

1 **Dominance rank predicts social network position across developmental stages**  
2 **in rhesus monkeys**

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14 **Running title:** Social rank predicts social network position

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**20 Abstract**

21 Social network analysis is increasingly common in studying the complex interactions  
22 among individuals. Across a range of primates, high-ranking adults are generally more socially  
23 connected, which results in better fitness outcomes. However, it still remains unclear whether  
24 this relationship between social network position and dominance rank emerges in infancy and  
25 whether, in species with a social transmission of dominance rank, social network positions are  
26 driven by the presence of the mother. To fill this gap, we first explored whether dominance ranks  
27 were related to social network position, measured via eigenvector centrality, in infants, juveniles,  
28 and adults in a troop of semi-free ranging rhesus macaques (*Macaca mulatta*). We then  
29 examined relationships between dominance rank and eigenvector centrality in a peer-only group  
30 of yearlings who were reared with their mothers in either a rich, socially complex environment of  
31 multigenerational (MG) kin support or a unigenerational (UG) group of mothers and their infants  
32 from birth through eight months. In experiment 1, we found that mother's network position  
33 predicted offspring network position, and that dominants across all age categories were more  
34 central in affiliative networks (social contact, social grooming, and social play). Experiment 2  
35 showed that high-ranking yearlings in a peer-only group were more central only in the social  
36 contact network. Moreover, yearlings reared in a socially complex environment of MG kin  
37 support were more central. Our findings suggest that the relationship between dominance rank  
38 and social network position begins early in life, and that complex early social environments can  
39 promote later social competency. Our data add to the growing body of evidence that the  
40 presence/absence of the mother and kin influence how dominance rank affects social network  
41 position. These findings have important implications for the role of caregivers in the social status  
42 of developing primates, which ultimately ties to health and fitness outcomes.

43 **Keywords:** eigenvector centrality, dominance rank, development, social network, rhesus  
44 macaques

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## 46 **Introduction**

47         Primates have a slow developmental trajectory, with maturation into adulthood requiring  
48 several years (Harvey & Clutton-Brock, 1985; Pereira & Fairbanks, 2002). Several hypotheses  
49 suggest that primate evolution has favored an extended juvenile period as a way for individuals  
50 to better learn a variety of skills needed for survival including proper foraging strategies  
51 (Agostini & Visalberghi, 2005; Janson & van Schaik, 1993; Rapaport & Brown, 2008), specific  
52 mechanisms to avoid predators (Ramakrishnan & Coss, 2001; Seyfarth, Cheney, & Marler,  
53 1980), and necessary social skills needed to integrate into the social group (Joffe, 1997; Shimada  
54 & Sueur, 2014). Given the vast array of challenges that developing primates must successfully  
55 overcome, it is perhaps not surprising that juveniles may be especially susceptible to mortality  
56 (Ross & Jones, 1999). While several studies have explored how young primates learn foraging  
57 and predator avoidance strategies (Hauser, 1988; Rapaport & Brown, 2008; van de Waal,  
58 Claidière, & Whiten, 2013), investigations on how infants develop their social skills to better  
59 integrate into the group's social networks are still scant (Barale, Rubenstein, & Beehner, 2015;  
60 Kulik, Amici, Langos, & Widdig, 2015). Yet, understanding how individuals acquire their social  
61 competence from infancy can shed new light on how social integration affects both human and  
62 nonhuman primate survival, health, and overall fitness across the lifespan (Brent, Ruiz-  
63 Lambides, & Platt, 2017; Kroenke, Kubzansky, Schernhammer, Holmes, & Kawachi, 2006;  
64 Lehmann, Majolo, & McFarland, 2015; Smith & Christakis, 2008; Vogt, Mullooly, Ernst, Pope,  
65 & Hollis, 1992).

66           Among all mammalian taxa, primates are one of the groups with the highest levels of  
67   sociality, reflected by a remarkable degree of gregariousness and an extraordinary variety of  
68   social systems (Kappeler & van Schaik, 2002). Many primate species, thus, engage in a complex  
69   network of social connections, and accumulating evidence indicates that individuals' fitness is  
70   affected not only by their direct social relationships, but also by their indirect social ties (e.g., if  
71   they are connected with individuals who have also a lot of social connections; Brent, 2015).  
72   Social network analysis is an increasingly common tool to analyze these elaborate ties (both  
73   direct and indirect) among individuals (Brent, 2015; Farine & Whitehead, 2015; McCowan,  
74   Anderson, Heagarty, & Cameron, 2008; McCowan et al., 2016; Pinter-Wollman et al., 2014;  
75   Sueur, Jacobs, Amblard, Petit, & King, 2011). Social network analysis has been used to study a  
76   wide variety of outcomes, ranging from disease transmission (Griffin & Nunn, 2011; MacIntosh  
77   et al., 2012; Rushmore et al., 2013) to social learning (Coelho et al., 2015; Hobaiter, Poisot,  
78   Zuberbühler, Hoppitt, & Gruber, 2014), and captive primate welfare (McCowan et al., 2008).  
79   However, to date, the vast majority of the research on nonhuman primate social networks has  
80   focused on adults, due either to the assumption that adult social networks are long established  
81   and therefore stable; to difficulties in recognizing juveniles and infants, especially as they are  
82   constantly changing and growing; or simply to the study questions at hand which may not  
83   warrant immature subjects. Therefore, although we are beginning to learn more about social  
84   networks in adults, relatively little is known about the social networks of developing primates.  
85   Yet, recent work suggests that examining the developmental trajectory of infant and juvenile  
86   networks can be key to understanding social networks in adults.

