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Title: Consistent individual variation across interaction networks indicates social personalities in lemurs

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Abstract: Consistent individual variation across interaction networks indicates social personalities in lemurs

#### ABSTRACT

Group members interact with each other in multiple ways, ranging from aggression to affiliation. It is not known, however, whether an individual's suite of social behaviors consistently co-varies through time and across different types of social interactions. Consistent social behavior would be advantageous in groups, especially when individuals need to remember conspecifics' social roles and preferences in order to keep track of group members' social relationships and predict their future behavior. Here, we address whether social behavior of individual ring-tailed lemurs (*Lemur catta*) is consistent through time and across four behaviors (aggression, grooming, contact calling, scent marking). We quantified variation in social behavior through four network centrality measures (out-degree, out-strength, betweenness, and eigenvector centrality). Comparing networks across two years revealed that network centrality remained consistent between years. Centrality was also consistent across networks: Lemurs with high centrality in one network also had high centrality in the other networks, even when we controlled for sex-based variation in behavior. Thus, regardless of their sex, some individuals were highly social in all four behaviors. They frequently groomed others, initiated aggressive interactions, and responded to others' contact calls and scent marks. Lemurs also had preferred social partners, and frequently interacted with the same individuals across multiple types of social behaviors and across years. In particular, lemurs frequently responded to the contact calls and the scent marks of the conspecifics they had frequently groomed. Together, these results demonstrate that individual variation in social behavior is not context specific, but instead persists through time and across multiple social interactions. Such consistent behavior provides evidence for social personalities, which may influence individuals' interaction styles including how socially active they are and with whom they interact.

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8 affiliation. It is not known, however, whether an individual's suite of social behaviors  
9 consistently co-varies through time and across different types of social interactions.  
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21 social in all four behaviors. They frequently groomed others, initiated aggressive  
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24 multiple types of social behaviors and across years. In particular, lemurs frequently  
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26 groomed. Together, these results demonstrate that individual variation in social behavior  
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28 interactions. Such consistent behavior provides evidence for social personalities, which  
29 may influence individuals' interaction styles including how socially active they are and  
30 with whom they interact.

31  
32  
33 **Keywords:**

34 Animal personalities, centrality measures, interaction networks, network metrics, ring-  
35 tailed lemurs, social centrality, social network analysis, social personalities, *Lemur catta*.

36

37 **INTRODUCTION**

38 Individual variation in social behavior has key consequences for resource access, mate  
39 choice, learning, disease transmission, decision-making, and fitness (Cameron et al.,  
40 2009; Croft et al., 2009; Frère et al., 2010; Krause et al., 2007; Lusseau & Conradt, 2009;  
41 Schülke et al., 2010; Seyfarth et al., 2012; Weidt et al., 2008; Wey et al., 2008). Some of  
42 this variation can be attributed to age, sex, dominance, and environmental factors  
43 (Monclus et al., 2012; Seyfarth et al., 2014; Silk et al., 2006a; Silk et al., 2006b;  
44 Taborsky & Oliveira, 2012; Thornton & Clutton-Brock, 2011). However, variation in  
45 social behavior may also result from some individuals being more social than others and  
46 thus initiating interactions more frequently or with more individuals regardless of their  
47 age, sex, or dominance status. Given that group members interact through multiple types  
48 of affiliative and aggressive behaviors, it is plausible that the preference for being social  
49 persists regardless of the type of social interaction. For instance, socially active  
50 individuals may frequently groom others while also frequently initiating aggressive  
51 interactions. This preference to be social may also remain stable through time.

52

53 Social differences that persist through time and across different behaviors may  
54 provide insight into social personality traits. In humans, social personalities are identified  
55 through consistencies in social activity levels and interaction styles, and are inferred from  
56 measures such as how many interaction partners an individual has, how frequently they  
57 interact with others, and the identities of their preferred interaction partners (Clifton,  
58 2013; Fang et al., 2015; Golbeck et al., 2011; John & Srivastava, 1999; Quercia et al.,

59 2012; Staiano et al., 2012). Thus, social personalities can be expressed two ways. First,  
60 individuals may display consistent social activity levels across all types of social  
61 interactions. Second, individuals may have preferred interaction partners that they  
62 frequently interact with during multiple types of social behaviors. Given the high  
63 complexity of animal interactions, an empirical approach similar to that of human social  
64 personalities can be utilized to study animal social personalities.

65

66         Social personalities would have immense consequences for how individuals  
67 navigate through the complex social environments that feature repeated interactions. On  
68 one hand, consistent behavior may reduce an individual's ability to quickly respond to  
69 changing conditions. Over the past decade, great progress has been made in  
70 understanding animal personalities (also referred to as "behavioral syndromes" or  
71 "temperament") from intra-individual consistencies in exploration, boldness, and activity  
72 levels (Bell, 2007; Biro & Stamps, 2008; David et al., 2011 ; Dingemanse & Reale, 2005;  
73 Koolhaas et al., 1999; Reale et al., 2010; Réale et al., 2007; Seyfarth et al., 2012; Sih et  
74 al., 2004a; Smith & Blumstein, 2008; Wolf & Weissing, 2012). However, consistent  
75 behavior frequently results in trade-offs, and can even lead to disadvantageous or  
76 maladaptive responses (Sih et al., 2004a; Sih et al., 2004b). On the other hand, consistent  
77 social behavior may be advantageous in a group setting, especially when group members  
78 need to remember each other's social roles and preferences. Doing so would allow them  
79 to keep track of their relationships with others, predict others' future behavior, and  
80 modify their own responses accordingly (Dall et al., 2005). If some individuals are highly

81 active during all types of social interactions, then such consistencies may create social  
82 niches which reflect individuals' roles in the social environment (Bergmuller &  
83 Taborsky, 2010). Individuals vary in their sociability (i.e. response to presence or absence  
84 of a conspecific) and aggressiveness (i.e. agonistic interactions towards others) (Réale &  
85 Dingemanse, 2010; Réale et al., 2007). Consistent variation in these traits may lead to  
86 social niches (Bergmuller & Taborsky, 2010; Montiglio et al., 2013) and can be  
87 beneficial at the population level by increasing behavioral diversity, which is essential for  
88 dealing with environmental changes (Caro & Sherman, 2011; Rubenstein, 2016).  
89 Furthermore, because reducing uncertainties during social interactions is highly  
90 advantageous (Barrett et al., 2012), keeping track of others' social personalities and  
91 niches may allow animals to reduce uncertainties about their social environment.

92

93         Identifying social personalities requires analyzing individual variation in social  
94 behavior through time and across behaviors. Social network analysis is a robust tool for  
95 quantifying individuals' network positions (i.e. centrality) by determining the extent of  
96 their connections and their social role in the group (Lusseau & Newman, 2004;  
97 Wassermann & Faust, 1994). Social individuals with high centrality in one behavior (e.g.  
98 aggression) may also have high centrality in other behaviors with a different function  
99 (e.g. grooming). Similar to inferring personality traits such as boldness, exploration, or  
100 neophobia from consistencies in behavioral measures through time and across contexts,  
101 we can infer social personality traits from consistencies in network centrality measures  
102 through time and across different contexts (Krause et al., 2010; Wilson et al., 2013).

103 Furthermore, social centrality can be defined in multiple ways depending on the question  
104 of interest. For instance, some centrality measures address the number of connections an  
105 individual has, some measures utilize the frequency of connections, while other measures  
106 account for the social importance of one's connections to determine their social centrality  
107 (Lusseau & Newman, 2004; Wassermann & Faust, 1994). Using multiple centrality  
108 measures allows analyzing different aspects of variation in social behavior.

109

110 Network position and centrality have multiple consequences (reviewed in (Krause  
111 et al., 2014)). Network position can influence information acquisition (Aplin et al., 2012;  
112 Kulahci et al., 2016), disease transmission (Duboscq et al., 2016; Godfrey et al., 2009;  
113 Rubenstein, 2015), and reproductive fitness (McDonald, 2007). Several studies have  
114 addressed whether network position stays consistent through time in association networks  
115 based on physical proximity (Aplin et al., 2015; Jacoby et al., 2014; Krause et al., 2016;  
116 Vander Wal et al., 2015). Other studies have addressed consistencies in one type of social  
117 interaction, for example aggressive interactions (Frumkin et al., 2016) including potential  
118 consistencies between social and defensive aggression (Blumstein et al., 2013). Yet, only  
119 a few studies have explored the consistencies across networks based on different types of  
120 social behaviors (Castles et al., 2014; Madden et al., 2011). Thus, whether or not network  
121 centrality and choice of interaction partners remain stable both through time and across  
122 different types of social behaviors has not yet been established.

123

124 We studied ring-tailed lemurs (*Lemur catta*) to detect individual consistencies  
125 through time and across different social behaviors. We constructed networks from four  
126 behaviors which included (1) grooming, (2) aggressive interactions, (3) contact calling,  
127 and (4) scent marking. Each of these behaviors has a different function. Affiliative  
128 interactions such as grooming are essential for forming social bonds and reducing  
129 aggression, as well as for stress reduction and hygiene maintenance (Barton, 1985; Cords,  
130 1997; Enquist & Leimar, 1993; Silk et al., 2006a; Silk, 2007). Lemurs with strong social  
131 bonds frequently groom each other to maintain these bonds ((Kulahci et al., 2015). In  
132 comparison to grooming, aggressive interactions are important in intra and inter-sexual  
133 competition, territoriality, group stability, and dominance in many species in addition to  
134 the ring-tailed lemurs (Clutton-Brock et al., 2006; Flack et al., 2006; Marler, 1976).

