

Current Biology

Knowledgeable lemurs become more central in social networks

--Manuscript Draft--

Manuscript Number:	CURRENT-BIOLOGY-D-17-01626R2
Full Title:	Knowledgeable lemurs become more central in social networks
Article Type:	Report
Corresponding Author:	Ipek G. Kulahci UCC Cork, IRELAND
First Author:	Ipek Kulahci
Order of Authors:	Ipek Kulahci Asif A. Ghazanfar Daniel Rubenstein
Abstract:	<p>Strong relationships exist between social connections and information transmission [1-9], where individuals' network position plays a key role in whether or not they acquire novel information [2, 3, 5, 6]. The relationships between social connections and information acquisition may be bidirectional if the ability to acquire novel information influences network position besides being influenced by it. Individuals who acquire information quickly and use it frequently may receive more affiliative behaviors than others, and thus achieve a more central network position. However, this possibility has not been theoretically or empirically addressed. To bridge this epistemic gap, we investigated whether ring-tailed lemurs' (Lemur catta) social centrality in affiliation networks changed after they learned how to solve a novel foraging task. Lemurs who engaged in frequent interactions before the learning experiment were more likely to observe and learn the task solution. Comparing social networks before and after the learning experiment revealed that the lemurs who were frequently observed solving the task received more affiliative behaviors than they did before—they became more central after the experiment. This change persisted even after the task was removed and it was not caused by those lemurs initiating more affiliative behaviors towards others. While the factors that influence variation in network position are not fully understood, our results suggest that cognitive variation can play a major role in social centrality, especially when observing and learning from others are advantageous.</p>

Knowledgeable lemurs become more central in social networks

Ipek G. Kulahci^{a, b, *}, Asif A. Ghazanfar^{a, c, d}, Daniel I. Rubenstein^a

a Department of Ecology & Evolutionary Biology, Princeton University, Princeton, NJ, U.S.A.

b Biological, Earth and Environmental Sciences, University College Cork, Ireland

c Princeton Neuroscience Institute, Princeton University, Princeton, NJ, U.S.A.

d Department of Psychology, Princeton University, Princeton, NJ, U.S.A.

* Lead contact (ipek.kulahci@gmail.com)

Keywords: Information acquisition, information transmission, learning, *Lemur catta*, network metrics, ring-tailed lemur, social centrality, social network analysis

1 **Summary**

2
3 Strong relationships exist between social connections and information transmission [1-9], where
4 individuals' network position plays a key role in whether or not they acquire novel information
5 [2, 3, 5, 6]. The relationships between social connections and information acquisition may be
6 bidirectional if learning novel information influences network position in addition to being
7 influenced by it. Individuals who acquire information quickly and use it frequently may receive
8 more affiliative behaviors [10, 11] and may thus have a central network position. However, the
9 potential influence of learning on network centrality has not been theoretically or empirically
10 addressed. To bridge this epistemic gap, we investigated whether ring-tailed lemurs' (*Lemur*
11 *catta*) centrality in affiliation networks changed after they learned how to solve a novel foraging
12 task. Lemurs who had frequently initiated interactions and approached conspecifics before the
13 learning experiment were more likely to observe and learn the task solution. Comparing social
14 networks before and after the learning experiment revealed that the frequently observed lemurs
15 received more affiliative behaviors than they did before—they became more central after the
16 experiment. This change persisted even after the task was removed and was not caused by the
17 observed lemurs initiating more affiliative behaviors. Consequently, quantifying received and
18 initiated interactions separately provides unique insights into the relationships between learning
19 and centrality. While the factors that influence network position are not fully understood, our
20 results suggest that differences in learning and knowledge state can play a major role in social
21 centrality, especially when learning from others is advantageous.
22

23 **Results**

24

25 Network connections predict individual variation in learning, including learning about the
26 location of novel resources [1-4], the solution of a novel task [5-7], and foraging techniques [8,
27 9]. Some individuals have higher network centrality than others either because they are highly
28 connected and have diverse and/or frequent connections, or because they occupy key network
29 positions by connecting the otherwise unconnected conspecifics [12, 13]. Central individuals
30 have better access to novel information than non-central individuals [2, 3, 5, 6]. However,
31 beyond age, sex, personality, and developmental stress [13-20], the factors that determine
32 individual variation in social centrality are not fully understood.

33

34 Here, we address the possibility that learning influences social centrality. When some
35 individuals acquire novel information before others do, such variation leads to an unequal
36 distribution of information within a group, where some individuals have knowledge that others
37 do not have. This provides opportunities for the naive individuals to observe and learn from the
38 informed conspecifics' behavior. Informed conspecifics may receive more affiliative behaviors
39 and thus become central after they acquire and repeatedly use information. As a result, there may
40 be feedback dynamics between social centrality and information acquisition, where network
41 position is influenced by learning in addition to influencing it.

42

43 To test if network position is influenced by learning, we compared individuals' centrality
44 before and after a foraging experiment in two free-ranging lemur groups. Strong social
45 associations and affiliative behaviors play a major role in determining the patterns of selective

46 observation and information transmission [6, 21, 22]. Consequently, we collected data on two
47 affiliative behaviors: approaching another individual to initiate close physical proximity, and
48 grooming. We then presented each group with a foraging task that could be solved by pulling a
49 drawer. The task included a single food item (grape) to reduce the likelihood of scrounging, so
50 that only the solver, but not the rest of the group, obtained the reward. We first determined if
51 socially central individuals were more likely to learn the task solution after observing others, and
52 then asked whether individuals' centrality changed after they learned the task solution. We
53 predicted that the lemurs who learn the task solution sooner than others, and solve it frequently
54 while others are observing, will receive more affiliative behaviors after the experiment than they
55 did before, and thus have higher social centrality.