87           First, recent studies have highlighted that adult social networks are not always stable over  
88   time (Borgeaud, Sosa, Sueur, & Bshary, 2017; Jarrett, Bonnell, Young, Barrett, & Henzi, 2018;

89 Vandeleest et al., 2017). Therefore, understanding the extent of changes in individuals' network  
90 positions and social ties across their lifespan is pivotal to have a better understanding of how  
91 these changes can reflect different fitness outcomes. Second, a handful of studies on both primate  
92 and non-primate species have shown that juveniles provide a meaningful contribution to the  
93 group social network as a whole, and their exclusion can significantly impact the assessment of a  
94 group network structure (e.g., olive baboons, *Papio Anubis*: Fedurek & Lehmann, 2017; orcas,  
95 *Orcinus orca*: Williams & Lusseau, 2006).

96         One potential mechanism that could relate to a juvenile's position in social networks is  
97 dominance rank. For primate species that live in large social groups, dominance rank is a  
98 pervasive factor in behavioral development. For example, across a variety of primate species,  
99 high-ranking individuals are preferred grooming partners, as dominants can offer low-ranking  
100 individuals rank-restricted services, such as tolerance and agonistic support, in exchange for  
101 grooming (Carne, Wiper, & Semple, 2011; Seyfarth, 1977). Consequently, dominance ranks are  
102 expected to influence an individual's position in the social network. Accordingly, across some  
103 primate species, high-ranking adults occupy more central (i.e., more socially connected)  
104 positions in their social networks (Borgeaud, Sosa, Sueur, & Bshary, 2017; Sueur & Petit, 2008;  
105 Sueur et al., 2011), and this relationship appears particularly strong in despotic species that  
106 display low levels of affiliation, more asymmetric aggression, steep dominance relationships, and  
107 low rates of post-conflict reconciliation (Sueur et al., 2011).

108         In primates characterized by social transmission of dominance rank, such as in  
109 cercopithecines (Berman, 1980; Cheney, 1977), a potential mechanism by which infants and  
110 juveniles can acquire their social network position may be through kin support and influence in  
111 their social interactions. In other words, if high-ranking mothers or kin are central in their social

112 networks and support their offspring in acquiring high ranks, then their offspring are expected to  
113 develop more central positions in the network as well. To date, however, evidence of maternal or  
114 kin influence of juveniles' acquisition of network positions has been limited. Berman,  
115 Rasmussen, & Suomi (1997) found, for instance, that rhesus macaque (*Macaca mulatta*) mothers  
116 in large groups bias their infant's interactions towards close kin, suggesting that the mother can  
117 have a significant impact on infant social networks. Turner, Bills, and Holekamp (2018) found  
118 that social networks vary based on rank in developing hyenas (*Crocuta crocuta*), a species  
119 characterized by maternal rank inheritance, but they did not directly test whether mother's  
120 presence or behavior influenced their offspring's social network position. Interestingly, Jarrett et  
121 al., (2018) found that juvenile vervet (*Chlorocebus pygerythrus*) networks did not map onto their  
122 mother's networks (which may have been explained by temporal shifts in the mothers'  
123 networks), although they did conclude that mother-daughter associations may influence both of  
124 their associations with others. Therefore, it still remains unclear: (1) whether the relationship  
125 between dominance rank and social network position emerges in infancy and juvenility and  
126 (2) whether this relationship, if present, is due to mothers' (and other close kin) presence, which  
127 may influence an infant's interactions with other group members.

128         The goals of this study were therefore two-fold: (1) we first examined whether  
129 dominance rank predicted an individual's position in its social networks in both immature  
130 (newborns to 2 years) and mature (3+ years) rhesus macaques in a naturalistic population (with  
131 mothers and multigenerational (MG) kin support; experiment 1); (2) we then explored the  
132 relationship between dominance rank and social network position in yearling rhesus macaques  
133 living in a peer-only group without the presence of adult kin, including their mothers  
134 (experiment 2). Rhesus macaques provide the ideal study model to address these questions. They

135 are female philopatric (i.e., females remain in their natal group while males emigrate at puberty),  
136 and are characterized by a highly nepotistic (i.e., social interactions are largely directed towards  
137 close kin) and despotic (i.e., frequent aggression and a linear, asymmetric dominance hierarchy)  
138 social system (Thierry, 2007). Rhesus monkey dominance rank is correlated with social network  
139 position, with top-ranking females being more central in the network (Sueur et al., 2011), and is  
140 acquired by a hearty system of matrilineal support in aggressive interactions (Berman, 1980),  
141 resulting in offspring ‘inheriting’ the rank of their mothers.

142         In experiment 1, we examined the development of the relationship between dominance  
143 rank and social network position in a naturalistic, MG population of rhesus macaques from  
144 infancy through adulthood. We first sought to replicate Sueur et al. (2011)’s results, predicting  
145 that high-ranking adults would be more central in their social networks (*prediction 1*). Similarly,  
146 if social network position is potentially inherited, then we predicted that mothers’ social network  
147 position should be correlated with their offspring’s network position (*prediction 2*) and that in  
148 infants and juveniles, like in their mothers, social network position would be related to  
149 dominance rank (*prediction 3*). In experiment 2, we examined the relationship between  
150 dominance rank and social network position in a yearling group of rhesus macaques recently  
151 formed after having been reared in social groups with their mothers for the first eight months of  
152 life. This peer group was formed by taking nine yearlings from the MG (mothers, siblings, aunts,  
153 grandmothers, great-grandmothers, cousins, etc.) field station and nine yearlings from  
154 unigenerational (UG; only same-aged mothers and their infants) groups and combining them into  
155 one social group, without the mothers. This yearling group was studied both immediately after  
156 group formation and hierarchy establishment, and following group relocation to a familiar  
157 environment for the UG subjects. This relocation resulted in a complete reversal of the hierarchy