135

136 While both grooming and aggression are direct interactions that involve physical  
137 contact, animals also interact indirectly through social signals. Social signals allow  
138 conspecifics to communicate when they are separated and are thus comparable to an  
139 interaction. Signals underlie individual recognition that is necessary for selectivity in  
140 interactions (Kulahci et al., 2014; Kulahci & Ghazanfar, 2013) and can greatly influence  
141 association and interaction networks (Snijders & Naguib, 2017). For instance, in many  
142 primate species including lemurs, contact calls are known as ‘cohesion calls’ because  
143 they allow group members to keep in touch over long distances (Macedonia, 1993).  
144 Additionally, lemur contact calls allow strongly bonded pairs to keep in touch and  
145 reinforce their bonds when they are physically separated from each other (Kulahci et al.,

146 2015). Besides contact calls, scent marks also allow conspecifics to keep in touch. Scent  
147 marks of many species carry individual signatures, and investigating a scent mark  
148 provides information on scent owner's identity, reproductive status, and location  
149 (Charpentier et al., 2008; Kappeler, 1998; Scordato & Drea, 2007). In lemurs, scent  
150 marking is critical in communication, reproductive status advertisement, and territoriality  
151 (Kappeler, 1998; Kulahci et al., 2014; Macedonia, 1986, 1993; Scordato & Drea, 2007).  
152 By focusing on four social behaviors with different functions, we aimed to determine  
153 whether individual variation in social activity levels and interaction partners persisted  
154 through time and across behaviors with different functional consequences.

155

156         We predicted that social variation that persisted through time and across different  
157 types of behaviors would indicate presence of social personalities in lemurs. We utilized  
158 two complementary approaches to infer social personalities. First, we analyzed  
159 consistencies in centrality metrics to explore whether individuals had consistently high  
160 (or low) centrality through time and across the four behaviors we studied. We predicted  
161 that some lemurs would be more social and thus have higher network centrality than  
162 others, and that this variation would be carried over through time and across different  
163 types of behaviors, resulting in consistencies in network centrality across all four  
164 behaviors we studied. Second, we analyzed whether individuals interacted with the same  
165 conspecifics through time and during different behaviors. If the pairs that interact  
166 frequently during one behavior also interact frequently during other behaviors, then this  
167 would result in correlations between the matrices of these networks, suggesting that

168 individuals had preferred partners they frequently interacted with during multiple  
169 behaviors. We predicted that lemurs would respond to the contact calls and the scent  
170 marks of the conspecifics they groomed. Because grooming reinforces social bonds,  
171 complementing grooming interactions with contact calling and scent marking would  
172 allow bonded lemurs to keep in touch and receive up to date information about each  
173 other. Alternatively, if we did not detect consistencies through time or different  
174 behaviors, then this would suggest that individual variation in social behavior is  
175 explained by other variables such as sex and/or age. For instance, if one of the factors that  
176 influenced variation in social behavior were age, then individuals' centrality and choice  
177 of interaction partners should differ between years instead of remaining consistent. This  
178 difference should be most noticeable when juveniles become adults.

179

## 180 **METHODS**

181

### 182 *Social network data*

183 Lemurs live in female dominated groups of up to 25 individuals (Jolly, 1966a, 1966b;  
184 Wilson & Hanlon, 2010). Such group sizes are perfect for network analyses, because they  
185 are large enough to detect individual variation, but also small enough to allow all  
186 individuals to be observed simultaneously to avoid sampling biases. We observed four  
187 ring-tailed lemur groups. Two groups (n=7, 8 individuals) semi free-ranged in large  
188 natural habitat enclosures at the Duke Lemur Center (NC, USA), while two larger groups  
189 (n=17, 21 individuals) free-ranged on St. Catherines Island (GA, USA) (**Table S1**). The

190 groups at Duke Lemur Center were separated from each other by chain-link fences,  
191 which allowed visual, acoustic, and olfactory contact but prevented inter-group  
192 movement. In contrast, lemurs at St. Catherines Island free-ranged on the island and were  
193 free to move between groups.

194

195 We observed two groups for two consecutive years (NHE4 n=9 in 2010 and n=7  
196 in 2011; YB n = 21 in 2011 and in 2012; **Table S1**). Each group was observed for a  
197 minimum of four times per week during two months (number of observation hours per  
198 group: 116, 105, 120, 107, 128, 120 hours respectively for n=9 (in 2010), n=7 (in 2011),  
199 8, 17, 21 (in 2011 and 2012) individuals). All lemurs were individually identifiable  
200 through visual features, collars, and tail shaves. We used all-occurrence sampling to  
201 collect social data, which we then converted into network matrices and analyzed in  
202 UCINET (version 6.624) (Borgatti et al., 2002). We constructed networks from four  
203 behaviors including grooming, aggression, contact calling, and scent marking. Each  
204 network had a distinct actor and a receiver (directed network) and also included  
205 information on how frequently an interaction occurred between each pair (weighted  
206 network). Procedures were consistent with the guidelines of, and approved by, the  
207 Institutional Animal Care and Use Committees at Duke University (A121-10-05) and  
208 Princeton University (Protocol #1868).

209

210 *Grooming* networks included both reciprocal grooming (two lemurs  
211 simultaneously groom each other) and non-reciprocal grooming (a directed interaction

212 where one lemur grooms another). We converted reciprocal grooming into directed  
213 grooming by adding the mutually grooming lemurs as both the actor and the receiver of  
214 the interaction. Each grooming bout was separated from others either by suspension of  
215 grooming for at least 5 minutes or by a change in grooming partners.

216

217 *Aggression* networks included chases and aggressive physical contact such as  
218 fights. The actor was the lemur initiating the aggressive interaction. If a lemur initiated an  
219 aggressive interaction towards a specific conspecific multiple times in a row, without  
220 engaging in an interaction with another group member, this was scored as a single  
221 aggressive interaction.

222

223 *Contact calling* networks were based on producing a vocal response after hearing  
224 a contact call. The lemurs producing a vocal response after hearing another lemur were  
225 the actors of the interaction. The lemurs vocalizing first and receiving responses were the  
226 recipients. We defined the responding lemurs as the actors, because although contact call  
227 responses are usually directed towards the lemur producing an initial call, it is not  
228 possible to determine with certainty whether the initial calls are directed towards the  
229 responding lemurs (Kulahci et al., 2015).

230

231 *Scent marking* networks were based on countermarking after investigating a  
232 previously placed mark at the same location. Lemurs marking the same place after  
233 investigating scent marks were defined as the actors of the interaction, and the lemurs

234 placing the initial marks were the recipients of the interaction. Scent marking data were  
235 collected only if we witnessed both the initial mark and the countermark within the same  
236 observational period. All countermarks were placed within a few minutes of the first  
237 mark during our observations. By quantifying networks based on multiple distinct  
238 behaviors, we aimed to obtain an accurate picture of each lemur's social activity levels  
239 and their preferences for specific interaction partners.

240

#### 241 *Network metrics*

242 To quantify individual variation in social behavior and to address whether some  
243 individuals were highly active regardless of the type of social behavior they engaged in,  
244 we calculated four network metrics (degree, strength, betweenness, and eigenvector  
245 centrality). Each metric addresses a different aspect of social centrality, such as the  
246 number of connections an individual has, or an individual's role in influencing the overall  
247 group structure by connecting the otherwise unconnected pairs.

248

249 The first measure, *degree*, is calculated from the number of direct connections an  
250 individual has (Freeman & Gosling, 2010). Individuals who are connected to more  
251 conspecifics have a higher degree than individuals who are connected to fewer  
252 conspecifics. We calculated degree from directed but unweighted networks, which we  
253 obtained by dichotomizing the network matrices. Any cell with a value of greater than  
254 "0" (i.e. when an interaction was present between two individuals) was entered as "1",  
255 while everything else (i.e. the absence of an interaction) was entered as "0". In directed

256 networks, *out-degree* indicates the number of group members towards whom an  
257 individual initiates an interaction, *in-degree* indicates the number of group members from  
258 whom an individual receives an interaction. We focused on *out-degree* to determine how  
259 socially active individuals are by quantifying the number of conspecifics towards whom  
260 they initiated interactions.

261

262 The second measure, *strength*, focuses on the frequency of interactions and is  
263 calculated from weighted networks. We focused on *out-strength* to determine the  
264 frequency that each lemur initiated interactions towards others. We used out-degree and  
265 out-strength to quantify whether certain individuals were more socially active than others  
266 through time and across different types of social behaviors.

267

268 The third centrality measure, *betweenness*, depends on the shortest path length,  
269 which is the least number of connections required to connect two individuals (Croft et al.,  
270 2008). Pairs that are directly connected have a shorter path length than pairs that are  
271 indirectly connected only through others. Betweenness reflects the number of shortest  
272 paths that go through an individual to connect other pairs (Borgatti et al., 2013; Lusseau  
273 & Newman, 2004). Individuals with high betweenness are critical in connecting the pairs  
274 that are not directly connected to each other (Freeman, 1979). An individual with low  
275 degree can have high betweenness if some of its neighbors are not otherwise connected to  
276 each other.