56
57 All lemurs in both groups (Windmill n=17, Yankee Bridge n=21) had multiple
58 opportunities to contact the task (mean \pm SE= 11.83 \pm 2.3 contacts with the task). The first lemurs
59 to solve the task in each group were juveniles (one male in Windmill, one female in Yankee
60 Bridge). The rest of the group members observed at least one conspecifics' task solving behavior
61 before solving the task for the first time themselves (excluding the initial solvers in each group,
62 frequency of observing an informed conspecific before solving for the first time mean \pm SE=
63 17.38 \pm 3.8 observations; number of informed conspecifics observed before solving mean \pm SE=
64 2.81 \pm 0.4 individuals). Across both groups, 22 lemurs solved the task, and some solved it more
65 frequently than others (n=12 in Windmill; n=10 in Yankee Bridge; task solving frequency
66 mean \pm SE= 32.77 \pm 12.3; **Table S1**). Observing conspecifics interact with the task increased
67 lemurs' interest in it, complementing a pattern that has previously been documented in meerkats
68 [23], squirrel monkeys [5], and ravens [6].

69

70 ***Socially central lemurs are more likely to learn after observing***

71
72 Individuals with high centrality in proximity and affiliation networks are more likely than others
73 to socially learn novel information, potentially because being connected provides more
74 opportunities for selectively attending to, and learning from, the conspecifics who tolerate them
75 in close proximity [5, 6, 21]. To determine whether individual variation in social centrality
76 influenced learning, we used network data that was collected before task presentation, and
77 calculated two centrality measures including *degree*, the number of connections, and *strength*,
78 the frequency of connections [13, 19, 24]. We distinguished between *indegree* (number of
79 conspecifics from whom an individual receives an interaction) and *outdegree* (number of
80 conspecifics towards whom an individual initiates an interaction). *Outstrength* and *instrength*
81 were defined similarly to indegree and outdegree, but included information on the frequency of
82 interactions.

83
84 Consistent with previous studies on information transmission [2, 3, 5, 6], we detected
85 positive relationships between individuals' network centrality and whether or not they acquired
86 novel information. When we excluded the first solver in each group, we found that the lemurs
87 who had initiated more affiliative behaviors were more likely to learn the task solution (**Figure**
88 **1**). Approach outdegree, in particular, predicted learning (Windmill: $F=8.71$, $p=0.013$, $n=17$;
89 Yankee Bridge: $F=8.339$, $p=0.01$, $n=21$). Neither sex nor age (adult or juvenile) influenced
90 whether or not lemurs learned the task solution (Logistic regression: $X^2= 4.708$, $p=0.095$; effect
91 of sex: $X^2= 0.745$, $p=0.388$, effect of age: $X^2= 3.428$, $p=0.064$).

92

93 *Frequently observed lemurs become more central in affiliation networks*

94

95 In each group, the first solver solved the task most frequently (**Table S1**). There was a positive
96 correlation between solving the task sooner than others and solving it frequently (data from both
97 groups, $F_{1,21}=11.565$, $p=0.003$; data from individual groups, Windmill: $F_{1,11}=14.539$, $p=0.003$,
98 $n=17$, Yankee Bridge: $F_{1,9}=7.41$, $p=0.026$, $n=21$). However, the frequency of solving the task,
99 but not learning it sooner, predicted how frequently each solver was observed by naïve
100 conspecifics (frequency of solving: Windmill: $F=477.351$, $p<0.001$, $n=17$; Yankee Bridge:
101 $F=506.919$, $p<0.001$, $n=21$; order of solving: Windmill: $F=0.454$, $p=0.517$, $n=17$; Yankee
102 Bridge: $F=0.006$, $p=0.939$, $n=21$).

103

104 To address whether social centrality increased after being observed while using novel
105 information, we compared individuals' centrality measures before and after the task learning
106 experiment. Because we were interested in the change in centrality rather than in its raw values,
107 we ranked each individual's centrality measures relative to their group members' measures. We
108 included both the initial solvers and the lemurs who learned after observing in this analysis. We
109 predicted that if the frequently observed lemurs receive more affiliative behaviors after learning
110 than they did before, then this change would be detected as an increase in indegree and
111 instrength. We also predicted that frequently observed lemurs' outdegree and outstrength would
112 remain the same. Out-measures indicate the behaviors that are initiated and are thus more likely
113 to reflect the degree to which individuals are social (e.g. their social personality traits [14, 25]).

114

115 Comparing centrality ranks before and after the learning experiment revealed that the
116 frequently observed lemurs had higher centrality (indegree and instrength) after the experiment
117 than they did before the experiment (**Table 1**). This increase was correlated with the frequency
118 of being observed, and was detected only for the frequently observed lemurs, but not for the
119 other lemurs who solved the task (**Figure 2**). Notably, receiving more affiliative behaviors, and
120 the corresponding increase in indegree and instrength, was not due to initiating more affiliative
121 behaviors towards others, as indicated by the lack of change in outdegree and outstrength (**Table**
122 **1**). In addition, an increase in received interactions did not result in an increase in interactions
123 that were given to others. Solving the task frequently while being observed was essential for
124 receiving more affiliative behaviors and becoming more socially central after the experiment.

125

126 **Discussion**

127

128 Some species, including primates, form long-term differentiated social bonds that are maintained
129 through affiliative behaviors [26-28]. However, the motivating factors and the underlying
130 mechanisms behind these bonds are not yet fully understood. Our study suggests that individual
131 differences in learning and using novel information may influence who bonds with whom.
132 Individuals who quickly and accurately acquire information, and use this information frequently,
133 may be perceived as reliable information sources or as successful individuals (e.g. successful
134 foragers, mates, group leaders, or cooperation partners). Being socially connected to successful
135 and knowledgeable individuals would be advantageous for future social learning opportunities,
136 as animals tend to observe and learn from those with whom they share affiliative connections [6,
137 21, 22].

