted betweenness  
197 measures how often an individual is situated on the shortest path between all others,  
198 taking into account the number and strength of these ties in equal proportions ( $\alpha =$

199 0.5) (Opsahl, 2009). A high weighted betweenness value indicates that an individual  
200 plays an important role in connecting other dyads and as such is considered central to  
201 its network. Eigenvector centrality is a measure of both direct and indirect network  
202 ties, reflecting the strength and quantity of social partners; individuals with high  
203 eigenvector centrality have many social partners who themselves also have many  
204 partners. Finally, clustering coefficient was used to assess to what extent individual  
205 survival depended on subgroup membership. The clustering coefficient indicates how  
206 well an individual is embedded into its local neighborhood, i.e. how well the  
207 individual's interaction partners are connected among themselves; the weighted  
208 version used here includes weights as based on interaction frequencies, using the  
209 arithmetic mean. A high value indicates strong local clustering (sub-group formation),  
210 whereby an individual's partners are well connected among themselves. Two  
211 individuals in the affiliation network (Spike and Jack; Figure 1) and one individual in  
212 the aggression network (Tony) were very peripheral, and due to their position the  
213 clustering coefficient could not be calculated. Thus, these individuals were not  
214 included into the respective analysis (see below), reducing the sample size to N=45  
215 (affiliation), N=46 (aggression) and N=44 (all variables together) respectively. All  
216 these network variables have been demonstrated to be important predictors of various  
217 aspects of animal behavior, survival and physiology. For example, binary degree  
218 centrality was found to predict survival in Barbary macaques (McFarland & Majolo,  
219 2013) and foals (Nunez et al., 2015), while Aplin et al., (2012) found that food patch  
220 discovery rate in birds was linked to eigenvector and betweenness centrality (see also  
221 Oh and Badyaev, 2010). Stanton et al., (2012) found that dolphin survival could be

222 predicted by eigenvector centrality. Betweenness centrality was also found to be  
223 important in predicting coalitionary aggression in chimpanzees (Gilby et al., 2013) and  
224 clustering coefficient has been shown to have implications for cooperation and disease  
225 transmission (Aplin et al., 2012; Gilby et al., 2013; Kurvers et al., 2014; Oh and  
226 Badyaev, 2010).

227

## 228 *Statistics*

229 In order to avoid different scaling ratios for the network parameters derived  
230 from groups of different sizes, we first scaled all network variables by subtracting the  
231 mean from each individual value and dividing this by the standard deviation. This  
232 enabled us to run the analysis for both groups combined, eliminating potential effects  
233 of group size on the network variables (e.g. individuals in a larger network can have,  
234 by definition, more interaction partners). We analyzed the data using a binary logistic  
235 regression model, with survivorship as dependent variable and individual network  
236 parameters as well as group, sex and rank as predictors. In order to minimize the  
237 problem of collinearity, we first ran a correlation analysis on all network parameters.  
238 Variables that were highly correlated (Spearman  $r > 0.8$ ) were not entered together into  
239 the model to avoid problems with collinearity. Instead, we ran the model multiple  
240 times, substituting variables, and selected the ones for which the final model had the  
241 lowest AIC values. In addition, we calculated variance inflation factors (VIF) for the  
242 network variables and excluded all network variables with  $VIFs > 10$  (Stanton and  
243 Mann, 2012). VIFs in the final models were all below 10, indicating low collinearity in  
244 our models. Because no previous assumptions regarding the importance of the network

245 parameters could be made, we used an information-theoretical approach, whereby we  
246 tested all possible models using the weighted AIC to select the best model to predict of  
247 individual survival. Because the percentage of feeding time has been shown to  
248 significantly predict macaque survival (McFarland and Majolo, 2013), we also  
249 included this variable in all our analyses in order to control for possible effects of  
250 network position on access to food. Including this variable also allowed us to assess if  
251 any of the network parameters were better predictors of macaque survival than feeding  
252 time alone.

253         We ran three separate logistic regression analyses: first we expanded on the  
254 analysis of McFarland & Majolo (2013) assessing the predictive effect of affiliation  
255 network position on survival. Secondly, we assessed in a separate analysis the  
256 predictive power of aggression network position on survival. Finally, in order to assess  
257 whether affiliation or aggression were stronger predictors of survival, we ran the  
258 analysis on all predictors simultaneously (affiliation and aggression) to obtain our final  
259 model. Regressions were run separately for two reasons: firstly, we wanted to expand  
260 on the original findings of McFarland & Majolo (2013), by further analyzing what  
261 properties of affiliation contribute to macaque survival. Secondly, as many studies only  
262 use affiliation networks, we were interested in finding out the predictive power of  
263 aggression network position on survival. Finally, running separate models in addition  
264 to the combined analysis helped overcome issues related to over-parameterization.  
265 Because individual social network measures are not independent for the members of  
266 one group, p-values from the logistic regression analyses might be anti-conservative.  
267 To address this issue we used node-permutations (n=999 permutations) in order to

268 compare the observed relationships between network variables and survival to those  
269 from randomized networks. Although node permutations may be more susceptible to  
270 type I or type II errors (Farine, 2014), there is no established method for performing  
271 permutations at the level of the data when using focal observations. We did this  
272 separately for all three best models described above. All analyses were run using R (R  
273 Development Core Team, 2008); network parameters were calculated using tnet  
274 (Opsahl, 2009), VIF calculations were done using the VIF function in the car  
275 package (Fox and Weisberg, 2011), binary logistic regressions were run using the step  
276 function in the nlme package (Pinheiro et al., 2015), and model selection was carried  
277 out based on Akaike Information Criterion (AIC) using the MuMIn package (Bartoń,  
278 2013).