277

278           The final measure, *eigenvector centrality*, is a more global measure than the  
279 previous three, because it depends on the centrality of one's neighbors. Highly connected  
280 individuals can have high eigenvector centrality only if the individuals they are connected  
281 to are also well-connected to others (Borgatti et al., 2013; Kasper & Voelkl, 2009;  
282 Newman, 2004). Both betweenness and eigenvector centrality are more global measures  
283 in comparison to out-degree and out-strength, and can provide insight into the social role  
284 that each individual plays in their group, either by connecting pairs or by sharing  
285 connections with others who play important roles in the group.

286

287           Overall, we calculated four measures for each of the four behaviors. These  
288 measures allowed us to quantify social centrality using different criteria, including the  
289 number of interaction partners (out-degree), frequency with which individuals initiated  
290 interactions (out-strength), their importance in connecting the otherwise unconnected  
291 pairs (betweenness), and the centrality of their interaction partners (eigenvector).

292

### 293 *Social network analyses*

#### 294 **Consistency of network centrality through time**

295 We compared individual centralities between two years to determine whether lemurs  
296 retained their centrality. We used data from two groups for this analysis (NHE4, YB,  
297 **Table S1**) because we did not have sufficient data for temporal comparisons from other  
298 groups. Only if the lemurs were in the same group during both years, were they included  
299 in temporal analyses. We used the R code from Wilson et al. (2013) to test consistencies

300 in network centrality. This network position consistency test ranks each individual based  
301 on a centrality metric of interest, and then analyzes whether individual ranks are  
302 correlated across networks. We used this test to determine whether individuals with high  
303 rank in one year also had high rank the next year. Using ranks is preferable to using raw  
304 metric values, because we are interested in whether or not some individuals consistently  
305 have higher centrality relative to others in their group. A significant p-value indicates that  
306 individual ranks are similar across networks, providing evidence for individual  
307 consistencies across networks of interest. Metrics arising from the same network are not  
308 independent of each other, and the test controls for the non-independent nature of  
309 network data by utilizing a randomization procedure (we ran 10000 randomizations)  
310 (Wilson et al., 2013). This test requires that all individuals in a network to have an equal  
311 probability of being observed, which was true in our study. We had four behaviors and  
312 four measures per behavior, giving us a total of 16 ranks per lemur. We used the  
313 Benjamini-Hochberg False Discovery Rate (FDR) to correct for multiple comparisons at  
314 the 0.05 level (Benjamini & Hochberg, 1995, 2000).

315

### 316 **Consistency of network centrality across different social behaviors**

317 To determine whether lemurs with high centrality in one type of social behavior also had  
318 high centrality in other social behaviors, we again used the network position consistency  
319 test from Wilson et al. (2013). We analyzed whether individual ranks were consistent  
320 across four behaviors (grooming, aggression, contact calling and scent marking). We  
321 used the FDR test to correct for multiple comparisons. Because metrics arising from the

322 same network are frequently correlated (Borgatti et al., 2013), we only compared the  
323 same metrics to each other. For example, while we compared grooming out-degree to  
324 out-degrees of aggression, contact calling, and scent marking, we did not compare  
325 grooming out-degree to out-strength, betweenness, or eigenvector from any network  
326 including the grooming network. If the same individuals consistently ranked high in  
327 multiple interactions, while others consistently ranked low, this would suggest that  
328 network centrality stays consistent regardless of the nature of the social connections  
329 between conspecifics, thus providing evidence in favor of social personalities.

330

331         Variation in group size may influence whether ranks stay consistent across  
332 different behaviors. Because our groups differed in size, we calculated *network density*  
333 for each network from each group. Low network density means that the majority of  
334 connections that could potentially exist in the network do not actually exist (Hanneman &  
335 Riddle, 2005). Larger groups are likely to have lower densities than smaller groups as the  
336 possibility of forming different connections increases as group size increases. We  
337 calculated network density from unweighted networks. In addition to density, we also  
338 analyzed the range of the centrality measures in each group. Smaller groups are likely to  
339 have less variation than larger groups, and this may potentially influence whether  
340 centrality measures stay consistent across networks.

341

342         Lemurs are a female-dominated species in which females stay in their natal group  
343 and interact frequently, while males disperse out into a new group when they reach

344 sexual maturity (Jolly, 1966a, 1966b; Wilson & Hanlon, 2010). It is possible that females  
345 are more social than males and have higher centrality ranks across all types of social  
346 interactions. To determine whether sex-based variation in social behavior was responsible  
347 for consistencies across behaviors, we used ANOVA to compare the centrality ranks of  
348 males to those of females. We then checked the p-values using a permutation test  
349 (“SimplePermutationTest” add-in for JMP) by running 1000 permutations on centrality  
350 ranks of males and females, and comparing the resulting p-values to those from our  
351 dataset. Females do not inherit their dominance status from their mothers (Nakamichi &  
352 Koyama, 1997) and lemur dominance hierarchies are subject to fluctuations. We  
353 therefore did not include dominance as a variable but focused on the role of sex-based  
354 differences in social behavior.

355

### 356 **Consistency of interaction partners through time**

357 We used the Quadratic Assignment Procedure (QAP) (Borgatti et al., 2013) to determine  
358 whether lemurs consistently interacted with the same group members through time. QAP  
359 runs a correlation test for the corresponding cells of each matrix, permutes the rows and  
360 the columns of one of the matrices, and runs the correlation again before repeating this  
361 procedure multiple times (we ran 10000 permutations). We used QAP to analyze whether  
362 individuals were consistent in their choice of interaction partners across years in two  
363 groups (NHE4, YB, **Table S1**). Only the networks based on the same social behavior  
364 were compared to each other (e.g. grooming network from the first year was only  
365 compared to grooming network from the following year).

366

367 **Consistency of interaction partners across different social behaviors**

368 We used QAP to analyze whether lemurs consistently interacted with the same set of  
369 conspecifics across different types of social behaviors. When analyzing weighted  
370 networks, QAP is informative about whether or not the pairs with strong connections in  
371 one network also have strong connections in the other networks. Running QAP with  
372 weighted networks allowed us to determine whether lemurs had social partners they  
373 frequently interacted with during multiple behaviors with different social functions.

374

375 **RESULTS**

376

377 **Network centrality was consistent across years**

378 In the two groups from which we had multiple years of data (n= 7, 21), the majority of  
379 the centrality ranks were consistent across years (**Table 1**; the Benjamini-Hochberg  
380 adjusted p-values are provided in **Table S2**). Individuals with high out-strength and  
381 eigenvector centrality in the grooming network in the first year also had high centrality  
382 ranks the following year (network position consistency test: grooming out-strength test  
383 score= 1,  $p < 0.001$ ,  $n=7$ ; grooming out-strength test score: 163.5,  $p=0.02$ ,  $n=21$ , grooming  
384 eigenvector test score: 4,  $p=0.008$ ,  $n=7$ ; grooming eigenvector test score: 104,  $p=0.001$ ,  
385  $n=21$ , **Table 1, Figure 1**). Betweenness ranks were consistent across years in only one of  
386 the groups but not in the other group (network position consistency test: grooming  
387 betweenness test score: 6.5,  $p=0.03$ ,  $n=7$ ; grooming betweenness test score: 212,  $p=0.07$ ,

388 n=21, **Table 1**). In one of the groups, scent marking ranks were not correlated between  
389 the two years (**Table 1**). Overall, for majority of the network measures, lemurs with high  
390 centrality in the first year also had high centrality in the following year, suggesting that  
391 individual variation in social behavior stayed consistent across years.

392

### 393 **Consistency of network centrality across multiple social behaviors**

394 To determine whether some individuals had high centrality regardless of the type of  
395 social behavior they engaged in, we compared each lemur's centrality rank across four  
396 behaviors. In the larger groups (n=17, 21 individuals), almost all of the centrality ranks  
397 were consistent across networks (**Table 2**; the Benjamini-Hochberg adjusted p-values are  
398 provided in **Table S3**). For instance, out-degree (network position consistency test, test  
399 score= 523.833, p=0.002), out-strength (test score= 505.625, p<0.001), eigenvector  
400 centrality (test score= 526.125, p=0.002), and betweenness (test score= 516.542,  
401 p=0.001) were consistent across behaviors (YB 2011, n=21). However, none of the ranks  
402 were consistent across behaviors in the smaller groups (n=7, 8 individuals). Networks  
403 from the smaller groups had higher densities than networks from the larger groups,  
404 indicating that lemurs in the smaller groups interacted with the majority of their group  
405 members (**Table S4**). The grooming networks, in particular, had the highest densities  
406 among all networks (grooming network density: 0.982, 0.861, 0.81, 0.449, 0.479, 0.319  
407 for n= 8, 9, 7, 17, 21, 21 individuals). Additionally, inter-individual variation in centrality  
408 measures was lower in smaller groups in comparison to those from the larger groups  
409 (**Tables S5, S6**).