138

139 When solving a task leads to the availability of multiple food items, such that individuals
140 other than the solvers can also obtain food [10, 11], individuals may associate or affiliate with
141 the solvers for increased tolerance and scrounging opportunities. Several primate species
142 frequently groom conspecifics who solve a task and provide food to the group [10, 11, 29]; some
143 even adjust their grooming based on how many conspecifics provide such benefits [11]. Our task
144 included only a single food item to reduce scrounging and food sharing, and we detected
145 centrality changes after the task was removed. Furthermore, the lemurs who groomed the
146 frequently observed individuals did not receive more grooming from these individuals. Thus, we
147 detected centrality changes in the absence of immediate benefits such as scrounging and mutual
148 grooming, suggesting that immediate benefits are unlikely to be responsible for knowledgeable
149 individuals' increase in centrality. Instead, our results support the idea that short-term benefits
150 cannot fully explain all of the affiliative interactions in animals [26]. Preferentially associating
151 and interacting with knowledgeable conspecifics may provide future and long-term benefits, and
152 this would have long-term consequences for social connections.

153

154 So, why did the frequently observed lemurs receive more affiliative interactions in the
155 absence of immediate benefits and without initiating more interactions themselves? Although our
156 design does not allow us to distinguish between potential mechanisms responsible for this
157 change, we offer a few potential explanations, some of which may be acting together to influence
158 the patterns we observed. One possibility is that the increased affiliation was due to carry-over
159 effects from the learning experiment. During the experiment, lemurs may have started to affiliate
160 with the conspecifics they observed, and this affiliation may have continued after task removal,

161 especially if observers continued to stay in close proximity and attend to the behaviors of those
162 they observed.

163

164 Another possibility is that using novel information successfully influences how
165 individuals are perceived by their conspecifics. Knowledgeable humans are considered
166 “prestigious” and receive social benefits [30]. Although social rank is assumed to be similar to
167 prestige [31], and some species preferentially learn from older or dominant individuals [32, 33],
168 dominant females in our study did not have high centrality nor did they solve the task (**Table**
169 **S1**). Thus, gaining information about the environment and contributing to group knowledge [34]
170 may be more important than dominance in determining who becomes influential and receives
171 affiliation. Because factors including rank, age, sex, and personality influence variation in
172 learning [21, 35-37] and in social centrality [13-20], carefully designed experiments are needed
173 to uncouple their effects on the relationships between learning and centrality. One promising
174 method involves manipulating the identity of the knowledgeable individuals, either through
175 selective access experiments that use automated or remote controlled devices [11] or through
176 training specific individuals on complicated tasks [10]. For example, low-ranking primates who
177 are presented as the only task-solvers and food-providers receive frequent affiliation from others
178 [10, 11]. A particularly exciting manipulation would involve choosing individuals based on their
179 learning ability. Explorative individuals tend to be innovative and learn novel information faster
180 [38, 39], and in some species, also have high centrality [20]. If a non-central individual, who is
181 neither explorative nor innovative, is presented as the only knowledgeable individual, and
182 becomes central after being observed, this would suggest that the centrality increase is due to
183 conspecifics’ social responses to that individual’s repeated use of information.

184

185 It is also possible that the frequently observed lemurs were perceived as successful
186 foragers. We cannot directly distinguish whether the increase in frequently observed lemurs'
187 centrality was due to their task learning ability, resulting in them being perceived as successful
188 solvers, or due to their ability to repeatedly gain food, resulting in them being perceived as
189 successful foragers. Cognitive abilities, such as learning ability, cannot be quantified directly but
190 are instead inferred from their influence on behavior [36, 40]. Individuals who successfully learn
191 about novel food and use this information while foraging are likely to become successful
192 foragers, and may receive increased attention and affiliation from conspecifics. To determine
193 whether the changes in centrality are due to the ability to solve the task (i.e. learning success) or
194 due to the ability to gain food (i.e. foraging success), additional experiments can be run, by
195 utilizing selective learning tasks that deliver food only to some solvers but not to the other
196 solvers, or by setting up selective foraging patches at which only some individuals can forage.

197

198 Changes in centrality after information transmission can affect the inferences we make
199 about the patterns of transmission through networks. For instance, if we find that central
200 individuals are more likely to learn novel information through social transmission, it is important
201 to rule out the possibility that those individuals became central only after acquiring and using
202 that information. Some options for ruling out this possibility include using network data that was
203 collected before information transmission (as done in our study) or using dynamic social
204 networks to quantify changes in centrality during and after transmission.

205

206 Distinguishing between initiated behaviors (quantified by out-measures) and received
207 behaviors (quantified by in-measures) can be highly informative in understanding the patterns of
208 social learning. The centrality changes we detected were based exclusively on in-measures;
209 frequently observed lemurs received more affiliative behaviors without initiating more affiliative
210 behaviors themselves. If naive individuals preferentially initiate interactions towards
211 knowledgeable individuals, then out-measures may be more informative than in-measures at
212 predicting who learns novel information when. To our knowledge, this possibility has not yet
213 been empirically incorporated into social learning and transmission studies.

214

215

216 **Conclusion**

217

218 We demonstrate that the relationships between social network centrality and learning are
219 bidirectional and based on feedback dynamics, such that in addition to centrality influencing who
220 learns novel information when, learning and using novel information influences centrality as
221 well. Individual differences in learning about the environment will lead to individual differences
222 in success at utilizing resources, and can thus play an important role in centrality, and ultimately
223 in social structure, by influencing social behaviors towards the knowledgeable conspecifics. We
224 strongly encourage studies that investigate the dynamic nature of centrality and the potential
225 ways in which it can be influenced by individual differences in acquiring and using novel
226 information.