279

## 280 **Results**

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

288

289 *Affiliation and survival*

290 Affiliation network parameters were largely uncorrelated with one another: of  
291 the five network parameters (binary degree and strength, betweenness, clustering  
292 coefficient and eigenvector centrality) only strength correlated above  $r_s=0.8$  with  
293 eigenvector centrality (Table 1S). In addition strength and eigenvector had VIFs above  
294 10. Thus, we excluded strength from the analysis, as it correlated highly with binary  
295 degree and eigenvector centrality. Following this, all VIFs were below 3. In order to  
296 assess if strength was a better predictor of survival than degree, we re-ran the model  
297 with strength instead of binary degree, and found that the AIC of the full model  
298 increased; thus, for further analyses binary degree was maintained. In the full model  
299 (AIC=60.02) only binary degree was significant ( $\beta= -1.51$ ,  $z=-2.22$ ,  $p=0.03$ ) while  
300 percentage feeding ( $\beta= 0.12$ ,  $z=-1.80$ ,  $p<0.08$ ) was close to significance (see Table 2S  
301 for full results). The best fit model (AIC=50.83;  $\Delta$  AIC to next best model = 1.69, see  
302 Table 3S) was one containing binary degree and percentage time feeding, both of  
303 which were also significant (Table 1; VIFs<2). Node-permutations confirmed that both  
304 parameter coefficients, as well as the p-values, were significantly different from  
305 randomized values (Table 2). Overall, this model correctly predicted the survival of  
306 macaques in 76.6% of cases. Thus, individuals with more affiliative partners and a  
307 higher percentage of feeding time were more likely to survive the exceptionally harsh  
308 winter (Figures 2), confirming the previously published results (McFarland & Majolo,  
309 2013). None of the other variables in the model were maintained during model  
310 selection.

311

312 *Aggression and survival*

313 From the network variables, strength and binary degree were strongly  
314 correlated with each other (Table 4S) and their VIFs were  $> 10$ . Thus, we only  
315 included one of the two variables in the model and subsequently maintained binary  
316 degree, as the AIC of the full model containing degree was lower compared to the  
317 model using strength ( $AIC_{\text{degree}} = 47.58$  vs  $AIC_{\text{strength}} = 50.48$ ; Table 5S). In addition,  
318 eigenvector centrality was strongly correlated with several other network parameters  
319 and had a high VIF value. Thus, we excluded eigenvector centrality from the analysis.  
320 After this, all remaining VIFs were below 5. In the full model, none of the variables  
321 reached significance, although clustering coefficient ( $\beta = 1.72$ ,  $z = 1.9$ ,  $p < 0.07$ ) and  
322 binary degree ( $\beta = -3.03$ ,  $z = -1.78$ ,  $p < 0.08$ ) were close to significance (see Table 5S for  
323 full results). The best model ( $AIC = 32.88$ ;  $\Delta AIC$  to next best model = 2.02, see Table  
324 6S), identified by the model selection procedure contained binary degree and clustering  
325 coefficient, both of which were also significant (see Table 1,  $VIFs < 2$ ). Node-  
326 permutations confirmed that both parameter coefficients as well as p-values were  
327 significantly different from randomized values (Table 2). This final model achieved an  
328 overall correct classification of macaques as survivors/non-survivors of 87%.  
329 Macaques that had aggressive interactions with many partners were more likely to  
330 survive (Fig. 3a), while those that had a high local clustering coefficient, i.e. those who  
331 had partners who themselves were strongly connected via aggression, had a lower  
332 chance of survival (Fig. 3b).

333

334 *Combined predictors of survival*



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

357

358 **Discussion**

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

370           Although a variety of network measures were used to assess social integration  
371 as well as quantitative aspects of sociality, we found that binary measures such as  
372 number of interaction partners were better predictors of macaque survival than  
373 variables including relationship strength. This was surprising, because it has previously  
374 been argued that relationship strength, and not the number of these relationships, is the  
375 most important component of primate social networks (Dunbar and Shultz, 2010;  
376 Fraser et al., 2008; Silk et al., 2009). Weighted network measures are expected to  
377 capture some aspects of the strength of social relationships, while binary measures  
378 capture the quantity. In our study, individuals that had more interaction partners in  
379 general had a survival advantage, suggesting that under these extreme conditions it is  
380 the quantity but not the ‘quality’ of these social relationships that is important,

381 confirming previous findings from McFarland & Majolo (2013). Similarly, a recent  
382 study on foal (*Equus caballus*) survival also found that binary degree was an important  
383 predictor for survival (Nunez et al., 2015). In some aspects, these results demonstrate  
384 the importance of weak links (i.e., infrequent social interactions) within the social  
385 network (see Granovetter, 1973), as they appear to enhance survival while the strength  
386 of the link appears to be less important. The significant correlation between affiliative  
387 degree and aggression degree (Table 7S) indicates that individuals with many  
388 aggressive partners also had many affiliative partners, suggesting that these individuals  
389 might in general be socially more integrated (Schino et al., 2005).