158 and a period of prolonged social instability (Wooddell, Kaburu, Murphy, Suomi, & Dettmer,  
159 2017a), since the UG subjects challenged the previously dominant MG subjects. In Wooddell et  
160 al. (2017a) we argued that this rank reversal is likely to be related to UGs' familiarity with the  
161 environment, as previous work across a broad range of social species has shown that familiarity  
162 with the environment can predict dominance rank (e.g., dark-eyed juncos, *Junco hyemalis*:  
163 Cristol & Ketterson, 1990; willow tit, *Parus montanus*: Koivula, Lahti, Orell, & Rytönen,  
164 1993). If factors other than kin support affect offspring's social network position, (e.g.,  
165 dominance rank), then high-ranking yearlings should be more central in their social networks  
166 following the formation of the peer-only group (*prediction 4*), and this should hold following a  
167 complete reversal of the hierarchy (i.e., previous low-ranked yearlings should now be more  
168 central; *prediction 5*).

## 169 **Materials and Methods**

170 All procedures here and below adhered to the NIH Guide for the Care and Use of  
171 Laboratory Animals, the American Society of Primatologists Principles for the Ethical Treatment  
172 of Nonhuman Primates, and were approved by the NICHD Animal Care and Use Committee.

### 173 *Subjects and housing*

#### 174 *Experiment 1*

175 Subjects were 79 rhesus macaques (*Macaca mulatta*) born from 1995 to 2015 and raised  
176 at the Laboratory of Comparative Ethology field station in Poolesville, MD. The troop was a  
177 large, MG group formed in the 1980s that consisted of three matriline. The dominance ranks of  
178 the matriline in order were: matriline 3, matriline 4, and matriline 1, with the exception of the  
179 alpha male, who was from matriline 1 (the lowest-ranking matriline). It is important to note that



180 the numbers of the matriline do not refer to ordinal rank, but rather to the laboratory's historical  
181 naming method for the matriline. Matriline 2 was removed in 2004 due to management reasons.  
182 Extensive matrilineal relationships have been documented in a previous publication (Wooddell,  
183 Kaburu, Suomi, & Dettmer, 2017b). The troop lived in a semi-naturalistic enclosure and  
184 exhibited the naturalistic social structure and dominance attainment classic of other free and  
185 semi-free ranging rhesus macaque groups. Subjects lived in a 5-acre (2-ha) wooded outdoor  
186 open-air enclosure with natural vegetation, foliage, and a pond (0.9 ha) with an island (0.07 ha),  
187 in addition to various enrichment such as jungle gyms, swings, perches, and tree huts. Three  
188 corncrib shelters (4.88 x 4.88 x 5.79 m) and three indoor runs (2.74 x 5.79 x 4.27 m) provided  
189 protection from inclement weather, but subjects had *ad libitum* access to all areas of the habitat  
190 (indoor and outdoor), unless for cleaning purposes. Purina Monkey Chow (#5038, St. Louis,  
191 MO), natural vegetation, and water were available *ad libitum* and a mixture of seeds, nuts, and  
192 fruit were provided twice a day. Subjects were exposed to both ambient light and temperature in  
193 the outdoor portion, but the indoor portions were set on a 12:12 light cycle at 25.6°C.

#### 194 *Experiment 2*

195 Subjects in experiment 2 were 18 rhesus macaque yearlings (born in 2015; 14 males; four  
196 females) studied from January to August 2016 following the formation of a peer group  
197 (Wooddell et al., 2017a). Briefly, nine of these subjects (six males, three females) were  
198 previously reared in one of three UG groups from birth in 2015 to January 2016. The UG groups  
199 consisted of 10-12 same-aged adult females, one adult male, and 1-4 several same-aged infants.  
200 The UG groups lived in indoor (2.44 x 3.05 x 2.21 m) and outdoor (2.44 x 3.0 x 2.44 m)  
201 enclosures equipped with perches, wood shavings, hanging barrels and were fed Purina High  
202 Protein Monkey Chow (#5045, St. Louis, MO) and fresh fruit and vegetables twice a day. The

203 outdoor portions were exposed to ambient light and temperature, and the indoor portions were on  
204 a 12:12 light cycle and constant temperature of 25.6°C. The other nine subjects (eight males, one  
205 female) were previously reared in the MG group in the field station from birth in 2015 and were  
206 nine (of the 18) of the infants in experiment 1. These subjects were removed in December 2015  
207 and January 2016 following a rare overthrow among the adult females in the troop at the field  
208 station, in which previously lower-ranking females attacked the dominant females and upended  
209 the social hierarchy (Wooddell et al., 2017b). In January 2016, these 18 yearlings (nine from the  
210 UG groups and nine from the MG field station group) were combined to create a peer-only  
211 group, in addition to one unrelated adult “grandfather” male. The group lived in a novel  
212 environment of an indoor run (7.3 x 3.4 x 3.7m) with *ad libitum* access to an outdoor corncrib  
213 (5.03 in diameter by 5.49 m high) from January to May 30, 2016. On May 31, 2016, the group  
214 was relocated to the rearing environment of the UG subjects (see above for description on  
215 housing details). Due to the familiarity of the environment for the UG (but not MG subjects), this  
216 relocation prompted a series of unstable dominance relationships, with an eventual complete  
217 reversal of the dominance hierarchy (see Wooddell et al., 2017a). The group resided in the  
218 indoor-outdoor runs familiar to the UG subjects until August 2016 when the study ended.