227

228 **Acknowledgments**

229 We thank St. Catherines Island for access to lemurs. We are grateful to R. Seyfarth and two
230 reviewers for comments on the manuscript. This study was funded by grants to IGK from
231 Animal Behavior Society, American Society of Mammalogists, American Society of
232 Primatologists, and Department of Ecology and Evolutionary Biology at Princeton University.
233 IGK was supported by ERC Consolidator Grant 617509 (to JL Quinn) while preparing the
234 manuscript.

235

236

237 **Author Contributions**

238 Conceptualization: IGK. Methodology: IGK, AAG, DIR. Investigation: IGK. Formal Analysis:
239 IGK. Writing- Original Draft: IGK. Writing- Review & Editing: IGK, AAG, DIR.

240

241

242 **Declaration of Interests**

243 The authors declare no competing interests.

244

245
246
247
248
249
250
251
252
253
254
255
256
257
258
259
260
261
262
263
264
265
266
267
268
269
270
271
272
273
274
275
276
277
278
279
280
281
282
283
284
285
286
287
288
289
290
291
292
293
294
295

REFERENCES

1. Atton, N., Hoppitt, W., Webster, M.M., Galef, B.G., and Laland, K.N. (2012). Information flow through threespine stickleback networks without social transmission. *Proc.R.Soc.B.* 279, 4272-4278.
2. Aplin, L.M., Farine, D.R., Morand-Ferron, J., and Sheldon, B.C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proc.R.Soc.B.* 279, 4199-4205.
3. Schakner, Z.A., Petelle, M.B., Tennis, M.J., Van der Leeuw, B.K., Stansell, R.T., and Blumstein, D.T. (2017). Social associations between California sea lions influence the use of a novel foraging ground. *Royal Society Open Science* 4, 160820.
4. Jones, T.B., Aplin, L.M., Devost, I., and Morand-Ferron, J. (2017). Individual and ecological determinants of social information transmission in the wild. *Anim.Behav.* 129, 93-101.
5. Claidiere, N., Messer, E.J., Hoppitt, W., and Whiten, A. (2013). Diffusion dynamics of socially learned foraging techniques in squirrel monkeys. *Current Biology* 23, 1251-1255.
6. Kulahci, I.G., Rubenstein, D.I., Bugnyar, T., Hoppitt, W., Mikus, N., and Schwab, C. (2016). Social networks predict selective observation and information spread in ravens. *Royal Society Open Science* 3, 160256.
7. Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A., and Sheldon, B.C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* 518, 538-541.
8. Allen, J., Weinrich, M., Hoppitt, W., and Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. *Science* 340, 485-488.
9. Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., and Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology* 12, e1001960.
10. Stambach, E. (1988). Group responses to specially skilled individuals in a *Macaca fascicularis* group. *Behaviour* 107, 241-266.
11. Fruteau, C., Voelkl, B., Van Damme, E., and Noë, R. (2009). Supply and demand determine the market value of food providers in wild vervet monkeys. *PNAS* 106, 12007-12012.
12. Wassermann, S., and Faust, K. (1994). *Social Networks Analysis*, (Cambridge, UK: Cambridge University Press).
13. Lusseau, D., and Newman, M.E. (2004). Identifying the role that animals play in their social networks. *Proc.R.Soc.B.*, S477-481.
14. Kulahci, I.G., Ghazanfar, A.A., and Rubenstein, D.I. (2018). Consistent individual variation across interaction networks indicates social personalities in lemurs. *Animal Behaviour* 136, 217-226.
15. Pike, T.W., Samanta, M., Lindstrom, J., and Royle, N.J. (2008). Behavioural phenotype affects social interactions in an animal network. *Proc.R.Soc.B.* 275, 2515-2520.
16. Boogert, N.J., Farine, D.R., and Spencer, K.A. (2014). Developmental stress predicts social network position. *Biology Letters* 10, 20140561.
17. Krause, J., James, R., Franks, D.W., and Croft, D.P. (2014). *Animal social networks*, (Oxford University Press, USA).
18. Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cole, E.F., Cockburn, A., and Sheldon, B.C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecol.Lett.* 16, 1365-1372.
19. Croft, D.P., James, R., and Krause, J. (2008). *Exploring animal social networks*, (Princeton University Press).
20. Snijders, L., van Rooij, E.P., Burt, J.M., Hinde, C.A., Van Oers, K., and Naguib, M. (2014). Social networking in territorial great tits: slow explorers have the least central social network positions. *Anim.Behav.* 98, 95-102.