390         Interestingly, when we combined the network parameters from the two  
391 behavioral networks the best predictors for Barbary macaque survival came from the  
392 aggression and not the affiliation network. Lea et al. (2010) reported evidence that  
393 agonistic relationships may positively influence fitness in yellow-bellied marmots and  
394 our results on Barbary macaques are in line with this. Similarly, Wey and Blumstein  
395 (2012) showed that affiliative bonds in marmots have a negative association with  
396 fitness while agonistic relationships, at least for males, positively affect fitness. In  
397 Barbary macaques we found that the number of aggressive interaction partners for an  
398 individual is positively linked to survival. *Although here we did not distinguish*  
399 *between the amount of aggression each individual gave or received as we used the*  
400 *overall number of agonistic interactions each dyad was involved in (i.e. the data were*  
401 *not directional), the fact that rank was not maintained in the model suggests that the*  
402 *aggression network does not simply reflect rank. Rank was not included into any of the*  
403 *best models and there is no indication that higher ranking (ie those that give? Receive?*

404 *A lot of aggression) individuals had a survival advantage.* This finding is intriguing, as  
405 it is often assumed that rank increases nutritional status (Soumah and Yokota, 1991;  
406 Vogel, 2005) which in turn should increase survival during periods of low food  
407 availability.

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

421         One of the strengths of social network analysis is that it can quantify not only  
422 direct interaction patterns but also indirect ones, such as clustering and betweenness. In  
423 our study, only clustering coefficient in the agonistic network was maintained in the  
424 best model, where it significantly predicted macaque survival. Figure 3B suggests that  
425 low local clustering is beneficial for survival in the context of aggression. Low local  
426 clustering indicates that the aggression partners of an individual are not particularly

427 aggressive amongst themselves, thus, they do not form aggressive clusters. This  
428 suggests that being involved in aggressive interactions with a high number of partners  
429 is beneficial but only if these partners are not aggressive amongst themselves.  
430 Clustering coefficient was also negatively correlated with feeding time as well as with  
431 rank (Table 7S), suggesting that higher ranking individuals tend to have highly  
432 clustered aggression networks. Clustering emerges as an increasingly important  
433 variable in animal social networks; e.g. clustering can aid or hinder the spread of  
434 diseases (Turner et al., 2008), personality will drive local network clustering in  
435 sticklebacks (Pike et al., 2008) and clustering coefficient in an association network was  
436 found to be negatively related with reproductive fitness in forked fungus beetles  
437 (Formica et al., 2012). The direction of the effect is the same as in our analysis, i.e.  
438 individuals in more cliquish environments appear to have a fitness disadvantage, at  
439 least in the context of aggression. However, other studies have shown that focused  
440 affiliation networks might convey an advantage in terms of e.g. stress relief (Wittig et  
441 al., 2008).

442       Together, the finding that the overall number of agonistic interaction partners,  
443 but not rank, predicted survival, suggests that having a larger aggression network  
444 provides a selection advantage, in the absence of any rank-related benefit. This may in  
445 part be explained by the fact that Barbary macaques are a relatively tolerant species,  
446 which may result in a more dispersed distribution of rank-related benefits among  
447 groups (Thierry, 2000). Variables like number of interaction partners, rank and feeding  
448 time are expected to be linked – if not statistically so, at least conceptually. Here, we  
449 found that both rank and feeding time were significantly correlated with network

450 variables in the aggression context but not in the affiliative context. Rank is assumed to  
451 give priority of access to food sources to individuals (Barton and Whiten, 1993;  
452 Bercovitch and Strum, 1993), but see Majolo et al., 2012), which in turn can influence  
453 feeding time. Rank is often (but not always) linked to (or based on) aggressive  
454 interactions and their outcomes (Bernstein, 1976). In addition, many affiliative  
455 interaction partners can improve foraging efficiency due to the increased feeding  
456 tolerance (Barrett et al., 1999; Marshall et al., 2012; McFarland and Majolo, 2013).  
457 Therefore, both the affiliative (i.e., feeding tolerance) and aggressive (i.e., priority of  
458 access) nature of social relationships – as well as their interaction – are likely to impact  
459 the amount of time an individual needs to spend feeding to fulfil their energetic  
460 requirements in the cold. Furthermore, rank can be difficult to measure and ranking  
461 individuals is often hampered by missing dyadic interactions (de Vries, 1995; Klass  
462 and Cords, 2011). As such, the methods currently used to assess rank might not always  
463 be suited to capture the dynamics and multidimensionality of dominance interactions in  
464 group living animals, especially when some dyads interact rarely or fail to do so all  
465 together. Recently, social network analysis, and especially a triad census, has been  
466 suggested as a potentially more powerful way of assessing dominance relationships in  
467 animals, especially when there is large proportion of dyads with no interaction data  
468 (e.g. Shizuka and McDonald, 2012). In addition, rank-related benefits can be very  
469 variable, and tend to lack cross-species consistency (Majolo et al., 2012). Indeed, some  
470 network measures of social integration might prove better predictors of individual  
471 fitness than rank (Gilby et al., 2013). Our findings of network parameters being  
472 stronger predictors of survival in wild Barbary macaques than rank reflect this view.

