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

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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.
10 Consistent social behavior would be advantageous in groups, especially when individuals
11 need to remember conspecifics' social roles and preferences in order to keep track of
12 group members' social relationships and predict their future behavior. Here, we address
13 whether social behavior of individual ring-tailed lemurs (*Lemur catta*) is consistent
14 through time and across four behaviors (aggression, grooming, contact calling, scent
15 marking). We quantified variation in social behavior through four network centrality
16 measures (out-degree, out-strength, betweenness, and eigenvector centrality). Comparing
17 networks across two years revealed that network centrality remained consistent between
18 years. Centrality was also consistent across networks: Lemurs with high centrality in one
19 network also had high centrality in the other networks, even when we controlled for sex-
20 based variation in behavior. Thus, regardless of their sex, some individuals were highly
21 social in all four behaviors. They frequently groomed others, initiated aggressive
22 interactions, and responded to others' contact calls and scent marks. Lemurs also had
23 preferred social partners, and frequently interacted with the same individuals across
24 multiple types of social behaviors and across years. In particular, lemurs frequently
25 responded to the contact calls and the scent marks of the conspecifics they had frequently
26 groomed. Together, these results demonstrate that individual variation in social behavior
27 is not context specific, but instead persists through time and across multiple social
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.

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- 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	0.009	0.003	0.001	0.008
Grooming	7	0.078	< 0.001	0.008	0.030
Scent marking	7	0.039	0.006	0.016	0.174
Contact calling	7	0.139	0.005	< 0.001	0.422
Aggression	21	< 0.001	< 0.001	0.663	0.003
Grooming	21	0.418	0.020	0.001	0.070
Scent marking	21	0.118	0.083	0.316	0.065
Contact calling	21	0.003	0.018	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

Group	N	OutDegree	OutStrength	Eigenvector	Betweenness
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	0.002	<0.001	0.626	0.048
SCI – YB (2011)	21	0.002	<0.001	0.002	0.001
SCI – YB (2012)	21	0.004	0.001	<0.001	<0.001

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
OutDegree	< 0.001	< 0.001	0.206	< 0.001
OutStrength	< 0.001	< 0.001	0.173	< 0.001
Eigenvector	0.214	< 0.001	0.389	0.002
Betweenness	< 0.001	< 0.001	0.228	0.001

858

859 **Table 3A**

860

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

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

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

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

Networks	N	p-value
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	0.049
Grooming – Contact calling	8	0.007
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	0.008
Grooming – Contact calling	17	<0.001
Scent marking – Contact calling	17	0.016
Aggression – Grooming	21	0.384
Aggression – Scent marking	21	0.222
Aggression – Contact calling	21	0.164
Grooming – Scent marking	21	0.004
Grooming – Contact calling	21	0.001
Scent marking – Contact calling	21	0.043

876

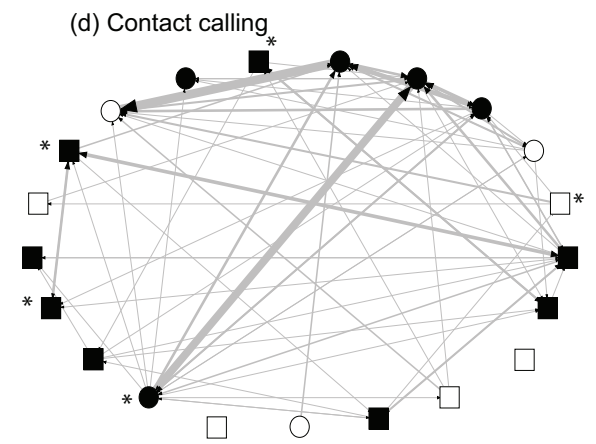
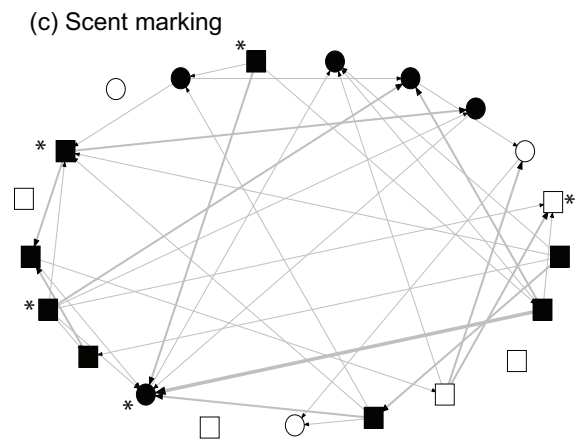
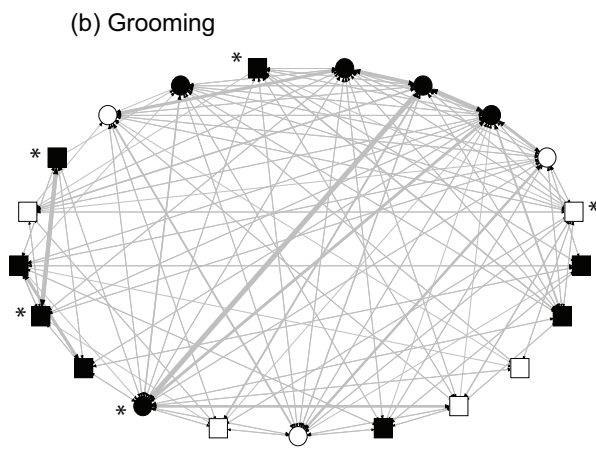
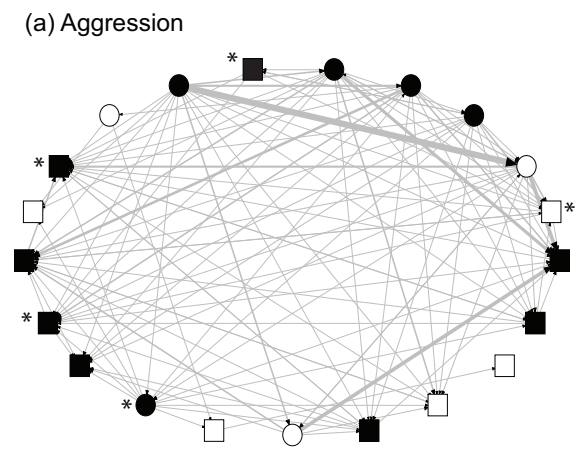
877 **Table 5.** Consistency in interaction partners across different networks. Significant p-
878 values from the QAP analysis are in bold. Lemurs' interaction partners remained
879 consistent across grooming, contact calling, and in some groups scent marking networks.