- 296 21. Coussi-Korbel, S., and Fragaszy, D.M. (1995). On the relation between social dynamics and
297 social learning. *Anim.Behav.* 50, 1441-1453.
- 298 22. Scheid, C., Range, F., and Bugnyar, T. (2007). When, what, and whom to watch? Quantifying
299 attention in ravens (*Corvus corax*) and jackdaws (*Corvus monedula*). *J.Comp.Psychol.* 121, 380-
300 386.
- 301 23. Hoppitt, W., Samson, J., Laland, K.N., and Thornton, A. (2012). Identification of learning
302 mechanisms in a wild meerkat population. *PLoS ONE* 7, e42044.
- 303 24. Borgatti, S.P., Everett, M.G., and Johnson, J.C. (2013). *Analyzing social networks*, (SAGE
304 Publications Limited).
- 305 25. Crofoot, M.C., Rubenstein, D.I., Maiya, A.S., and Berger-Wolf, T.Y. (2011). Aggression,
306 grooming and group-level cooperation in white-faced capuchins (*Cebus capucinus*): insights from
307 social networks. *Am. J. Primatol* 73, 821-833.
- 308 26. Seyfarth, R.M., and Cheney, D.L. (2012). The evolutionary origins of friendship.
309 *Annu.Rev.Psychol* 63, 153-177.
- 310 27. Silk, J.B., Alberts, S.C., and Altmann, J. (2003). Social Bonds of Female Baboons Enhance Infant
311 Survival. *Science* 302, 1231.
- 312 28. Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig,
313 R.M., Seyfarth, R.M., and Cheney, D.L. (2010). Strong and Consistent Social Bonds Enhance the
314 Longevity of Female Baboons. *Current Biology* 20, 1359-1361.
- 315 29. Borgeaud, C., and Bshary, R. (2015). Wild vervet monkeys trade tolerance and specific
316 coalitionary support for grooming in experimentally induced conflicts. *Current Biology* 25, 3011-
317 3016.
- 318 30. Henrich, J., and Gil-White, F.J. (2001). The evolution of prestige: Freely conferred deference as a
319 mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* 22, 165-196.
- 320 31. Laland, K.N. (2004). Social learning strategies. *Animal Learning & Behavior* 32, 4-14.
- 321 32. Horner, V., Proctor, D., Bonnie, K.E., Whiten, A., and de Waal, F.B. (2010). Prestige affects
322 cultural learning in chimpanzees. *PLoS ONE* 5, e10625.
- 323 33. Kendal, R., Hopper, L.M., Whiten, A., Brosnan, S.F., Lambeth, S.P., Schapiro, S.J., and Hoppitt,
324 W. (2015). Chimpanzees copy dominant and knowledgeable individuals: implications for cultural
325 diversity. *Evol. Hum. Behav.* 36, 65-72.
- 326 34. McComb, K., Moss, C., Durant, S.M., Baker, L., and Sayialel, S. (2001). Matriarchs as
327 repositories of social knowledge in African elephants. *Science* 292, 491-494.
- 328 35. Sih, A., and Del Giudice, M. (2012). Linking behavioural syndromes and cognition: a
329 behavioural ecology perspective. *Phil. Trans. R. Soc. B* 367, 2762-2772.
- 330 36. Shettleworth, S. (2010). *Cognition, evolution, and behavior*, (NY: Oxford University Press).
- 331 37. Thornton, A., and Lukas, D. (2012). Individual variation in cognitive performance:
332 developmental and evolutionary perspectives. *Phil. Trans. R. Soc. B* 367, 2773-2783.
- 333 38. Benson-Amram, S., and Holekamp, K.E. (2012). Innovative problem solving by wild spotted
334 hyenas. *Proc.R.Soc.B.* 279, 4087.
- 335 39. Miller, R., Schwab, C., and Bugnyar, T. (2016). Explorative innovators and flexible use of social
336 information in common ravens (*Corvus corax*) and carrion crows (*Corvus corone*). *J. Comp.*
337 *Psychol.* 130, 328.
- 338 40. Thornton, A., Isden, J., and Madden, J.R. (2014). Toward wild psychometrics: linking individual
339 cognitive differences to fitness. *Behav.Ecol.* 25, 1299-1301.
- 340 41. Borgatti, S.P., Everett, M.G., and Freeman, L.C. (2002). *Ucinet 6 for Windows: Software for*
341 *social network analysis*, (Harvard: Analytical Technologies).
- 342 42. Kulahci, I.G., Rubenstein, D.I., and Ghazanfar, A.A. (2015). Lemurs groom-at-a-distance through
343 vocal networks. *Animal Behaviour* 110, 179-186.
- 344 43. Borgatti, S.P., Everett, M.G., and Johnson, J.C. (2018). *Analyzing social networks*, 2nd Edition,
345 (SAGE).
- 346

347 **Figure Legends**

348

349 **Figure 1. Central lemurs are more likely to learn the task solution.**

350 The lemurs who learned (white) were highly social and had engaged in more affiliative
351 interactions than the lemurs who did not learn (gray). Node size: outdegree, numbers: order of
352 learning. Networks are constructed from data collected before the task learning experiment. See
353 also Table S1.

354

355

356 **Figure 2. Frequently observed lemurs become more central in affiliation networks.**

357 Data shown from the frequently observed lemurs in Windmill (n=17). Because of high inter-
358 individual variation in the frequency of being observed, we plotted ranks instead of raw values.
359 The most frequently observed lemur was assigned a rank of 1 (x-axis). A negative change in
360 centrality rank (y-axis) indicates that the lemur became more central after the experiment. See
361 also Table S1.

362

363
364
365

Centrality measure	F value	P value
Approach Indegree	5.197	0.036
Approach Instrength	5.647	0.033
Approach Outdegree	0.874	0.370
Approach Outstrength	0.2	0.662
Groom Indegree	8.487	0.012
Groom Instrength	4.788	0.047
Groom Outdegree	0.238	0.631
Groom Outstrength	1.512	0.239

366
367

368 **Table 1. The frequency of being observed predicts the increase in social centrality.**

369 The frequently observed lemurs had higher indegree and instrength after the experiment than
370 they did before, while their outdegree and outstrength did not change. The p-values are generated
371 from a permutation-based node-level regression test. Significant changes are indicated in bold.

372

373

374 **STAR METHODS**

375

376 **CONTACT FOR REAGENT AND RESOURCE SHARING**

377 Further information and requests for resources should be directed to and will be fulfilled by the
378 Lead Contact, Ipek G. Kulahci (ipek.kulahci@gmail.com).

379

380 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

381 We worked with two groups of free-ranging ring-tailed lemurs (*Lemur catta*) at the St.
382 Catherines Island (GA, USA). The first group (Yankee Bridge n=21; 8 females, 13 males; 12
383 juveniles, 9 adults) was studied June-August 2012, while the second group (Windmill n=17; 7
384 females, 10 males; 7 juveniles, 10 adults) was studied July-October 2013 (**Table S1**). Lemurs
385 were individually identifiable through facial variation, visual features, collars, and tail shaves.
386 All lemurs were habituated to the experimenter (IGK), allowing observations and task
387 presentation to take place without disturbing their behavior. All procedures were approved by the
388 Institutional Animal Care and Use Committee at Princeton University (Protocol # 1868).