473

474 **Conclusion**

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

482

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655 **Figure Legends**

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

659

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

668

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

677





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

	<b>B±SE</b>	<b>Wald z</b>	<b>P</b>	<b>AIC</b>
<b>Affiliation (N=45)</b>				
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	
<i>Model overall</i>				50.83 (60.02)
<i>76.6% correct</i>				
<b>Aggression (N=46)</b>				
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	
<i>Model overall</i>				32.88 (47.58)
<i>87.0% correct</i>				

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

682

683

684

685 Table 2: Permutation results for variable coefficients and p-values of the best models  
 686 (affiliation, aggression and combined).  
 687

	<b>Proportion observed B &lt; randomized B</b>	<b>Proportion observed p &gt; randomized p</b>
<b>Best model affiliation</b>		
Binary degree <sub>Aff</sub>	0.996	0.026
Feed	0.998	0.002
<b>Best model aggression</b>		
Binary degree <sub>Agg</sub>	0.998	0.009
Clustering <sub>Agg</sub>	0.017	0.039
<b>Best model combined</b>		
Binary degree <sub>Agg</sub>	1	0.005
Clustering <sub>Agg</sub>	0.002	0.03

688  
 689 Subscript Agg = aggression network, Aff = affiliation network; note the best model  
 690 overall is identical to the aggression model  
 691  
 692

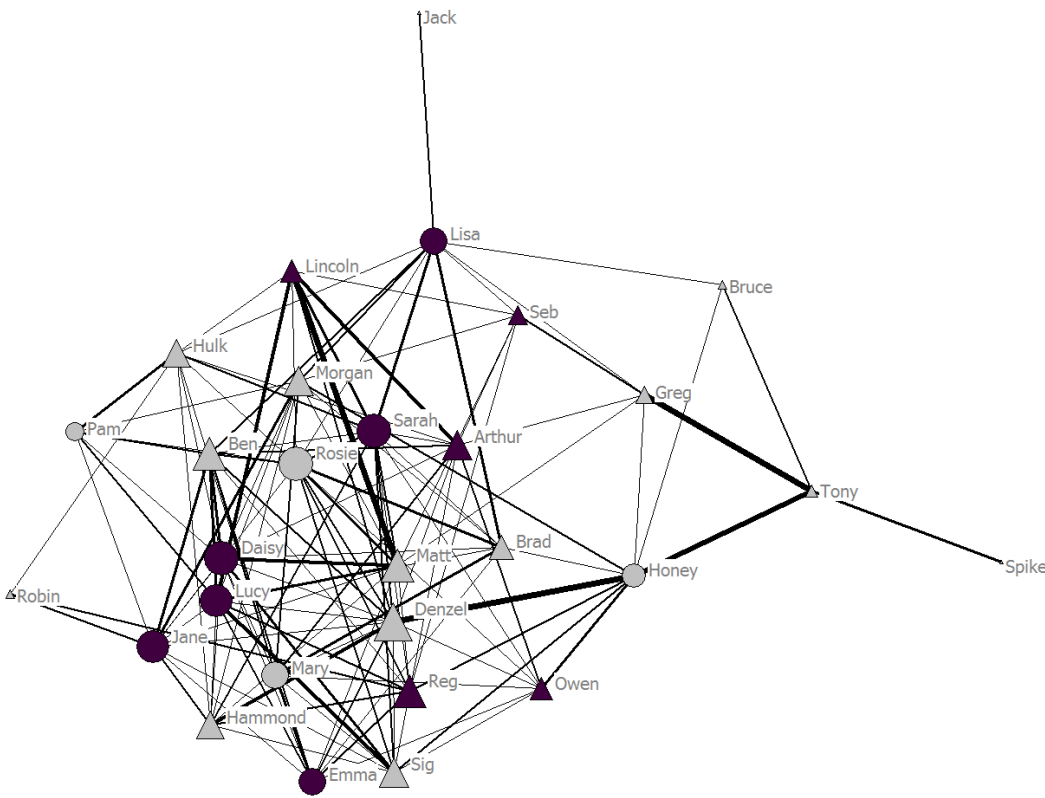
693 Table 3: The two best models predicting macaque survival resulting from the model  
 694 selection procedure combining the affiliation and aggression network variables. N=44

	<b>B±SE</b>	<b>Wald z</b>	<b>P</b>	<b>AIC</b>
<b>Best model</b>				
Constant	1.52 ± 0.65	2.34	0.019	
Binary degree <sub>Agg</sub>	-2.03 ± 0.79	-2.58	0.01	
Clustering <sub>Agg</sub>	1.60 ± 0.78	2.05	0.041	
<i>Model overall</i>				38.85(49.6)
<b>2nd best model</b>				
Constant	1.81 ± 0.75	2.42	0.016	
Binary degree <sub>Agg</sub>	-2.17 ± 0.85	-2.58	0.01	
Clustering <sub>Agg</sub>	1.89 ± 0.80	2.36	0.019	
Clustering <sub>Aff</sub>	-0.84 ± 0.63	-1.34	0.18	
<i>Model overall</i>				38.45 (49.6)