219 *Behavioral data collection: social affiliation*

220 For experiment 1, LJW collected data from 36 adult subjects (4 males, 32 females; ages  
221 3-18 years,  $M \pm SD: 8.19 \pm 3.34$  years), 25 juvenile subjects (11 males, 14 females, age at the  
222 beginning of the study: 1-2 years; 404-904 days:  $602.36 \pm 169.13$  days), and 18 infant subjects  
223 (14 males, four females; age at the beginning of the study: 31-64 days;  $45 \pm 10.29$  days). Infants  
224 were distinguished from juveniles by age, as infants were heavily dependent on the mother,  
225 being only a month or two old at the start of the study, whereas juveniles were relatively

226 independent and were well over a year (or two) old at the start of the study. Adult behavioral  
227 data were collected 1-2 times per week in both AM (900-1200) and PM sessions (1200-1700) via  
228 modified frequency sheets (Novak, Kinsey, Jorgensen, & Hazen, 1998) from November 2014 to  
229 July 2015 using a 5-minute continuous focal animal sampling method (Altmann, 1974). Each 5-  
230 minute interval was broken into 20, 15-second intervals in which the frequencies of all behaviors  
231 (social and nonsocial) were recorded in chronological order. For the purposes of this study, we  
232 only analyzed social behaviors, which included social contact (i.e., within 30-cm of another  
233 individual), social grooming (i.e., picking and spreading apart the fur), and social play (i.e.,  
234 rough and tumble wrestling, play chasing, open mouth play faces). For each social behavior, the  
235 behaviors were mutually exclusive for a dyad (i.e., an individual was not in social contact with  
236 the individual they were grooming, but they could be in social contact with a different  
237 individual). For each of these behaviors, we also recorded the identities of the social partners to  
238 construct social networks so as to analyze the number of intervals that focal animals interacted  
239 with other individuals. A total of 1,528 adult observations were recorded ( $M=42.44 \pm 9.43$ ),  
240 totaling 127.33 hours. Behavioral data on juveniles and infants were recorded in both AM and  
241 PM sessions following the identical coding scheme as the adult behavioral collection. For  
242 juveniles, data were collected twice per week from September to December 2015. A total of 728  
243 juvenile observations ( $M=29.12 \pm 1.09$ ) were recorded, totaling 60.67 hours. Behavioral data on  
244 infants were recorded 2-3 times per week across both AM and PM sessions from June to  
245 December 2015. The infants were born from March to May of 2015 so the observations reflected  
246 approximately the first 3-8 months of life (or slightly earlier for the later born infant). A total of  
247 1,067 infant observations were recorded ( $59.28 \pm 4.32$ ), totaling 88.92 hours. Total observation  
248 time for the field station was thus 277 hours.

249 For the peer group in experiment 2, each yearling (age at the beginning of the study: 188-  
250 296 days:  $274.44 \pm 24.85$  days) was observed twice per week in both AM and PM sessions by  
251 one of three observers (inter-observer reliability  $\geq 85\%$  for at least 3 consecutive sessions),  
252 following identical procedures as in experiment 1. We collected a total of 615 observations  
253 ( $M=34.17 \pm 1.25$ ) while the monkeys were housed in the new environment following peer group  
254 formation, totaling 51.25 hours. Following relocation to the previous rearing environment of the  
255 UG subjects in May 2016, and during subsequent hierarchical instability, 360 observations were  
256 recorded ( $M=20 \pm 0.34$ ), totaling 30 hours. Total observation time for the peer group across both  
257 housing conditions (and periods of decreasing stability) was thus 81.25 hours. It is important to  
258 note that nine of the infants from the field station were eventually relocated to the peer-group  
259 following the overthrow in the field station, thus they are included in both experiments (1 and 2).  
260 These infants were therefore studied continuously from approximately three months of age to 1.5  
261 years across different environments.

262 *Behavioral data collection: dominance hierarchies*

263 To construct dominance hierarchies, we used all observations of aggressive (threat, chase,  
264 attack) and submissive (displacement, fear grimace) interactions recorded via both focal animal  
265 sampling and *ad libitum* sampling (Altmann, 1974). For the field station, a total of 10,994  
266 dominance interactions were recorded from November 2014 to December 2015 among all group  
267 members (infants, juveniles, and adults). For the peer-group, a total of 5,835 dominance  
268 interactions were recorded (after group formation: 2,604; after group relocation and instability:  
269 3,231). We constructed dominance hierarchies via Elo-rating, a method commonly used to detect  
270 temporal fluctuations in dominance rank over time (Neumann et al., 2011), which we have  
271 previously utilized for both of the current study populations (Wooddell et al., 2017a; 2017b). For

272 all experiments, we used the *elo.sequence* function (Neumann et al., 2011) in R software (version  
273 3.3.3) with the initial value set at 1,000 and the k factor set at 200. An Elo-rating is generated for  
274 both the winner and loser after each interaction, with more points attributed to the interaction in  
275 which the outcome was unexpected (i.e., a lower-ranking animal winning against a higher-  
276 ranking animal) than expected interactions. Higher Elo-ratings reflect higher dominance ranks.  
277 Therefore, a total of 21,988 Elo-ratings were used to generate dominance ranks for experiment 1,  
278 and 11,670 Elo-ratings were generated to determine dominance ranks for experiment 2. Average  
279 Elo-ratings were used in analyses. It is important to note that we used the infant and juveniles'  
280 own dominance ranks (instead of their mothers') based off of their dominance interactions,  
281 which allowed us to examine both an inheritance of dominance rank and social network position.