389

390 **METHOD DETAILS**

391

392 **Network data**

393 We used all occurrence sampling to collect social interaction data on two affiliative behaviors:
394 approaching a conspecific to initiate close physical proximity and grooming. Groups were
395 observed before and after, but not during, the task experiment (number of observation hours:
396 Windmill before experiment= 48 hours, after experiment= 45 hours; Yankee Bridge before

397 experiment=54 hours, after experiment=51 hours). We recorded similar number of interactions
398 before and after the experiment (Windmill approach: 220 interactions before, 230 interactions
399 after; Windmill groom: 210 interactions before, 233 interactions after; Yankee Bridge approach:
400 173 interactions before, 135 interactions after; Yankee Bridge groom: 146 interactions before,
401 151 interactions after). Social interaction data were converted into network matrices and
402 analyzed in UCINET (version 6.647) [41]. Social network data were collected outside of the task
403 experiment to avoid potential influences of the task and the reward on who initiated social
404 behaviors towards whom and how frequently.

405
406 In approach networks, the lemur who approached a conspecific and sat in close physical
407 proximity (within one body width or closer) was the actor of the interaction. The lemur who was
408 approached was the receiver of the interaction. Approach networks included only the instances
409 that did not result in another interaction, allowing us to prevent including the same data in
410 multiple networks. For instance, if a lemur approached a conspecific and started grooming her,
411 then this interaction was only entered into the grooming network but not into the approach
412 network. In grooming networks, the lemur who groomed another was the actor of the interaction,
413 while the lemur who was groomed was the recipient. Lemurs engage in both directed grooming
414 (one lemur grooms another) and mutual grooming (two lemurs groom each other) [14, 42].
415 Mutual grooming data were converted into directed grooming data by including both of the
416 participating lemurs as the actor and the receiver.

417

418

419 **Task presentation**

420 The foraging task was a transparent Plexiglas box (20x20x20cm) that included a single grape to
421 minimize scrounging. Each group was presented with a single box. All lemurs were free to
422 participate in the experiment by approaching and contacting the box during each of the sessions,
423 and we did not exclude any lemurs from the task-learning experiment. Multiple sessions were
424 run on each day. The session lengths varied based on group movement, weather conditions,
425 short-term environmental disturbances, and changes in lemurs' motivation. A session began
426 when a lemur approached the box and ended when no lemurs were within a 1 meter radius of the
427 box for three minutes. Each session had multiple trials. Trials ended when the grape was taken.
428 All sessions were recorded with an HD camcorder (Panasonic HC-V700) placed on a tripod at
429 the same height as the task. The videos were scored for i) who solved the task, ii) the latency of
430 the first solution for each lemur, iii) frequency of solving, and iv) who observed whose solving
431 behavior. Only the lemurs facing the box within a 2m radius as the box was being opened were
432 counted as observers, to ensure that all the lemurs who were classified as observers had a clear
433 view of the task solution.

434

435 **QUANTIFICATION AND STATISTICAL ANALYSIS**

436 We used the permutation-based node-level regression test in UCINET (version 6.647) [41] to
437 analyze whether lemurs with high social centrality were more likely than others to learn the task
438 solution (we ran 10000 permutations). For this analysis, we excluded the first solver in each
439 group, as we were interested in how social centrality influenced the likelihood of observing and
440 learning information that was already present in the group. Data from two groups were analyzed

441 separately. We used logistic regression to determine whether sex or age (adult versus juvenile)
442 influenced learning.

443

444 To determine which factor predicted the frequency of being observed by naïve
445 conspecifics, we entered both the frequency of solving and the temporal order of learning into a
446 model, together with the frequency of being observed (dependent variable).

447

448 To analyze the relationships between the change in centrality ranks (dependent variable)
449 and the frequency of being observed (rank; independent variable) (**Table 1**), we used the node-
450 level regression in UCINET (version 6.647) [41]. This regression procedure combines targeted
451 hypothesis testing with randomization tests to deal with the non-independence of network data,
452 by repeatedly permuting the dependent variable (centrality measures) to calculate the p-values
453 [43]. We ran 10000 permutations.