410

411 Females had higher centrality than males in all networks except the scent marking  
412 network, where the difference between the sexes was not significant (regression results;  
413 **Table 3A**). When we checked the p-values using a permutation test, we found that the  
414 majority of the p-values from the permutation test were consistent with those we obtained  
415 from our dataset, thereby confirming our observational p-values. The only variation were  
416 insignificant differences in scent-marking out-degree ( $p=0.211$  versus  $0.206$ ) and scent  
417 marking betweenness ( $p=0.228$  versus  $0.224$ ). Despite sex-based differences in social  
418 behavior, analyzing females' ranks separately from males' ranks revealed that intra-  
419 individual consistencies in centrality still persisted even after accounting for behavioral  
420 differences between sexes (network consistency test results; **Table 3B**; the Benjamini-  
421 Hochberg adjusted p-values are provided in **Table S7**). This suggests that even though  
422 sex played a major role in determining variation in lemur social centrality, with females  
423 being more central than males, intra-individual consistencies across networks were not  
424 exclusively due to sex-based differences.

425

#### 426 **Lemurs' choice of interaction partners was consistent through time**

427 To address whether individuals interacted with the same conspecifics through time, we  
428 analyzed the similarities between network matrices from two consecutive years. QAP  
429 analysis revealed that lemurs were highly consistent in their interaction partners across  
430 years. In both groups, lemurs initiated aggressive interactions towards the same  
431 conspecifics during both years (QAP,  $r=0.982$ ,  $p<0.001$ ,  $n=7$ ;  $r=0.22$ ,  $p=0.014$ ,  $n=21$ ),

432 groomed the same conspecifics ( $r=0.993$ ,  $p<0.001$ ,  $n=7$ ;  $r=0.519$ ,  $p<0.001$ ,  $n=21$ ), and  
433 responded to the calls of the same conspecifics ( $r=0.918$ ,  $p<0.001$ ,  $n=7$ ;  $r=0.191$ ,  
434  $p=0.031$ ,  $n=21$ ). Scent marking in one group ( $n=21$ ) was an exception to this trend. Only  
435 in one group but not the other group, lemurs investigated the marks of the same  
436 conspecifics during both years ( $r=0.662$ ,  $p<0.001$ ,  $n=7$ ;  $r=-0.005$ ,  $p=0.652$ ,  $n=21$ ; **Table**  
437 **4**). These results revealed that lemurs had high temporal consistency in their choice of  
438 interaction partners for the majority of the social interactions we analyzed.

439

#### 440 **Lemurs engaged in multiple types of interactions with their preferred partners**

441 We used QAP to determine whether lemurs interacted with same conspecifics during  
442 multiple social behaviors. In all groups except one, lemurs responded to the calls of, and  
443 investigated the scents of, the conspecifics they frequently groomed (**Table 5**). Even  
444 though the relationship between grooming, vocalizations and scent marks was not  
445 significant in one of the groups, there was a strong trend in the same direction as in the  
446 other groups ( $n=7$ ; grooming versus scent marking,  $p=0.059$ ; grooming versus contact  
447 calling,  $p=0.057$ ). In addition, in two groups, lemurs investigated the scent marks of the  
448 conspecifics they frequently vocalized in response to (QAP,  $r=0.2$ ,  $p=0.016$ ,  $n=17$ ;  
449  $r=0.122$ ,  $p=0.043$ ,  $n=21$ ). In comparison, there were no correlations between aggression  
450 networks and any other network in any of the groups. Overall, lemurs attended and  
451 responded to the social signals of the same conspecifics they groomed, demonstrating  
452 that their choice of interaction partners stayed consistent across multiple social behaviors  
453 that have different social functions.

454

455 **DISCUSSION**

456

457 We demonstrate that individual variation in social behavior persists through time and  
458 across multiple interaction networks. Lemurs' network centrality and choice of  
459 interaction partners were consistent between years. In the larger groups, lemurs with high  
460 centrality in one network also had high centrality in the other networks, even when we  
461 controlled for sex-based differences in social behavior. These central lemurs frequently  
462 groomed conspecifics, initiated aggressive interactions, and responded to the contact calls  
463 and the scents of many conspecifics, suggesting that some individuals are highly social  
464 regardless of the context in which their interactions occur. Lemurs also had preferred  
465 interaction partners; they frequently groomed, kept in vocal contact with, and  
466 investigated the scent marks of their preferred partners. Network consistencies through  
467 time and across different behaviors provide evidence of social personalities, which may  
468 underlie individual variation in interaction styles, including how socially active  
469 individuals are and their choice of interaction partners.

470

471         Social differences are likely to have major consequences both at the individual  
472 level and at the group level. For example, in pigtailed macaque (*Macaca nemestrina*)  
473 groups, a small set of group members play a key role in reducing within-group conflicts  
474 and in maintaining the stability of the group structure (Flack et al., 2006). Similarly,  
475 highly social individuals have a major influence on group-level processes such as

476 transmission of disease or information (Rubenstein, 2015). Consistent social differences  
477 may shape how animals respond to their environment (Wilson et al., 2013; Wolf &  
478 Krause, 2014). Social centrality correlates with exploration in great tits (*Parus major*)  
479 (Aplin et al., 2013), and has been shown to predict future breeding success in juvenile  
480 manakins (*Pipra filicauda*) (McDonald, 2009; Ryder et al., 2008) and the tendency to  
481 give alarm calls in yellow-bellied marmots (*Marmota flaviventris*) (Fuong et al., 2015).  
482 Therefore, consistent social variation that persists through time and across behaviors may  
483 significantly impact how individuals and groups adapt to changing conditions.

484

485         Knowing the past behaviors and the preferences of group members would allow  
486 animals to predict others' future behavior and to adjust their own responses accordingly  
487 (Dall et al., 2005; Drewe et al., 2009; Madden et al., 2009; Wassermann & Faust, 1994;  
488 Wolf & Krause, 2014). One of the exciting but relatively unexplored questions in social  
489 cognition is whether animals know about and keep track of conspecifics' social centrality  
490 (Seyfarth & Cheney, 2015). If centrality stays stable across different types of interactions,  
491 then this may allow animals to reliably predict conspecifics' behavior, keep track of their  
492 relationships, and adjust their own behavior accordingly. Therefore, it is possible that in  
493 addition to dominance, kinship, age, and sex, social personalities provide key information  
494 that shapes animals' social decisions and relationships. For example, chacma baboons  
495 (*Papio hamadryas ursinus*) use different strategies when approaching conspecifics with  
496 different personalities (i.e. nice, aloof, loner) (Seyfarth et al., 2012), suggesting that they  
497 do in fact pay attention to, and keep track of, different personality types in their group

498 and their own relationships with them. Such personality differences also have fitness  
499 consequences and tend to influence how well individuals respond to social events  
500 (Seyfarth et al., 2012). By remembering the personalities of their group members and  
501 their relationships with others, animals can make informed decisions about how to best  
502 respond to their social environment.

503

504         Despite these important consequences of social personalities, and despite the  
505 growing interest in personalities and in networks, only a limited number of empirical  
506 studies have addressed whether network centrality metrics stay stable through time and  
507 across contexts. Some of these studies have focused on the consistencies in association  
508 networks of fission-fusion populations. For example, a long-term study has demonstrated  
509 that bighorn sheep (*Ovis canadensis*) have consistent network centrality across years  
510 (Vander Wal et al., 2015). Another long-term study has shown that great tits occupy  
511 consistent positions in foraging networks, as evidenced by both short-term (weekly) and  
512 long-term (yearly) data. However, because great tit social data were based on a gambit of  
513 the group approach, it is possible that these consistencies were influenced by variation in  
514 space use (Aplin et al., 2015). Similarly, individual guppies also occupy consistent  
515 network positions, and some of these consistencies were explained in part by the  
516 tendency to be social and in part by sex-specific preferences (Krause et al., 2016).  
517 Additional studies have analyzed interaction networks to identify consistencies. For  
518 example, aggression network metrics of small spotted sharks (*Scyliorhinus canicula*)  
519 were shown to stay consistent across different habitats. However, it is possible that these

520 consistencies were driven by individual preferences for specific group sizes (Jacoby et  
521 al., 2014). In yellow-bellied marmots, measures of defensive aggression (i.e. aggression  
522 during live trapping) were found not to correlate with measures of social aggression  
523 (Blumstein et al., 2013). Furthermore, comparison of grooming, dominance, and foraging  
524 competition networks in meerkats (*Suricata suricatta*) showed that network centrality and  
525 partner choice are not always consistent across networks (Madden et al., 2011). Similarly,  
526 a three-year study on chacma baboons revealed high temporal variation between  
527 grooming, affiliative interaction, and proximity networks (Castles et al., 2014). However,  
528 the same study also demonstrated consistencies between grooming networks and  
529 networks based on other affiliative interactions (Castles et al., 2014).

530

531         Our study adds to these previous results to demonstrate social consistencies  
532 through time and across multiple types of social behaviors with different functions.  
533 Accounting for multiple types of behaviors is critical when determining whether social  
534 differences remain consistent. Analyzing multiple behaviors provides more accurate  
535 picture of each individual's social tendencies, including their preference to be social and  
536 their choice of interaction partners. Furthermore, consistencies in interaction partners  
537 across multiple behaviors can have far reaching implications at the group level.  
538 Repeatedly interacting with the same conspecifics during different behaviors provides  
539 increased opportunities for forming and maintaining strong social bonds. For example,  
540 strongly-bonded ring-tailed lemurs use vocalizations to keep in contact with each other  
541 (Kulahci et al., 2015). Such strong social bonds, which are reinforced through multiple

542 behaviors, could be one of the driving factors behind stable relationships between  
543 conspecifics. The ability to form and maintain strong social relationships plays a critical  
544 role in fitness (Seyfarth & Cheney, 2012), and may even be one of the precursors to the  
545 evolution of cooperation (Allen et al., 2017).