## 282 *Social network analysis*

283 In experiment 1, we analyzed only adult-adult interactions to construct adult social  
284 networks. To construct peer networks, we used juvenile-juvenile interactions (1-2 years old) to  
285 construct juvenile social networks, and only infant-infant interactions to construct infant social  
286 networks. We chose to examine three types of affiliative social networks independently – social  
287 contact, social grooming, and social play networks – as each of these networks can provide  
288 different social mechanisms depending on age. For example, social grooming is primarily done  
289 by adult females, and can serve to strengthen and maintain bonds (Dunbar, 1991) necessary for  
290 group cohesion (Lehmann, Korstjens, & Dunbar, 2007) and coalition formation (Borgeaud &  
291 Bshary, 2015; Schino, 2007). Social play on the other hand, is done by primarily immature  
292 primates, especially males, and serves to maintain bonds (Poirier & Smith, 1974), and possibly  
293 assess rivals (Paquette, 1994), and promote social competence (Palagi, 2018; Pellis, Burghardt,  
294 Palagi, & Mangel, 2015). Social contact likely has similar functions across all ages. For adults,

295 we constructed two types of networks: social contact and social grooming. We could not analyze  
296 adult social play networks because play was never recorded between adult dyads. Contrarily, for  
297 juveniles, we analyzed all three affiliative networks. And finally, for infants, we analyzed only  
298 social contact and social play networks, because social grooming between infant dyads was only  
299 observed once. In experiment 2, we used all peer interactions in addition to interactions with the  
300 adult male, but excluded the adult male from statistical analysis. We constructed all three types  
301 of affiliative networks for this peer group in experiment 2. For all experiments, we used  
302 weighted, undirected networks for all affiliative networks.

303 To construct social networks, we used the *Statnet* and *SNA* packages (Handcock, Hunter,  
304 Butts, Goodreau, & Morris, 2006) in R software (version 3.3.3). We used the ‘*evcent*’ function to  
305 calculate eigenvector centrality for each individual and for each social behavior. This network  
306 metric reflects the number and strength of an individual’s direct connections as well as the  
307 centrality of the neighbors the subject is connected to (Bonacich, 2007; Kasper & Voelkl, 2009;  
308 Newman, 2004; Farine & Whitehead, 2015; Sueur et al., 2011). In other words, individuals can  
309 have high eigenvector centrality values either if they have a higher number of connections, or if  
310 their neighbors have a higher number of connections, or both (Farine & Whitehead, 2015).  
311 Eigenvector centrality is a common metric analyzed in social networks and has previously been  
312 reported to be associated with dominance rank in adult rhesus macaques (Sueur & Petit, 2008;  
313 Sueur et al., 2011). For visual illustrations of the social networks, we used Cytoscape (v 3.5.1).

#### 314 *Development of a rank-related relationship*

315 To examine when a possible relationship emerged between dominance rank and  
316 eigenvector centrality in infancy, we additionally combined and analyzed the social data into 4-  
317 week bins. Given that the infants were studied for 29-weeks, the last bin contained 5-weeks. For

318 each 4-week bin, we combined all affiliative data (social contact, social grooming, and social  
319 play) among peers in order to obtain enough data for network construction and constructed social  
320 networks as above. We then ran simple Spearman correlations to test whether Elo-ratings were  
321 correlated with eigenvector centrality in each 4-week bin to analyze when this relationship  
322 emerged.

### 323 *Statistical analysis*

324 In order to assess whether adult dominance rank predicted adult social network position  
325 (prediction 1), we used the ‘lm’ function in R to run two regression models (one for social  
326 contact and one for social grooming). To this end, we set eigenvector centrality as the dependent  
327 variable, while individuals’ Elo-rating values, age and sex were set as predictors. We square-root  
328 transformed social contact eigenvector values in order to normalize their distribution.

329 In order to assess whether mothers’ social network predicts their offspring’s social  
330 network position (prediction 2), we ran a linear mixed model analysis (LMM) with the ‘lmer’  
331 function implemented in the R package *lmerTest*. Offspring’s social play eigenvector was set as  
332 the outcome variable. We set the mothers’ social grooming and social contact eigenvector  
333 centrality measures, infants’ sex and age, and the interactions between infants’ sex and mothers’  
334 grooming and social contact eigenvectors as predictors. In this model, each mother’s ID was  
335 included as random factor in order to control for pseudoreplications due to a single mother  
336 birthing multiple offspring (n=43 offspring, n=30 unique mothers).

337 To test prediction 3 (i.e., that dominance rank also predicts social network position in  
338 infants and juveniles), we ran multiple regression models via the ‘lm’ function where eigenvector  
339 values from social contact, social grooming (juveniles only), and social play were set as outcome

340 variables. Infants' and juveniles' Elo-rating, sex, age, and their interaction were set as predictors.  
341 For this analysis, juvenile social grooming and social play eigenvector values and infant social  
342 play eigenvector centrality values were squared-root transformed, while both juvenile and infant  
343 social contact eigenvector centrality values were log-transformed to achieve normal distribution.  
344 Furthermore, for the analysis conducted on infant networks, an interaction between sex and  
345 mother's Elo-rating was not tested due to a strongly male-biased sex ratio (14 males, four  
346 females).