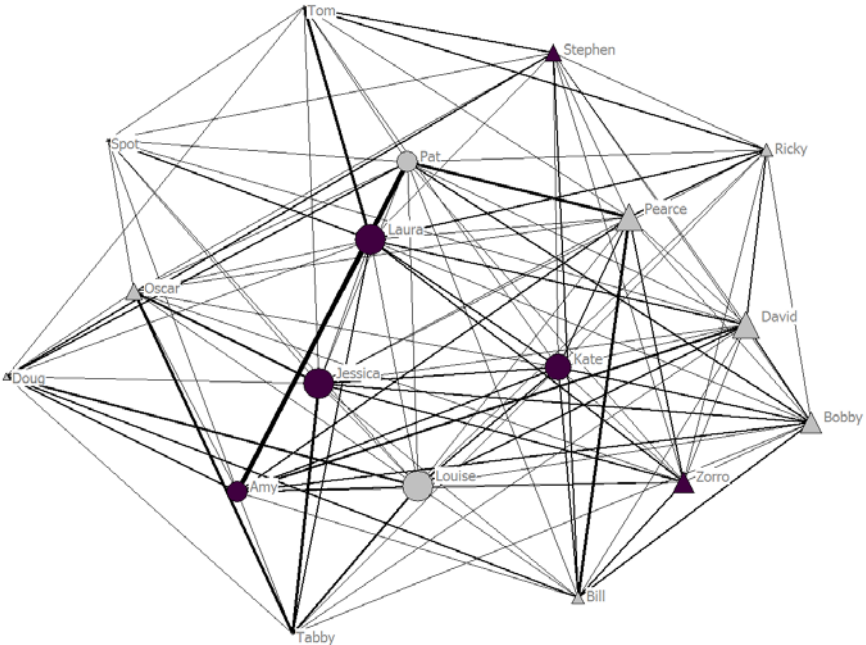
695 AIC – value in () represents value of the full model, including all predictors