454

455

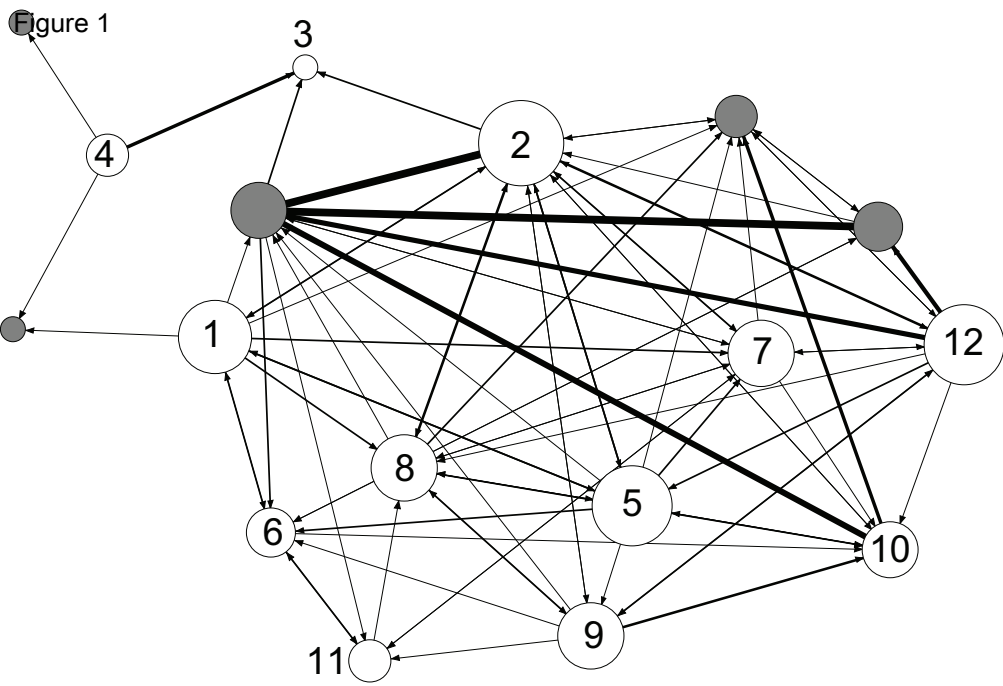
456 **DATA AND SOFTWARE AVAILABILITY**

457 The data used in the analyses reported in this paper are available at Mendeley Data at

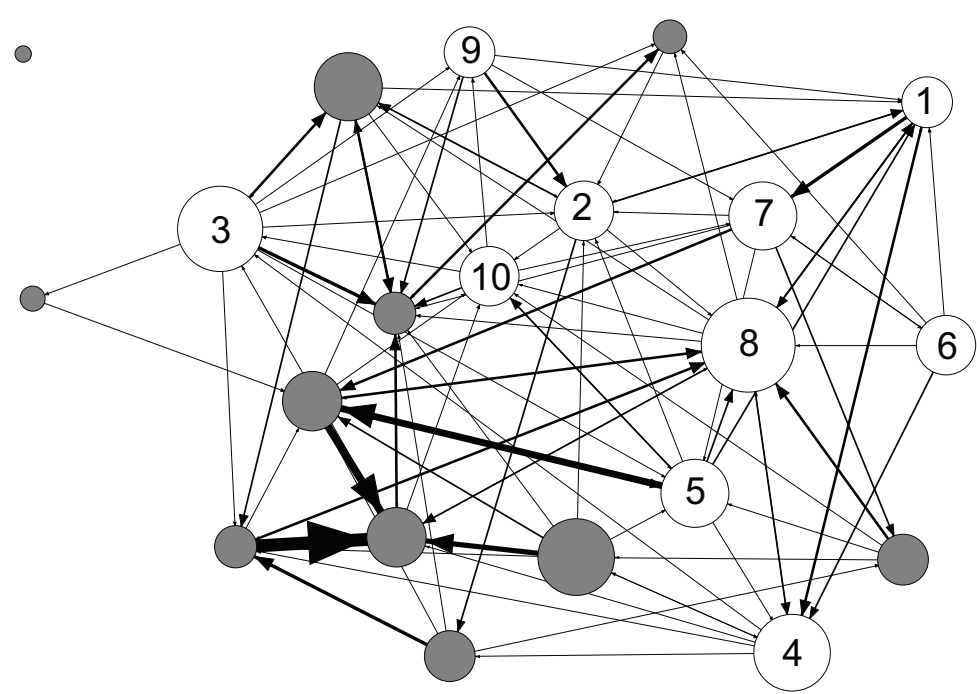
458 <http://dx.doi.org/10.17632/3h6cg9z87c.2>.