347 Finally, in order to test the relationship between yearling's rank and social network  
348 position in the peer-only groups (predictions 4 and 5), we ran an LMM model where the social  
349 contact, social grooming, and social play eigenvector values were included as dependent  
350 variables in separate models, whereas early social experience (MG vs UG), sex, age, Elo-rating,  
351 and period (before vs after relocation) were set as fixed factors. IDs were included as random  
352 factors.

353 For all models, we took an information theoretic (I-T) approach to model selection and  
354 selected only the best set of candidate models on the basis of AIC scores (Burham et al, 2011).  
355 We did this by using the function 'stepAIC' implemented in the R package *Mass* for the  
356 regression models and the function 'step' in the R package *lmerTest* for the LMM models. Only  
357 the results from the best models (i.e., those with the lowest AIC scores) are presented in the  
358 tables.

359 Network metrics are not independent because each individual's network metric (e.g.,  
360 eigenvector centrality) inevitably depends on other individuals' position in the network. This  
361 lack of independency violates some of the assumptions of many statistical tests. In order to take  
362 this into account, test statistics originated from observed data need to be compared with a



363 distribution of test statistics generated from random networks (Farine, 2017). In the current  
364 study, for each of the above-mentioned models (regression and LMMs), we generated 100  
365 networks where we randomly swapped the identity of the recipient in the social interactions, and  
366 then ran the models (regressions or LMMs) where eigenvector centrality values calculated from  
367 each of these random networks were set as outcome variables. We then generated a distribution  
368 of estimates from the models and examined where the estimate calculated from the observed data  
369 falls in relation to such distribution. In order to calculate whether the regression and LMM  
370 analyses from the observed data significantly differ from the analysis calculated from random  
371 networks, we calculated one-tailed p values by comparing the number of the random estimates  
372 that were higher than the observed estimate.

### 373 **Results**

#### 374 *Experiment 1: Relationship between social network position and dominance rank across the* 375 *lifespan in a naturalistic population*

376 Adult eigenvector values ranged from 0.026 to 0.338 ( $M \pm SD$ :  $0.15 \pm 0.07$ ) for social  
377 contact and 0.01 to 0.36 ( $0.147 \pm 0.08$ ) for social grooming. Social contact and social grooming  
378 eigenvector values were positively correlated for adults (Pearson correlation:  $r=0.46$ ,  $p=0.005$ ,  
379  $n=36$ ). The best model with grooming eigenvector as the outcome variable explained almost 60%  
380 of its variation ( $F(1,34)=52.51$ ,  $p<0.001$ ,  $R^2=0.595$ ), and contained exclusively adults' Elo-  
381 rating, which had a significant positive effect on grooming eigenvector centrality ( $\beta= 0.00013$ ,  
382  $SE= 0.00002$ ,  $t= 7.247$ ,  $p<0.001$ ; Table 1). This suggests that, among adult rhesus macaques,  
383 dominance rank significantly predicted grooming network position (Figure 1a). Similarly, our  
384 analysis of social contact showed that both Elo-rating and sex were part of the best model, which  
385 explained about 16% of the variation in individuals' social contact eigenvector values

386 (F(2,33)=4.236,  $p = 0.023$   $R^2=0.156$ ). In this model, Elo-rating had a significant positive effect  
387 on social contact eigenvector ( $\beta= 0.00009$ , SE= 0.00003,  $t= 2.714$ ,  $p=0.01$ ; Table 1). Both  
388 models were significantly different from a random distribution (Figures S1 and S2). This  
389 indicates that high-ranking adults had a greater number of social connections than low-ranking  
390 adults, supporting prediction 1.

391 When we tested prediction 2, we found that the best model included exclusively the  
392 interaction between mothers' grooming eigenvector (but not mothers' social contact eigenvector)  
393 and offspring (infants and juveniles) sex, which significantly explained 40% of the variance of  
394 offspring play network eigenvector centrality ( $\beta = 2.45$ , SE = 0.83,  $t = 2.94$ ,  $p = 0.005$ , Table 2).  
395 This model was significantly different from a random distribution (Figure S3), and revealed that  
396 a positive relationship between mother's grooming eigenvector centrality and offspring's play  
397 eigenvector centrality is present only in males but not females (Figure 2).

398 Mother's Elo-rating positively predicted juvenile's Elo-ratings (F(1,23)=34.82,  $p<0.001$ ,  
399  $R^2=0.602$ ,  $\beta=0.78$ ), indicating an inheritance of dominance rank. Juvenile eigenvector values  
400 ranged from 0.007 to 0.515 ( $0.124 \pm 0.161$ ) for social contact, 0 to 2.06 ( $0.203 \pm 0.419$ ) for  
401 social grooming, and  $0.001 \pm 0.479$  ( $0.14 \pm 0.146$ ) for social play. Only social contact and social  
402 play eigenvector values were positively correlated ( $r=0.53$ ,  $p=0.007$ ,  $n=25$ ). For social grooming,  
403 only age predicted eigenvector centrality ( $\beta=0.0008$ , SE= 0.0002,  $t=3.29$ ,  $p=0.003$ ; Table 1),  
404 whereas for social contact, Elo-rating was part of the best model ( $\beta= 0.0002$ , SE= 0.0001,  $t=2.22$ ,  
405  $p=0.036$ ; Table 1; which was also significantly different from a random distribution; see Figure  
406 S4). This model explained about 14% of the variation in juvenile social contact eigenvector  
407 (F(1,23)=4.911,  $p = 0.037$ ,  $R^2=0.140$ ). For social play, the top model included an interaction  
408 between Elo-rating and sex, which explained 43% of the variance (F(3,21)=7.144,  $p = 0.002$ ,

409  $R^2=0.434$ ) and was significantly different from a random distribution (Figure S3). Collectively,  
410 these results indicate that while older juveniles were more central in social grooming networks,  
411 more dominant juveniles were more central in social contact networks, and high-ranking juvenile  
412 males had a greater number of well-connected social partners than low-ranking males (Figures  
413 1b and 3).