696

697 Figure 1 A: Group L

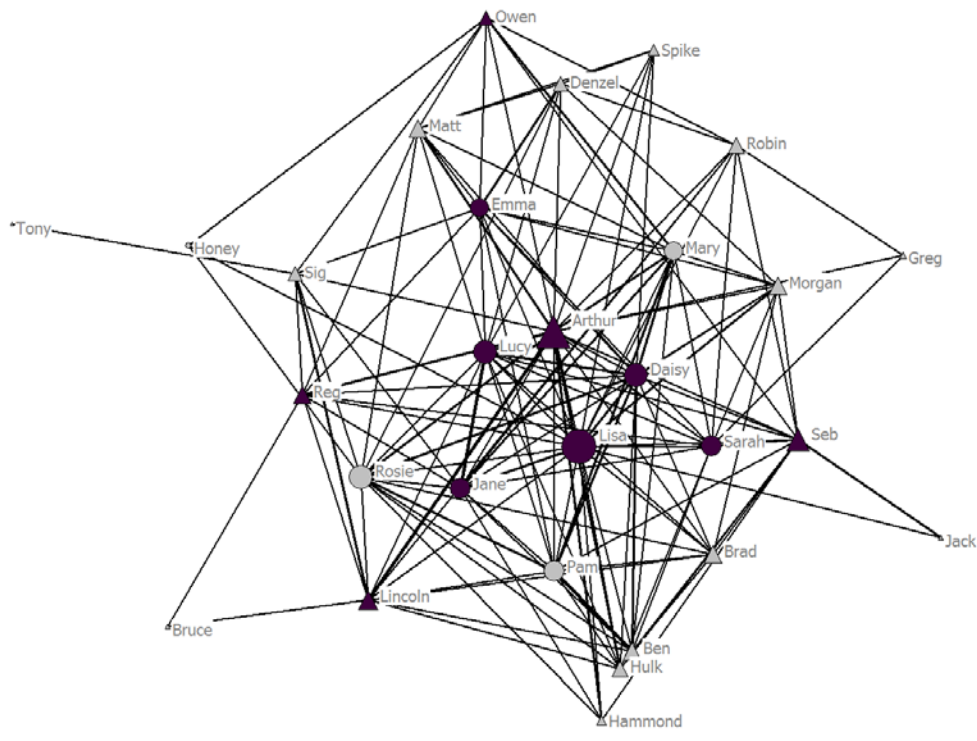


698  
699 Group F

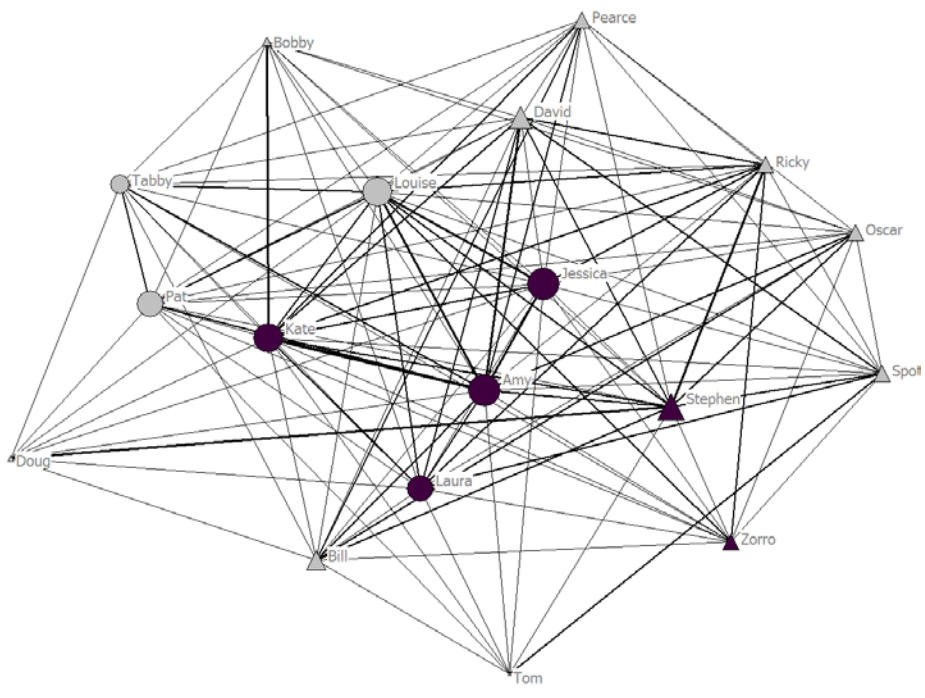


700

701 B  
702 Group L

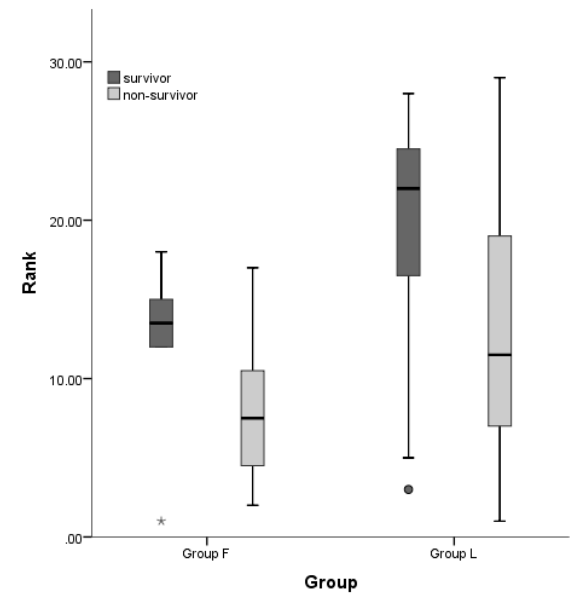
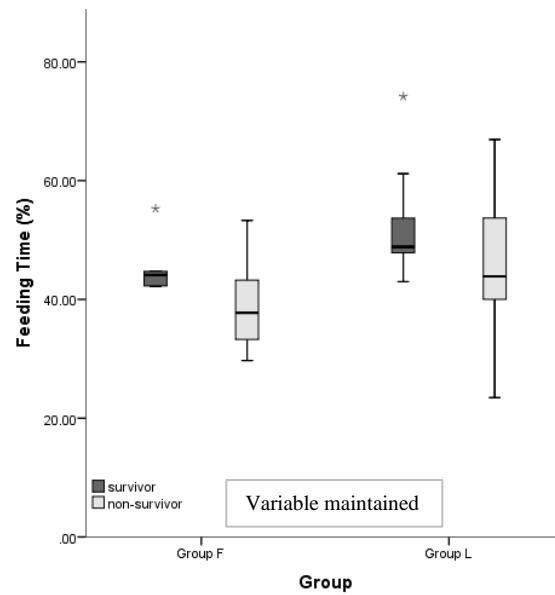
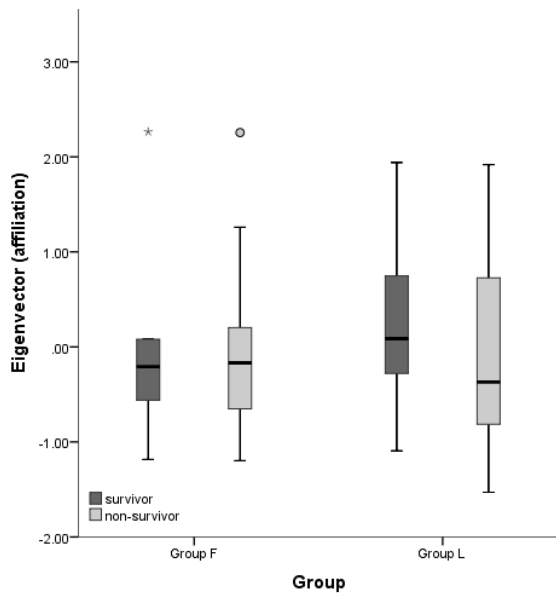
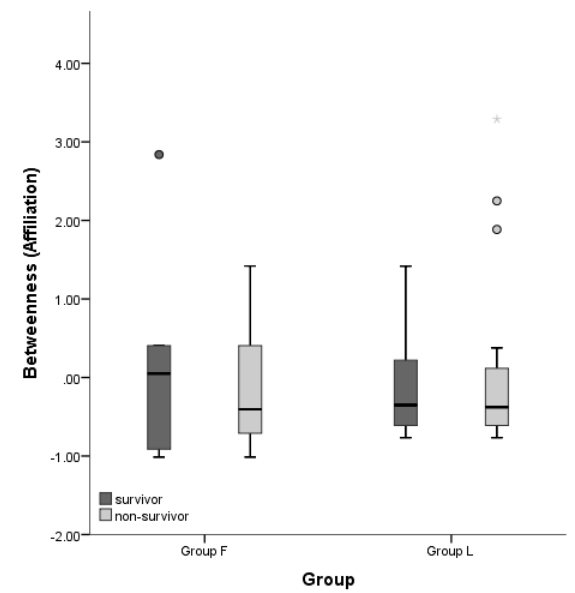
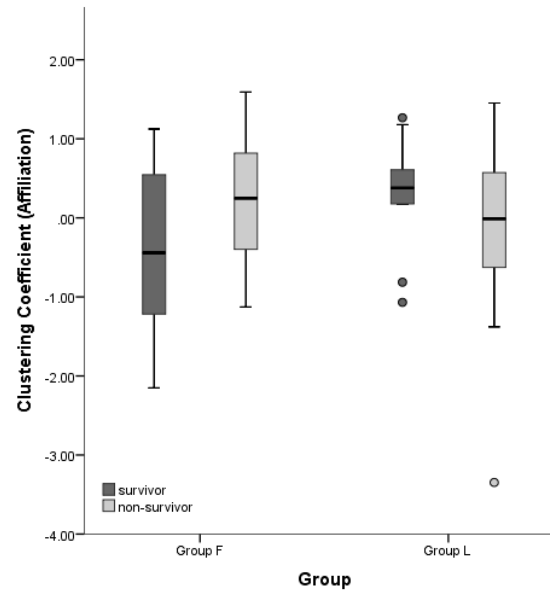
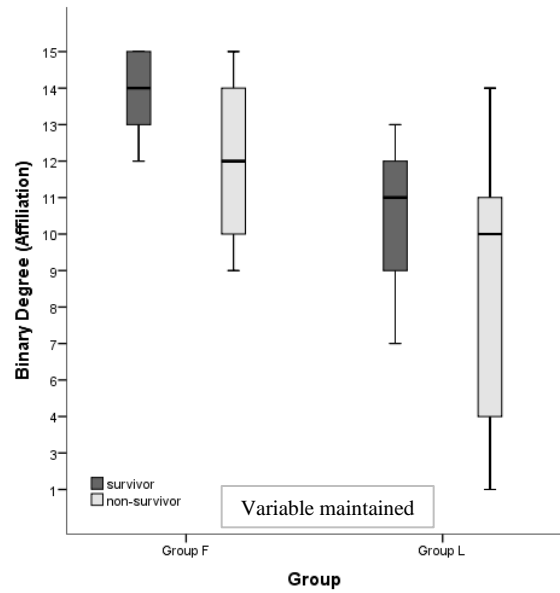