546

547         Network position and centrality are likely to be influenced by factors such as sex,  
548 age, and group structure (Krause et al., 2014). Such confounding factors can make it  
549 difficult to infer social personalities. Our group sizes varied from 7 to 21 individuals.  
550 Smaller groups were more connected than the larger groups, as evidenced by the high  
551 network densities and the low inter-individual variation in centrality measures. Running  
552 additional studies is essential for distinguishing whether this difference in results is due to  
553 a lack of confidence arising from a small sample size or due to a real biological  
554 difference arising from group size differences. Still, this variation outlines the importance  
555 of studying groups with differing sizes to fully understand how group size and structure  
556 influence social consistencies. Besides group size, sex can also play a role in  
557 consistencies in network centrality. For instance, in our study populations, females had  
558 higher centrality than males. However, analyzing females' centrality ranks separately  
559 from males' ranks revealed that intra-individual consistencies across different social  
560 behaviors still existed even after we controlled for sex-based differences. Furthermore,  
561 centrality ranks remained consistent across two years, during which some juveniles  
562 reached adulthood. If age were the only factor responsible for differences in centrality,  
563 then the centrality ranks of these juveniles should have changed when they became

564 adults. Together, these patterns suggest that social consistencies can still be present even  
565 beyond the influence of factors that are known to affect social behavior.

566

567         Our temporal analyses spanned two years of data and provided evidence that  
568 interaction partners stay consistent through time. Even though two years does not include  
569 all possible group composition changes such as multiple births and deaths, the promising  
570 results from our study suggest that assessing social personalities through consistencies in  
571 time and across different social behaviors is a fruitful direction for those studies that have  
572 access to longitudinal data from multiple years. In our study, the main exception to the  
573 temporal consistencies was the scent marking network in one group (n=21, **Tables 1, 4**).  
574 In this group, scent marking ranks were not consistent between years and the central  
575 lemurs from the first year did not occupy central positions during the following year.  
576 Similarly, lemurs did not mark the same conspecifics' marks during both years. Adult  
577 males frequently investigate and counter-mark conspecifics' marks, therefore the scent  
578 marking networks are highly dependent on the behavior adult males. However, to keep  
579 network matrices comparable, data from some adult males (e.g. those switching groups  
580 between years) were removed from the temporal analyses. It is possible that removing  
581 data from adult males reduced our power to detect consistencies in the scent marking  
582 networks. This was not an issue in the other group (n=7), which was in a different field  
583 site where movement between groups was restricted. It is therefore important to account  
584 for the ecology of the species of interest when looking at temporal consistencies in long-  
585 term data sets, especially when group composition changes significantly between years.

586

587           Quantifying social personalities through networks is a new approach in animal  
588 behavior. Yet, human studies have already provided evidence that network metrics  
589 reliably reflect social personalities by demonstrating that the five main personality traits  
590 (extraversion, neuroticism, agreeableness, conscientiousness, and openness (John &  
591 Srivastava, 1999)) strongly correlate with the consistencies in network centrality  
592 measures (Clifton, 2013; Fang et al., 2015; Golbeck et al., 2011; Quercia et al., 2012;  
593 Staiano et al., 2012). In contrast, only a handful of animal studies, the majority of which  
594 have focused on proximity networks, have addressed consistencies in animal social  
595 networks. Here, we demonstrate consistencies in both social centrality (particularly in  
596 larger groups) and in choice of interaction partners, both through time and across multiple  
597 types of social behaviors. We suggest that quantifying animal social personalities through  
598 networks presents a highly fruitful direction. The positive results from our study  
599 encourage further exploration of social personalities in the long-term datasets, where  
600 major life history events and significant group changes should provide additional  
601 insights. By combining network analysis with social personality studies and carefully  
602 designed social cognition experiments, we can address how knowledge of conspecifics'  
603 social personalities can help animals make social decisions.

## 604 REFERENCES

- 605  
606 Allen, B., Lippner, G., Chen, Y.-T., Fotouhi, B., Momeni, N., Yau, S.-T., & Nowak, M. A. (2017).  
607 Evolutionary dynamics on any population structure. *Nature*, *544*(7649), 227-230.
- 608 Aplin, L., Farine, D., Morand-Ferron, J., & Sheldon, B. (2012). Social networks predict patch discovery in  
609 a wild population of songbirds. *Proc. R. Soc. B.*, rspb20121591.
- 610 Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013).  
611 Individual personalities predict social behaviour in wild networks of great tits (*Parus major*).  
612 *Ecology Letters*, *16*(11), 1365-1372.
- 613 Aplin, L. M., Firth, J. A., Farine, D. R., Voelkl, B., Crates, R. A., Culina, A., . . . Sheldon, B. C. (2015).  
614 Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal*  
615 *Behaviour*, *108*, 117-127.
- 616 Barrett, L., Henzi, S. P., & Lusseau, D. (2012). Taking sociality seriously: the structure of multi-  
617 dimensional social networks as a source of information for individuals. *Philosophical transactions*  
618 *of the Royal Society of London. Series B, Biological sciences*, *367*(1599), 2108-2118. doi:  
619 10.1098/rstb.2012.0113
- 620 Barton, R. (1985). Grooming site preferences in primates and their functional implications. *International*  
621 *Journal of Primatology*, *6*(5), 519-532.
- 622 Bell, A. M. (2007). Future directions in behavioural syndromes research. *Proceedings of the Royal Society*  
623 *B: Biological Sciences*, *274*(1611), 755-761.
- 624 Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful  
625 approach to multiple testing. *Journal of the royal statistical society. Series B (Methodological)*,  
626 289-300.
- 627 Benjamini, Y., & Hochberg, Y. (2000). On the adaptive control of the false discovery rate in multiple  
628 testing with independent statistics. *Journal of educational and Behavioral Statistics*, *25*(1), 60-83.
- 629 Bergmuller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in*  
630 *Ecology & Evolution*, *25*(9), 504-511.
- 631 Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends*  
632 *in Ecology & Evolution*, *23*(7), 361-368.
- 633 Blumstein, D. T., Petelle, M. B., & Wey, T. W. (2013). Defensive and social aggression: repeatable but  
634 independent. *Behavioral Ecology*, *24*(2), 457-461. doi: 10.1093/beheco/ars183
- 635 Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). *Ucinet 6 for Windows: Software for social*  
636 *network analysis*: Harvard: Analytical Technologies.
- 637 Borgatti, S. P., Everett, M. G., & Johnson, J. C. (2013). *Analyzing social networks*: SAGE Publications  
638 Limited.
- 639 Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase  
640 reproductive success in feral horses. *PNAS*, *106*(33), 13850-13853.
- 641 Caro, T., & Sherman, P. W. (2011). Endangered species and a threatened discipline: behavioural ecology.  
642 *Trends in Ecology & Evolution*, *26*(3), 111-118.
- 643 Castles, M., Heinsohn, R., Marshall, H. H., Lee, A. E. G., Cowlshaw, G., & Carter, A. J. (2014). Social  
644 networks created with different techniques are not comparable. *Animal Behaviour*, *96*, 59-67.
- 645 Charpentier, M. J., Boulet, M., & Drea, C. M. (2008). Smelling right: the scent of male lemurs advertises  
646 genetic quality and relatedness. *Molecular Ecology*, *17*(14), 3225-3233. doi: 10.1111/j.1365-  
647 294X.2008.03831.x
- 648 Clifton, A. (2013). Variability in personality expression across contexts: A social network approach.  
649 *Journal of Personality*.
- 650 Clutton-Brock, T., Hodge, S., Spong, G., Russell, A., Jordan, N., Bennett, N., . . . Manser, M. (2006).  
651 Intrasexual competition and sexual selection in cooperative mammals. *Nature*, *444*(7122), 1065.
- 652 Cords, M. (1997). Friendships, alliances, reciprocity and repair. In A. Whiten & R. W. Byrne (Eds.),  
653 *Machiavellian Intelligence II: Extensions and Evaluations* (pp. 24-49). Cambridge: Cambridge  
654 University Press.

655 Croft, D., Krause, J., Darden, S., Ramnarine, I., Faria, J., & James, R. (2009). Behavioural trait assortment  
656 in a social network: patterns and implications. *Behavioral Ecology and Sociobiology*, *63*(10),  
657 1495-1503.

658 Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*: Princeton University Press.

659 Dall, S. R., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its  
660 use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, *20*(4), 187-193.

661 David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches,  
662 *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, *81*(1), 219-224.

663 Dingemanse, N. J., & Reale, D. (2005). Natural selection and animal personality. *Behaviour*, *142*, 1159-  
664 1184.

665 Drewe, J. A., Madden, J. R., & Pearce, G. P. (2009). The social network structure of a wild meerkat  
666 population: 1. Inter-group interactions. *Behavioral Ecology and Sociobiology*, *63*(9), 1295-1306.