414 Infant eigenvector values ranged from 0.03 to 0.4998 ( $0.185 \pm 0.151$ ) for social contact  
415 and 0.037 to 0.539 ( $0.185 \pm 0.150$ ) for social play, and both were positively correlated (Pearson  
416 correlation:  $r=0.60$ ,  $p=0.008$ ,  $n=18$ ). Mother's Elo-rating positively predicted her infant's Elo-  
417 rating ( $F(1,16)=29.14$ ,  $p<0.001$ ,  $R^2=0.65$ ,  $\beta=0.80$ ), indicating an inheritance of dominance rank.  
418 The analysis of infant social contact network position showed that the best model explained 51%  
419 of social contact eigenvector variation ( $F(1,16)=$ ,  $p<0.001$ ,  $R^2=0.507$ ) and included exclusively  
420 infant Elo-rating ( $\beta=0.002$ ,  $SE=0.00005$ ,  $t=4.30$ ,  $p<0.001$ ; Table 1). Similarly, the best model in  
421 which social play eigenvector was set as the outcome variable explained 43% of its variation  
422 ( $F(2,15)=$ ,  $p=0.006$ ,  $R^2=0.428$ ), and included infant Elo-rating which had a significantly positive  
423 effect on their network position ( $\beta=0.0003$ ,  $SE=0.0001$ ,  $t=3.29$ ,  $p=0.005$ ; see Table 1 and  
424 Figures 1c and 4). Both models were significantly different from a random distribution (Figures  
425 S5 and S6). High-ranking infants thus had a greater number of well-connected social partners  
426 than low-ranking infants. These results indicate that the relationship between eigenvector  
427 centrality and dominance rank emerged early in life, supporting prediction 3. We constructed 7,  
428 4-week bins and ran simple Spearman correlations between infant Elo-rating and eigenvector  
429 centrality. Within the first 4-weeks of data collection (representing the first 2-3 months of life  
430 depending on age at the start of the study), a correlation already emerged ( $r=0.49$ ,  $p=0.047$ ), and  
431 remained steady for the first 4, 4-week bins (weeks 5-8 of data collection:  $r=0.482$ ,  $p=0.04$ ,

432 weeks 9-12 of data collection:  $r=0.49$ ,  $p=0.04$ , weeks 13-16 of data collection:  $r=0.74$ ,  $p<0.001$ ).  
433 The relationship between eigenvector centrality and infant Elo-rating was not significant in  
434 weeks 17-20 and 21-24 ( $p=0.30$  and  $0.09$  respectively), but was again significant in weeks 25-29  
435 ( $r=0.54$ ,  $p=0.02$ ). In other words, high-ranking infants had more developed social networks than  
436 low-ranking infants very shortly after birth.

437 *Experiment 2: Relationship between social network position and dominance rank in a newly*  
438 *formed peer group*

439 After yearling group formation and before group relocation, eigenvector values ranged  
440 from 0.066 to 0.409 ( $0.198 \pm 0.129$ ) for social contact, 0.006 to 0.604 ( $0.163 \pm 0.175$ ) for social  
441 grooming, and 0.057 to 0.344 ( $0.219 \pm 0.089$ ) for social play. After group relocation and social  
442 instability, eigenvector values ranged from 0.129 to 0.322 ( $0.222 \pm 0.060$ ) for social contact,  
443 0.016 to 0.585 ( $0.158 + 0.167$ ) for social grooming, and 0.014 to 0.422 ( $0.202 + 0.125$ ) for social  
444 play. Both before and after social instability, social contact and social grooming eigenvector  
445 values were positively correlated to each other (before:  $r=0.72$ ,  $p=0.001$ ; after:  $r=0.684$ ,  
446  $p=0.002$ ), but both social contact (before:  $r=-0.608$ ,  $p=0.007$ ; after:  $r=-0.660$ ,  $p=0.003$ ) and social  
447 grooming eigenvector values (before:  $r=-0.530$ ,  $p=0.023$ ; after:  $r=-0.518$ ,  $p=0.028$ ) were  
448 inversely correlated with social play eigenvector values. Interestingly, the negative correlation  
449 between social contact and social play is in sharp contrast to what was found in the naturalistic  
450 population, where a positive correlation between these two variables was found. For the social  
451 contact network, the best model included yearling early social experience (MG or UG:  $\beta = -0.14$ ,  
452  $SE = 0.020$ ,  $t = -6.719$ ,  $p < 0.001$ ; Table 3) and Elo-rating ( $\beta = 0.00010$ ,  $SE = 0.000015$ ,  $t =$   
453  $6.591$ ,  $p < 0.001$ ; Table 3), and this model was significantly different from a random distribution  
454 (Figure S7). In contrast, contrary to our predictions, Elo-rating did not predict yearling

455 eigenvector values for social grooming and social play networks, as for both analyses, the best  
456 models included early social experiences and sex (Table 3). Collectively, these results indicate  
457 that only for the social contact network, high-ranking yearlings were more central than low-  
458 ranking yearlings, but only during a specific period (partially supporting prediction 4, failing to  
459 support prediction 5). Furthermore, eigenvector values after group formation were predictive of  
460 eigenvector values after group relocation and instability (social contact:  $F(1,16)=21.92$ ,  $p<0.001$ ,  
461  $R^2=0.58$ ,  $\beta=0.76$ ; social grooming:  $F(1,16)=51.68$ ,  $p<0.001$ ,  $R^2=0.76$ ,  $\beta=0.87$ ; social play:  
462  $F(1,16)=10.74$ ,  $p=0.005$ ,  $R^2=0.40$ ,  $\beta=0.63$ ), indicating that network positions remained stable  
463 over time, although dominance ranks changed significantly (see Wooddell et al., 2017a for the  
464 change in dominance ranks over time).