703  
704 Group F

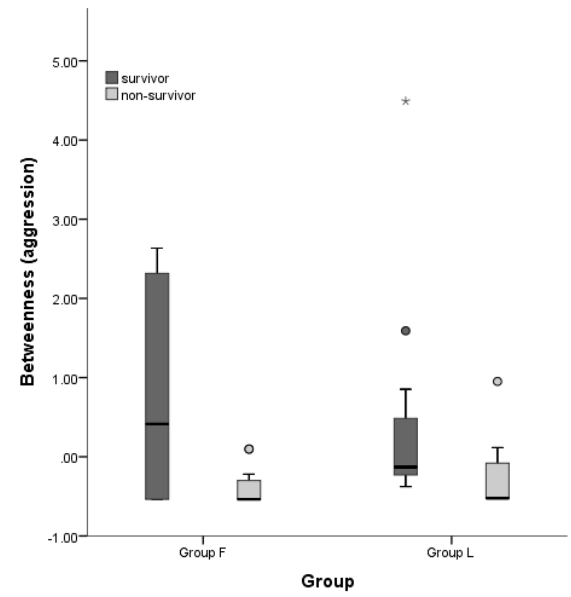
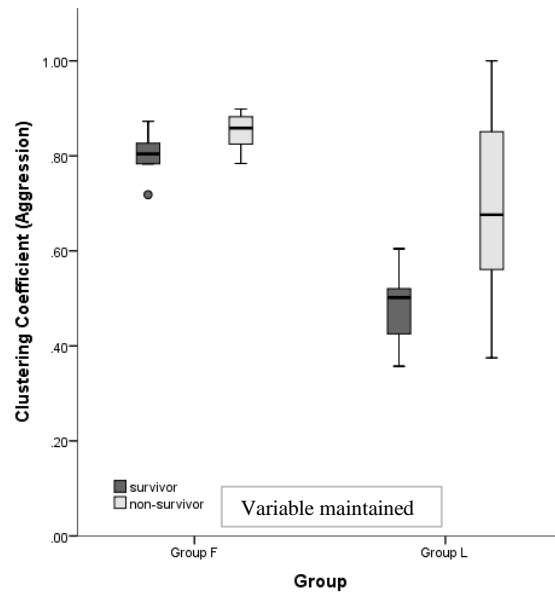
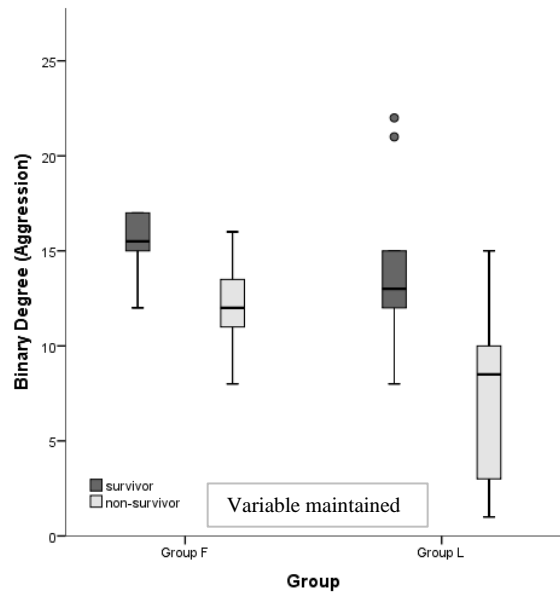