667 Duboscq, J., Romano, V., Sueur, C., & MacIntosh, A. J. (2016). Network centrality and seasonality interact  
668 to predict lice load in a social primate. *Scientific reports*, *6*, 22095. doi: 10.1038/srep22095

669 Enquist, M., & Leimar, O. (1993). The evolution of cooperation in mobile organisms. *Animal Behaviour*,  
670 *45*(4), 747-757.

671 Fang, R., Landis, B., Zhang, Z., Anderson, M. H., Shaw, J. D., & Kilduff, M. (2015). Integrating  
672 personality and social networks: A meta-analysis of personality, network position, and work  
673 outcomes in organizations. *Organization Science*.

674 Flack, J. C., Girvan, M., De Waal, F. B., & Krakauer, D. C. (2006). Policing stabilizes construction of  
675 social niches in primates. *Nature*, *439*(7075), 426-429.

676 Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: a review and evaluation of  
677 past research. *American Journal of Primatology*, *72*(8), 653-671.

678 Freeman, L. C. (1979). Centrality in social networks conceptual clarification. *Social networks*, *1*(3), 215-  
679 239.

680 Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010). Social and genetic  
681 interactions drive fitness variation in a free-living dolphin population. *PNAS*, *107*(46), 19949-  
682 19954.

683 Frumkin, N. B., Wey, T. W., Exnicios, M., Benham, C., Hinton, M. G., Lantz, S., . . . Karubian, J. (2016).  
684 Inter-annual patterns of aggression and pair bonding in captive American flamingos  
685 (*Phoenicopterus ruber*). *Zoo biology*, *35*(2), 111-119.

686 Fuong, H., Maldonado-Chaparro, A., & Blumstein, D. T. (2015). Are social attributes associated with  
687 alarm calling propensity? *Behavioral Ecology*, *26*(2), 587-592. doi: 10.1093/beheco/aru235

688 Godfrey, S. S., Bull, C. M., James, R., & Murray, K. (2009). Network structure and parasite transmission in  
689 a group living lizard, the gidgee skink, *Egernia stokesii*. *Behavioral Ecology and Sociobiology*,  
690 *63*(7), 1045-1056. doi: 10.1007/s00265-009-0730-9

691 Golbeck, J., Robles, C., Edmondson, M., & Turner, K. (2011). *Predicting personality from twitter*. Paper  
692 presented at the Privacy, security, risk and trust.

693 Hanneman, R. A., & Riddle, M. (2005). *Introduction to social network methods*. . California: University of  
694 California, Riverside.

695 Jacoby, D. M. P., Fear, L. N., Sims, D. W., & Croft, D. P. (2014). Shark personalities? Repeatability of  
696 social network traits in a widely distributed predatory fish. *Behavioral Ecology and Sociobiology*,  
697 1-9.

698 John, O. P., & Srivastava, S. (1999). The Big Five trait taxonomy: History, measurement, and theoretical  
699 perspectives. *Handbook of personality: Theory and research*, *2*(1999), 102-138.

700 Jolly, A. (1966a). *Lemur behavior*: The University of Chicago Press.

701 Jolly, A. (1966b). Lemur social behavior and primate intelligence. *Science*, *153*(3735), 501-506.

702 Kappeler, P. M. (1998). To whom it may concern: the transmission and function of chemical signals in  
703 *Lemur catta*. *Behavioral Ecology and Sociobiology*(42), 411-421.

704 Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, *50*(4), 343-356.

705 Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., . . .  
706 Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology.  
707 *Neuroscience & Biobehavioral Reviews*, *23*(7), 925-935.

708 Krause, J., Croft, D., & James, R. (2007). Social network theory in the behavioural sciences: potential  
709 applications. *Behavioral Ecology and Sociobiology*, 62(1), 15-27.

710 Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical  
711 Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4099-4106.

712 Krause, J., James, R., Franks, D. W., & Croft, D. P. (2014). *Animal social networks*: Oxford University  
713 Press, USA.

714 Krause, S., Wilson, A. D., Ramnarine, I. W., Herbert-Read, J. E., Clément, R. J., & Krause, J. (2016).  
715 Guppies occupy consistent positions in social networks: mechanisms and consequences.  
716 *Behavioral Ecology*, 28(2), 429-438.

717 Kulahci, I. G., Drea, C. M., Rubenstein, D. I., & Ghazanfar, A. A. (2014). Individual recognition through  
718 olfactory-auditory matching in lemurs. *Proceedings of the Royal Society B: Biological Sciences*,  
719 281(1784), 20140071.

720 Kulahci, I. G., & Ghazanfar, A. A. (2013). Multisensory recognition in vertebrates (especially primates). In  
721 P. Belin, S. Campanella & T. Ethofer (Eds.), *Integrating face and voice in person perception* (pp.  
722 3-27): Springer New York.

723 Kulahci, I. G., Rubenstein, D. I., Bugnyar, T., Hoppitt, W., Mikus, N., & Schwab, C. (2016). Social  
724 networks predict selective observation and information spread in ravens. *Royal Society Open  
725 Science*, 3(7), 160256. doi: 10.1098/rsos.160256

726 Kulahci, I. G., Rubenstein, D. I., & Ghazanfar, A. A. (2015). Lemurs groom-at-a-distance through vocal  
727 networks. *Animal Behaviour*, 110, 179-186.

728 Lusseau, D., & Conradt, L. (2009). The emergence of unshared consensus decisions in bottlenose dolphins.  
729 *Behavioral Ecology and Sociobiology*, 63(7), 1067-1077.

730 Lusseau, D., & Newman, M. E. (2004). Identifying the role that animals play in their social networks.  
731 *Proceedings of the Royal Society B: Biological Sciences*, 271 Suppl 6, S477-481.

732 Macedonia, J. M. (1986). Individuality in a contact call of the ringtailed lemur (*Lemur catta*). *American  
733 Journal of Primatology*, 11, 163-179.

734 Macedonia, J. M. (1993). The vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia primatologica*,  
735 61(4), 186-217.

736 Madden, J. R., Drewe, J. A., Pearce, G. P., & Clutton-Brock, T. H. (2009). The social network structure of  
737 a wild meerkat population: 2. Intragroup interactions. *Behavioral Ecology and Sociobiology*,  
738 64(1), 81-95.

739 Madden, J. R., Drewe, J. A., Pearce, G. P., & Clutton-Brock, T. H. (2011). The social network structure of  
740 a wild meerkat population: 3. Position of individuals within networks. *Behavioral Ecology and  
741 Sociobiology*, 65(10), 1857-1871. doi: 10.1007/s00265-011-1194-2

742 Marler, P. (1976). On animal aggression: The roles of strangeness and familiarity. *American Psychologist*,  
743 31(3), 239.

744 McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *Proceedings of the  
745 National Academy of Sciences*, 104(26), 10910-10914.

746 McDonald, D. B. (2009). Young-boy networks without kin clusters in a lek-mating manakin. *Behavioral  
747 Ecology and Sociobiology*, 63(7), 1029-1034.

748 Monclus, R., Cook, T., & Blumstein, D. T. (2012). Masculinized female yellow-bellied marmots initiate  
749 more social interactions. *Biology Letters*, 8(2), 208-210. doi: 10.1098/rsbl.2011.0754

750 Montiglio, P.-O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: personality,  
751 social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal  
752 Society of London B: Biological Sciences*, 368(1618), 20120343.

753 Nakamichi, M., & Koyama, N. (1997). Social relationships among ring-tailed lemurs (*Lemur catta*) in two  
754 free-ranging troops at Berenty reserve, Madagascar. *International Journal of Primatology*, 18(1),  
755 73-93. doi: 10.1023/a:1026393223883

756 Newman, M. E. (2004). Analysis of weighted networks. *Physical Review E*, 70, 056131.

757 Quercia, D., Lambiotte, R., Stillwell, D., Kosinski, M., & Crocrot, J. (2012). *The personality of popular  
758 facebook users*. Paper presented at the Proceedings of the ACM 2012 conference.