459

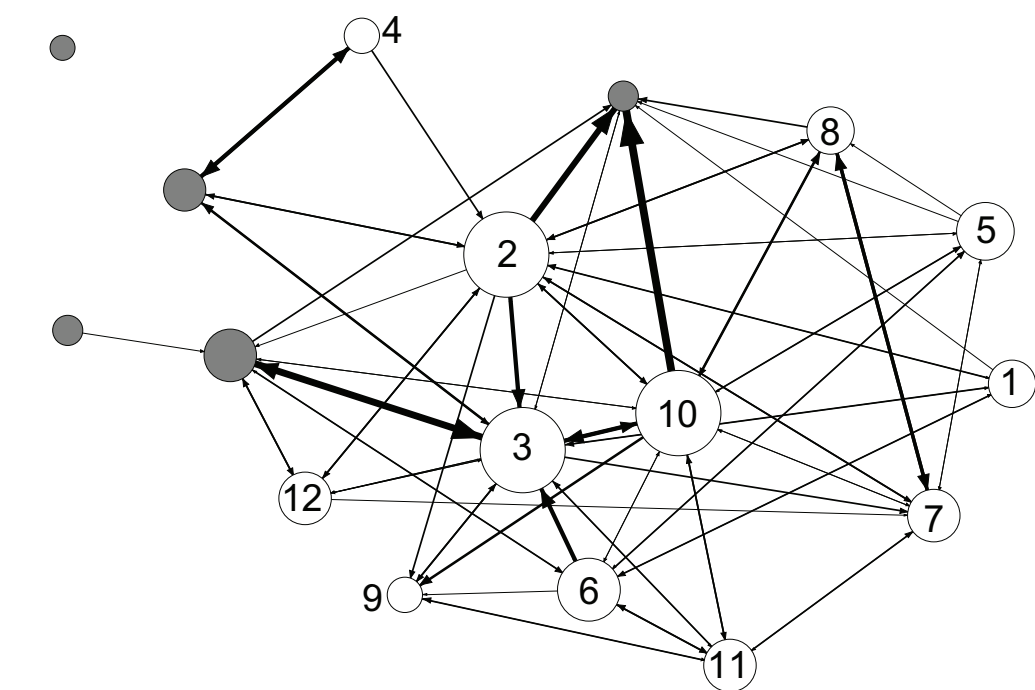
Figure 1



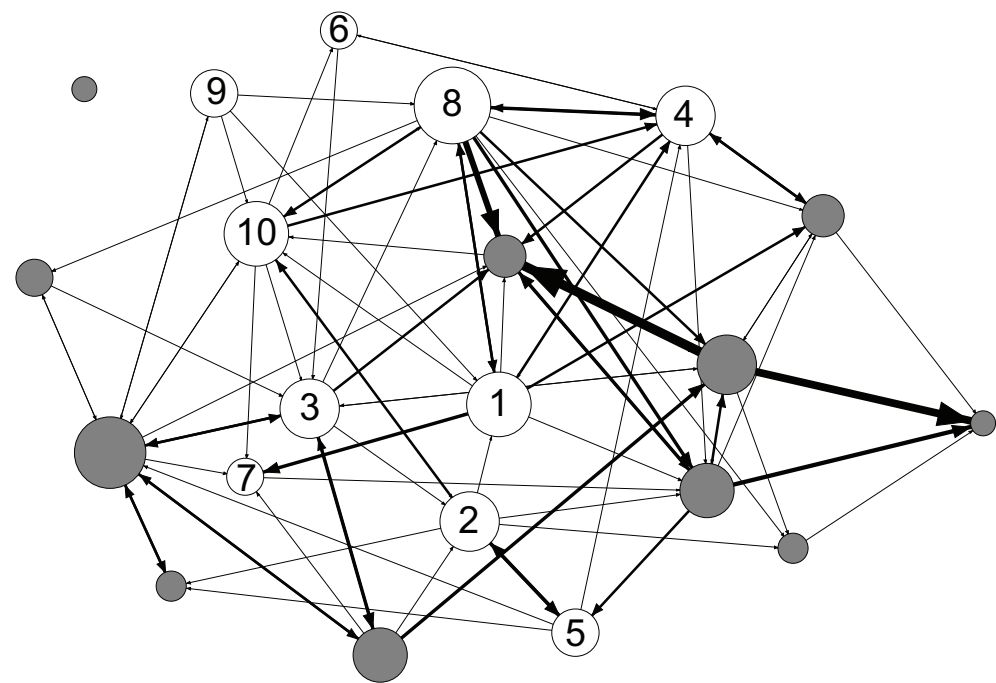
Approach (WM)



Approach (YB)

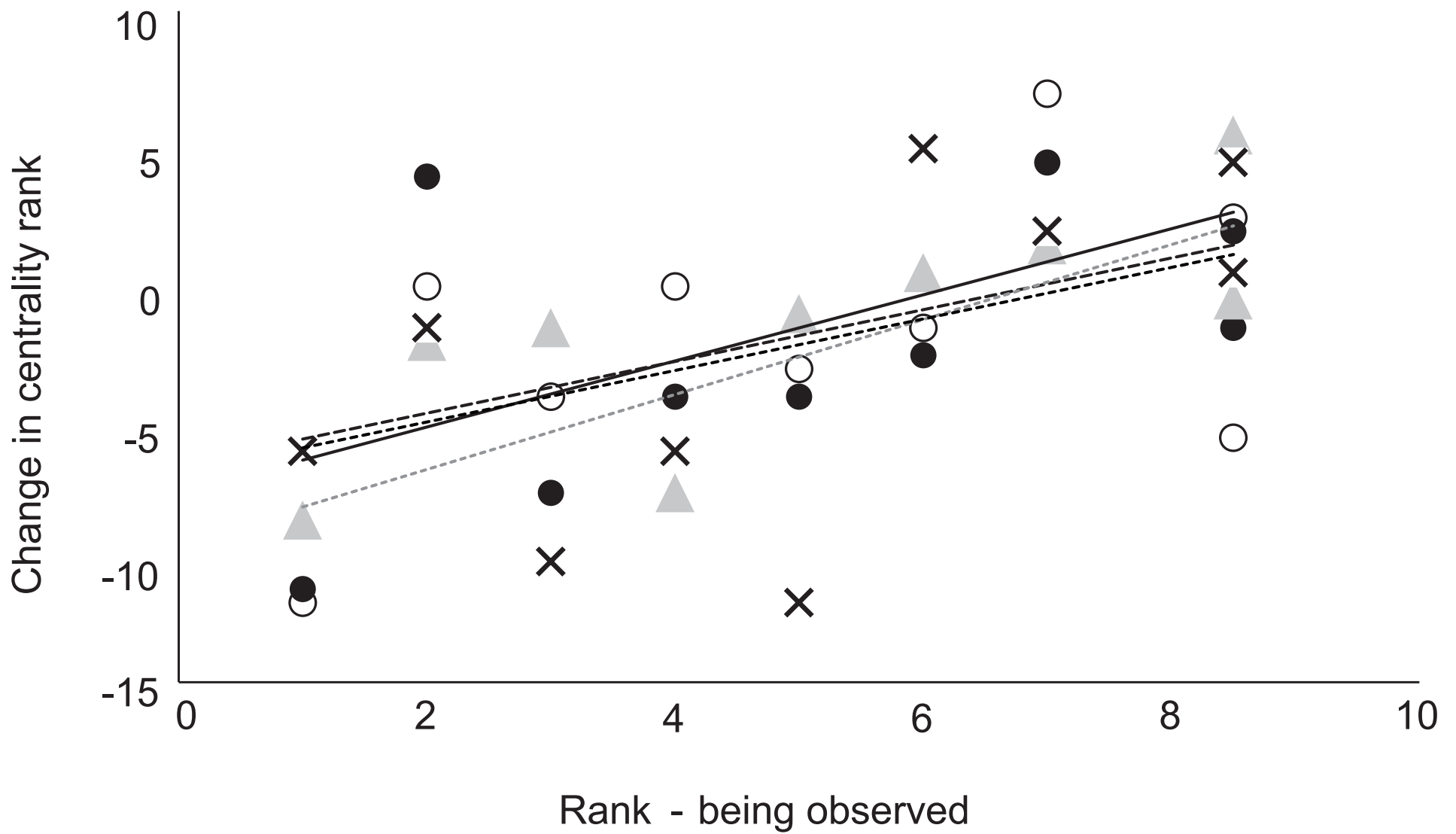


Groom (WM)



Groom (YB)

Figure 2



○ Approach indegree

● Approach instrength

▲ Groom indegree

× Groom instrength