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706 Figure 2  
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709 Figure 3  
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714 Supplementary Data

715

716 Table 1S: Results of Spearman Rank correlation analysis between network parameters

717 from the affiliation network (N=45 for Clustering coefficient, N=47 for all others);

718 strength was subsequently excluded from the analysis due to the high correlation with the

719 other metrics.

<b>Affiliation network</b>		Strength (weighted degree)	Betweenness (weighted)	Clustering Coefficient (weighted)	Eigenvecto r 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

720 The asterisk indicate a significant correlation with  $p < 0.01$ .

721

722

723

724 Table 2S: Logistic regression results predicting macaque survival based on the affiliation  
 725 network (N=45), model 1 uses binary degree, model 2 uses strength instead.  
 726

<b>Affiliation: Full model 1</b>	<b>B</b>	<b>Wald z</b>	<b>P</b>	<b>AIC</b>
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	
<b>Binary degree</b>	<b>-1.51</b>	<b>-2.22</b>	<b>0.03</b>	
Clustering	-0.34	-0.63	0.53	
Betweenness	0.06	0.11	0.91	
Eigenvector	0.06	0.12	0.91	
<i>Feeding</i>	<i>0.12</i>	<i>-1.80</i>	<i>0.07</i>	

727

<b>Affiliation: Full model 2</b>	<b>B</b>	<b>Wald z</b>	<b>P</b>	<b>AIC</b>
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	
<i>Feeding</i>	<i>-0.10</i>	<i>-1.68</i>	<i>0.09</i>	

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

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735 Table 3S  
 736 Model selection results (variable coefficients) for all models with an AIC difference of  $\Delta < 3$  to the best fit model containing  
 737 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

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

741

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

<b>Aggression network</b>		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**

747 The asterisks indicate a significant correlation with  $p < 0.01$ .

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757 Table 5S: Logistic regression results predicting macaque survival based on the aggression  
 758 network (N=46); model 1 uses binary degree, model 2 uses strength instead.  
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<b>Aggression: Full model 1</b>	<b>B</b>	<b>Wald z</b>	<b>P</b>	<b>AIC</b>
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	

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<b>Aggression: Full model 2</b>	<b>B</b>	<b>Wald z</b>	<b>P</b>	<b>AIC</b>
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	
<b>Clustering</b>	<b>2.09</b>	<b>2.15</b>	<b>0.03</b>	
Betweenness	0.35	0.35	0.73	
Feeding	0.03	0.49	0.62	

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

765 Table 6S

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

768

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

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

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

<b>Aggression network</b>		Feeding time (%)	Degree (binary)	Degree (weighted)	Betweenness (weighted)	Clustering Coefficient (weighted)	Eigenvector centrality	Rank
<b>Affiliation network</b>	Feeding time (%)	$r_s$ -	<b>0.415</b>	<b>0.459</b>	<b>0.591</b>	<b>-0.469</b>	<b>0.370</b>	<b>0.496</b>
	Degree (binary)	$r_s$ -0.091	<b>0.592</b>	0.539	-0.277	0.159	<b>0.560</b>	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	<b>0.378</b>	<b>0.303</b>	-0.166	0.101	<b>0.328</b>	0.161
	Rank	$r_s$ .496	<b>0.552</b>	<b>0.492</b>	<b>0.442</b>	<b>-0.280</b>	<b>0.436</b>	-

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

776

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 <sub>agg</sub>	-4.32	-1.78	<i>0.08</i>	
<b>Clustering<sub>agg</sub></b>	<b>2.67</b>	<b>2.19</b>	<b>0.03</b>	
Betweenness <sub>agg</sub>	-0.09	-0.09	0.93	
Binary degree <sub>aff</sub>	-1.18	-0.94	0.35	
Clustering <sub>aff</sub>	-2.13	-1.68	<i>0.09</i>	
Betweenness <sub>aff</sub>	-0.25	-0.25	0.80	
Eigenvector <sub>aff</sub>	1.07	1.29	0.19	
Feeding	0.02	0.20	0.84	

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

780



781 Table 9S. Model selection results (variable coefficients) for all models with an AIC difference of  $\Delta < 3$  to the best fit model containing  
 782 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

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