- 759 Réale, D., & Dingemanse, N. J. (2010). Personality and individual social specialisation. In T. Székely, A. J.  
760 Moore & J. Komdeur (Eds.), *Social behaviour: genes, ecology and evolution* (pp. 417-441):  
761 Cambridge University Press.
- 762 Reale, D., Dingemanse, N. J., Kazem, A. J. N., & Wright, J. (2010). Evolutionary and ecological  
763 approaches to the study of personality. *Philosophical Transactions of the Royal Society B:*  
764 *Biological Sciences*, 365(1560), 3937-3946.
- 765 Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal  
766 temperament within ecology and evolution. *Biological Reviews*, 82(2), 291-318.
- 767 Rubenstein, D. I. (2015). Networks of terrestrial ungulates: linking form and function. In J. Krause, R.  
768 James, D. W. Franks & D. P. Croft (Eds.), *Animal Social Networks* (pp. 184-196). Oxford: Oxford  
769 University Press.
- 770 Rubenstein, D. I. (2016). Anthropogenic impacts on behavior: the pros and cons of plasticity. In O. Berger-  
771 Tal & D. Saltz (Eds.), *Conservation Behavior: Applying Behavioral Ecology to Wildlife*  
772 *Conservation and Management* (pp. 121-146). Cambridge: Cambridge University.
- 773 Ryder, T. B., McDonald, D. B., Blake, J. G., Parker, P. G., & Loiselle, B. A. (2008). Social networks in the  
774 lek-mating wire-tailed manakin (*Pipra filicauda*). *Proceedings of the Royal Society B: Biological*  
775 *Sciences*, 275(1641), 1367-1374.
- 776 Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success  
777 in male macaques. *Current Biology*, 20(24), 2207-2210.
- 778 Scordato, E. S., & Drea, C. M. (2007). Scents and sensibility: information content of olfactory signals in  
779 the ringtailed lemur, *Lemur catta*. *Animal Behaviour*, 73(2), 301-314.
- 780 Seyfarth, R. M., & Cheney, D. L. (2012). The Evolutionary Origins of Friendship. *Annual Review of*  
781 *Psychology*, 63(1), 153-177. doi: doi:10.1146/annurev-psych-120710-100337
- 782 Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. *Animal Behaviour*, 103, 191-202.
- 783 Seyfarth, R. M., Silk, J. B., & Cheney, D. L. (2012). Variation in personality and fitness in wild female  
784 baboons. *PNAS*, 109(42), 16980-16985.
- 785 Seyfarth, R. M., Silk, J. B., & Cheney, D. L. (2014). Social bonds in female baboons: the interaction  
786 between personality, kinship and rank. *Animal Behaviour*, 87(0), 23-29.
- 787 Sih, A., Bell, A., & Johnson, J. C. (2004a). Behavioral syndromes: an ecological and evolutionary  
788 overview. *Trends in Ecology & Evolution*, 19(7), 372-378.
- 789 Sih, A., Bell, A., Johnson, J. C., & Ziemba, R. E. (2004b). Behavioral Syndromes: An Integrative  
790 Overview. *The Quarterly Review of Biology*, 79(3), 241-277. doi: 10.1086/422893
- 791 Silk, J., Altmann, J., & Alberts, S. (2006a). Social relationships among adult female baboons (*Papio*  
792 *cynocephalus*) I. Variation in the strength of social bonds. *Behav Ecol Sociobiol*, 61(2), 183-195.
- 793 Silk, J. B. (2007). Social components of fitness in primate groups. *Science*, 317(5843), 1347-1351.
- 794 Silk, J. B., Alberts, S. C., & Altmann, J. (2006b). Social relationships among adult female baboons (*Papio*  
795 *cynocephalus*) II. Variation in the quality and stability of social bonds. *Behav. Ecol. Sociobiol.*, 61,  
796 197-204.
- 797 Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral*  
798 *Ecology*, 19(2), 448-455.
- 799 Snijders, L., & Naguib, M. (2017). Communication in animal social networks: A missing link? *Advances in*  
800 *the Study of Behavior*, 49, 297-359.
- 801 Staiano, J., Lepri, B., Aharony, N., Pianesi, F., Sebe, N., & Pentland, A. (2012). *Friends don't lie: inferring*  
802 *personality traits from social network structure*. Paper presented at the Proceedings of the 2012  
803 ACM Conference.
- 804 Taborsky, B., & Oliveira, R. F. (2012). Social competence: an evolutionary approach. *Trends in Ecology &*  
805 *Evolution*, 27(12), 679-688. doi: 10.1016/j.tree.2012.09.003
- 806 Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group  
807 behaviour in mammal societies. *Philosophical transactions of the Royal Society of London. Series*  
808 *B, Biological sciences*, 366(1567), 978-987. doi: 10.1098/rstb.2010.0312
- 809 Vander Wal, E., Festa-Bianchet, M., Réale, D., Coltman, D. W., & Pelletier, F. (2015). Sex-based  
810 differences in the adaptive value of social behavior contrasted against morphology and  
811 environment. *Ecology*, 96(3), 631-641. doi: 10.1890/14-1320.1

812 Wassermann, S., & Faust, K. (1994). *Social Networks Analysis*. Cambridge, UK: Cambridge University  
813 Press.  
814 Weidt, A., Hofmann, S. E., & König, B. (2008). Not only mate choice matters: fitness consequences of  
815 social partner choice in female house mice. *Animal Behaviour*, 75(3), 801-808.  
816 Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: a  
817 promising tool for the study of sociality. *Animal Behaviour*, 75(2), 333-344.  
818 Wilson, A. D. M., Krause, S., Dingemanse, N. J., & Krause, J. (2013). Network position: a key component  
819 in the characterization of social personality types. *Behavioral Ecology and Sociobiology*, 67(1),  
820 163-173.  
821 Wilson, D. E., & Hanlon, E. (2010). *Lemur catta* (Primates: Lemnidae). *Mammalian Species*, 42, 58-74.  
822 Wolf, M., & Krause, J. (2014). Why personality differences matter for social functioning and social  
823 structure. *Trends in Ecology & Evolution*, 29(6), 306-308.  
824 Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends*  
825 *in Ecology & Evolution*, 27(8), 452-461.  
826

827 **FIGURE LEGENDS**

828

829 **Figure 1.** Networks of four behaviors during two consecutive years from one of the  
830 groups. The circular layout is based on lemur names and is used for ease of comparison  
831 between behaviors and years. Line thickness is proportional to the interaction frequency.  
832 Node shape is based on sex (circles represent females, squares represent males), and node  
833 color is based on age (black nodes are adults, white nodes are juveniles). An asterisk next  
834 to a node indicates that lemur was present in the group during only one year.

835

836

Network	N	OutDegree	OutStrength	Eigenvector	Betweenness
Aggression	7	<b>0.009</b>	<b>0.003</b>	<b>0.001</b>	<b>0.008</b>
Grooming	7	0.078	<b>&lt;0.001</b>	<b>0.008</b>	<b>0.030</b>
Scent marking	7	0.039	<b>0.006</b>	<b>0.016</b>	0.174
Contact calling	7	0.139	<b>0.005</b>	<b>&lt;0.001</b>	0.422
Aggression	21	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.663	<b>0.003</b>
Grooming	21	0.418	<b>0.020</b>	<b>0.001</b>	0.070
Scent marking	21	0.118	0.083	0.316	0.065
Contact calling	21	<b>0.003</b>	<b>0.018</b>	0.065	0.068

837

838 **Table 1.** The majority of the network centrality measures were consistent over time. The  
 839 p-values are obtained from the network position consistency test. P-values in bold are the  
 840 results that were deemed significant in the FDR test and indicate the measures that were  
 841 similar between the two years. The Benjamini-Hochberg FDR adjusted p-values are  
 842 provided in **Table S2**. Except scent marking network measures from one group (n=21),  
 843 the majority of the measures were correlated between years in both groups.

844

845

846

<b>Group</b>	<b>N</b>	<b>OutDegree</b>	<b>OutStrength</b>	<b>Eigenvector</b>	<b>Betweenness</b>
DLC – NHE2	8	0.148	0.072	0.574	0.249
DLC – NHE4 (2010)	9	0.470	0.661	0.619	0.424
DLC – NHE4 (2011)	7	0.493	0.605	0.823	0.138
SCI – WM	17	<b>0.002</b>	<b>&lt;0.001</b>	0.626	0.048
SCI – YB (2011)	21	<b>0.002</b>	<b>&lt;0.001</b>	<b>0.002</b>	<b>0.001</b>
SCI – YB (2012)	21	<b>0.004</b>	<b>0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>

847

848 **Table 2.** Individual centrality was consistent across four behaviors in the larger groups.

849 The p-values are obtained from the network position consistency test. P-values in bold  
850 are the results that were deemed significant in the FDR test and indicate the measures that  
851 were similar between all four behaviors. The Benjamini-Hochberg FDR adjusted p-  
852 values are provided in **Table S3**. DLC and SCI are the study sites (DLC: Duke Lemur  
853 Center, SCI: St. Catherines Island). NHE2, NHE4, WM, YB are the group name  
854 abbreviations. YB (n=21) group size stayed the same between years, even though the  
855 group composition changed due to births and male movement between groups.

856

857

Metric	Aggression	Grooming	Scent marking	Contact calling
<b>OutDegree</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.206	<b>&lt;0.001</b>
<b>OutStrength</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.173	<b>&lt;0.001</b>
<b>Eigenvector</b>	0.214	<b>&lt;0.001</b>	0.389	<b>0.002</b>
<b>Betweenness</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.228	<b>0.001</b>

858

859 **Table 3A**

860

Group	N	Sex	OutDegree	OutStrength	Eigenvector	Betweenness
SCI- WM	17	Females	<b>0.001</b>	<b>0.002</b>	0.796	0.190
		Males	0.642	0.176	0.453	0.276
SCI- YB (2011)	21	Females	<b>0.011</b>	0.044	<b>0.024</b>	<b>0.009</b>
		Males	<b>0.005</b>	<b>0.001</b>	<b>0.007</b>	0.088
SCI- YB (2012)	21	Females	0.130	0.137	<b>&lt;0.001</b>	<b>0.034</b>
		Males	<b>0.007</b>	<b>0.004</b>	0.137	<b>0.010</b>

861

862 **Table 3B**863 **Table 3.** Sex-based differences in network centrality. Significant p-values are in bold.

864 Even though females had higher centrality than males in all networks except the scent

865 marking network (regression results; 3A), individual consistencies for the majority of the

866 measures persisted when data from males and females were analyzed separately using the

867 network position consistency test (3B). The Benjamini-Hochberg FRD adjusted p-values

868 for Table 3B are provided in **Table S7**.