1 **ACKNOWLEDGMENTS**

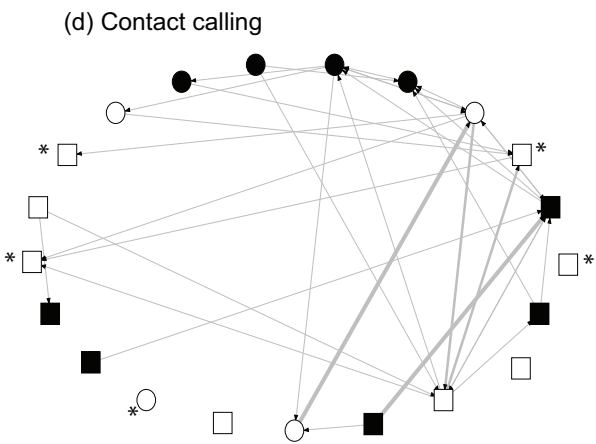
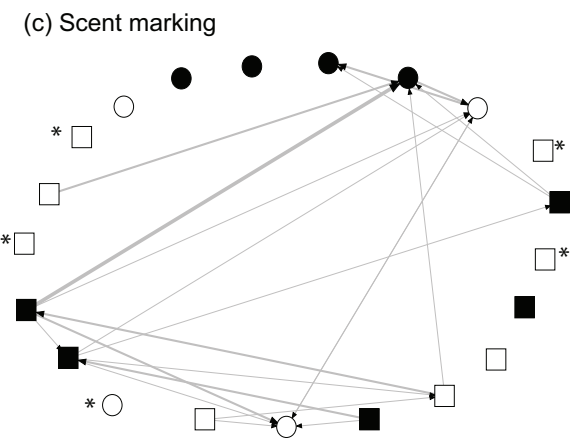
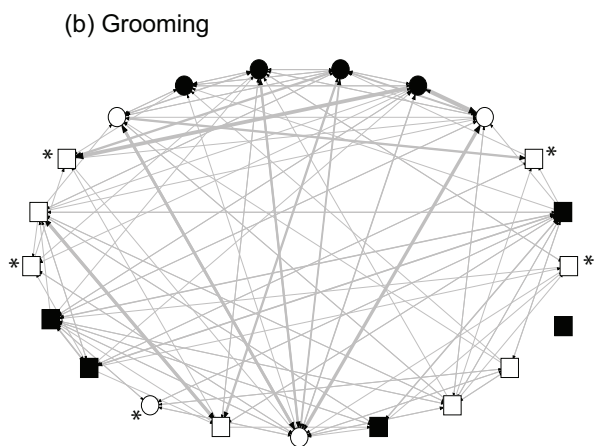
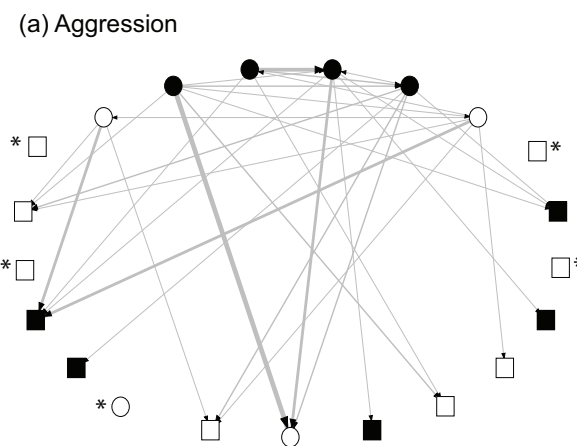
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2012 Networks



○ Female □ Male Node color: Age * Not present in both years