869

<b>Network</b>	<b>N</b>	<b>r value</b>	<b>P-value</b>
Aggression	7	0.982	<b>&lt;0.001</b>
Grooming	7	0.993	<b>&lt;0.001</b>
Scent marking	7	0.662	<b>&lt;0.001</b>
Contact calling	7	0.918	<b>&lt;0.001</b>
Aggression	21	0.220	<b>0.014</b>
Grooming	21	0.519	<b>&lt;0.001</b>
Scent marking	21	-0.005	0.652
Contact calling	21	0.191	<b>0.031</b>

870

871 **Table 4.** Lemurs' interaction partner choices were consistent through time. Results are  
872 from the QAP analysis in which similarities between the matrices of four behaviors were  
873 analyzed. Significant p-values are indicated in bold.

874

<b>Networks</b>	<b>N</b>	<b>p-value</b>
Aggression – Grooming	7	0.280
Aggression – Scent marking	7	0.133
Aggression – Contact calling	7	0.319
Grooming – Scent marking	7	0.059
Grooming – Contact calling	7	0.057
Scent mark – Contact calling	7	0.366
Aggression – Grooming	8	0.078
Aggression – Scent marking	8	0.249
Aggression – Contact calling	8	0.535
Grooming – Scent marking	8	<b>0.049</b>
Grooming – Contact calling	8	<b>0.007</b>
Scent marking – Contact calling	8	0.425
Aggression – Grooming	17	0.312
Aggression – Scent marking	17	0.356
Aggression – Contact calling	17	0.083
Grooming – Scent marking	17	<b>0.008</b>
Grooming – Contact calling	17	<b>&lt;0.001</b>
Scent marking – Contact calling	17	<b>0.016</b>
Aggression – Grooming	21	0.384
Aggression – Scent marking	21	0.222
Aggression – Contact calling	21	0.164
Grooming – Scent marking	21	<b>0.004</b>
Grooming – Contact calling	21	<b>0.001</b>
Scent marking – Contact calling	21	<b>0.043</b>

876

877 **Table 5.** Consistency in interaction partners across different networks. Significant p-  
878 values from the QAP analysis are in bold. Lemurs' interaction partners remained  
879 consistent across grooming, contact calling, and in some groups scent marking networks.

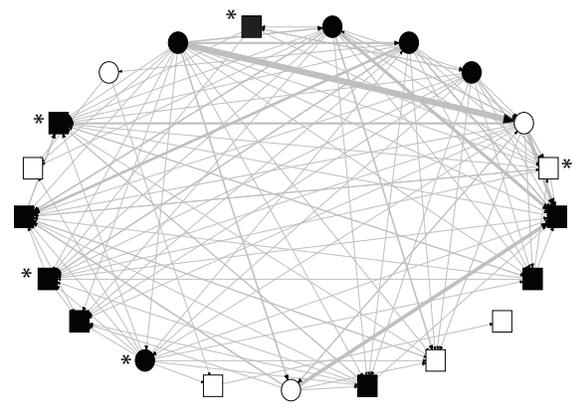
1 **ACKNOWLEDGMENTS**

2

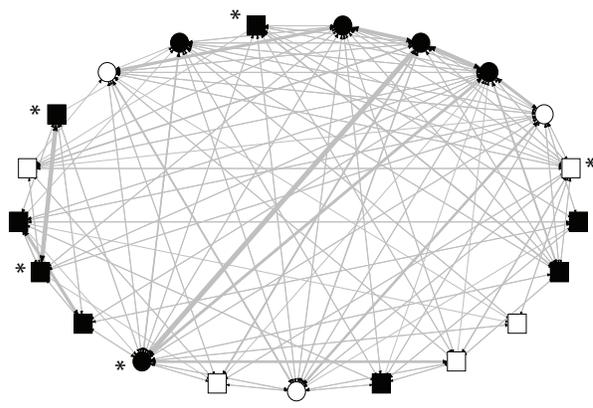
3 We thank Duke Lemur Center and St. Catherines Island. This study was funded by grants to IGK  
4 from the Animal Behavior Society, American Society of Mammalogists, American Society of  
5 Primatologists, and the Department of Ecology & Evolutionary Biology at Princeton University.

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7 Lemur Center publication #1359.

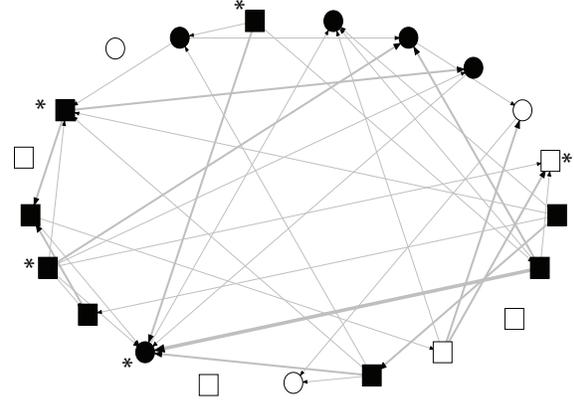
(a) Aggression



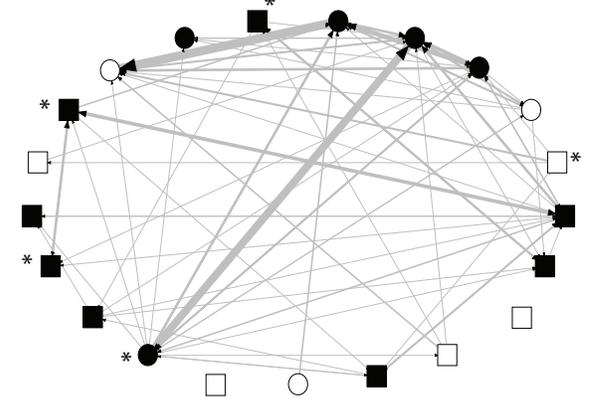
(b) Grooming



(c) Scent marking

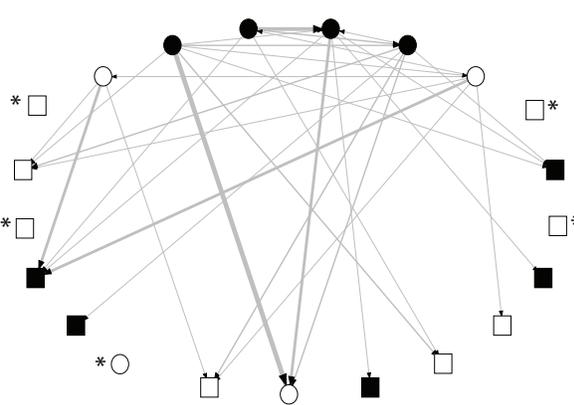


(d) Contact calling

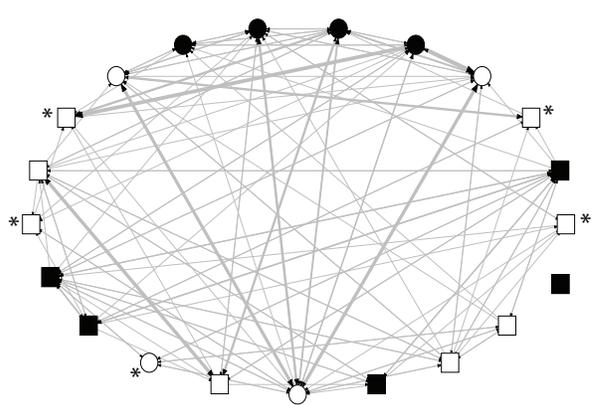


## 2012 Networks

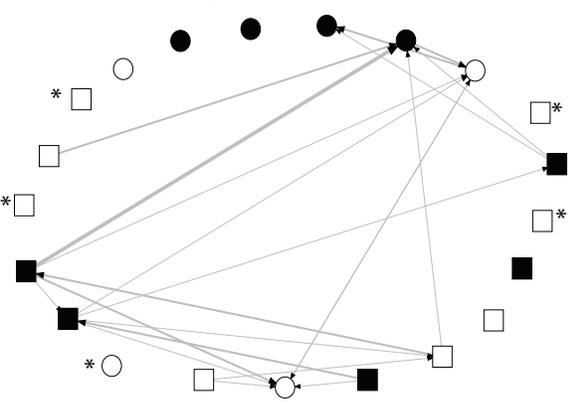
(a) Aggression



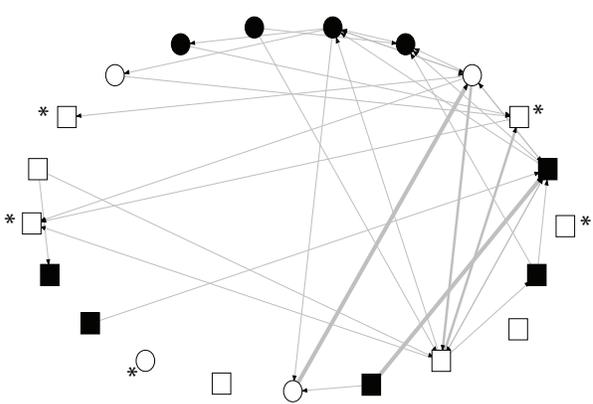
(b) Grooming



(c) Scent marking



(d) Contact calling



○ Female

□ Male

Node color: Age

\* Not present in both years