## 465 **Discussion**

466         Similar to previous findings (Sueur & Petit, 2008; Sueur et al., 2011), in experiment 1  
467 high-ranking adult macaques were more central in both social contact and social grooming  
468 networks. This is not surprising, given that high-ranking adults can provide benefits to others,  
469 including tolerance and agonistic support in exchange for grooming (Carne et al., 2011; Seyfarth,  
470 1977), making them attractive as social partners, even in groups of related females in which  
471 maternal lineage and dominance rank are independent (Snyder-Mackler et al., 2016).  
472 Unfortunately, we did not have a large enough sample size of adult males ( $n=4$ ) to test for sex  
473 effects of social networks. However, some research suggests that high-ranking adult male  
474 macaques are likely to be more central as well (Sade, Altmann, Loy, Hausfater, & Breuggeman,  
475 1988; Sueur & Petit, 2008; Sueur, Petit, et al., 2011), confirming previous work showing that the  
476 fitness consequences of strong social bonds are not just limited to females (males: Schülke,  
477 Bhagavatula, Vigilant, & Ostner, 2010; Young, Majolo, Heistermann, Schülke, & Ostner, 2014;

478 females: Brent et al., 2017; Silk et al., 2010; Silk, Alberts, & Altmann, 2003). Future research  
479 should continue to examine the social network positions of both males and females across the  
480 lifespan.

481         Intriguingly, we found that a mother's position in the social grooming network predicted  
482 her son's position in the peer social play network, indicating a potential inheritance of social  
483 networks (see also: Brent et al., 2013; Goldenberg, Douglas-Hamilton, & Wittemyer, 2016; Ilany  
484 & Akçay, 2016). The reason why a mother's position in the grooming network is related to her  
485 son's position in the play network, rather than his grooming network, likely has to do with their  
486 life-history stages and the relative importance of each social behavior in each stage of life. For  
487 adults, grooming is a primary behavior to maintain bonds and form alliances (Borgeaud &  
488 Bshary, 2015; Dunbar, 1991; Lehmann et al., 2007; Schino, 2007), whereas social play can serve  
489 these same functions for young primates, especially males (Palagi, 2018; Paquette, 1994; Pellis  
490 et al., 2015; Poirier & Smith, 1974). To the best of our knowledge, we are unaware of any study  
491 examining whether infants exchange play for agonistic support, which is an exciting avenue for  
492 future research. Therefore, the grooming network for adults may be *functionally* similar to the  
493 play network for young primates. In this case, high-ranking juveniles may be attractive social  
494 partners in play, much the same way as high-ranking adults are attractive partners in social  
495 grooming. Alternatively, infants could play around their mothers while they are grooming one  
496 another or play with close kin that share similar dominance ranks, resulting in similar networks  
497 (Berman, 1982). A further alternative scenario might be that mothers could actively initiate or  
498 prevent social interactions of their infants (Berman et al., 1997). Unfortunately, we were unable  
499 to tease apart the direct mechanisms by which offspring inherit similar network positions as the  
500 mother, which needs to be tested with future studies.

501 Similarly, mothers' dominance ranks predicted the infants' position in their social  
502 networks, and this emerged during the first four weeks of data collection. How might social  
503 networks already be constructed around dominance rank at such an early age, when infants are  
504 still heavily dependent on the mother? Our findings indicate that the networks are at least in  
505 some way being influenced by the mother's presence soon after, if not immediately after, birth.  
506 Although the networks between mothers and infants are somewhat independent (as the mothers'  
507 networks contained only adults and the infant networks contained only infants), infants could  
508 still be associating with similar individuals as their mothers (e.g., the infants of those mothers).  
509 High-ranking infants may therefore be associating with a plethora of other individuals, simply  
510 because their mother is. As the mother has a strong influence on the social networks of her  
511 infants (Berman 1982, Berman et al., 1997; Maestriperi, 2018), future research should analyze  
512 social interactions with or without the mother in close proximity. This will allow us to  
513 investigate to what extent networks change depending on the mother's nearby association and  
514 possible involvement.

515 In the naturalistic population, we found that high-ranking juvenile males were more  
516 central in social play networks, but high-ranking females were not. This is at first surprising,  
517 given that females remain in their natal groups, and males emigrate at puberty. Our findings  
518 suggest that juvenile males may find additional benefits of integration into peer social networks  
519 than females. For example, previous research has indicated that groups of same-aged (and often  
520 related) male macaques may emigrate together (van Noordwijk & van Schaik, 2001) and form  
521 alliances with one another (de Ruiter & Geffen, 1998; Gerber, Krützen, de Ruiter, van Schaik, &  
522 van Noordwijk, 2015), which can increase the chances of a successful integration, thereby  
523 increasing reproductive fitness (Schülke et al., 2010). Strengthening peer relationships may

524 therefore be an especially adaptive strategy for juvenile males. Moreover, it may be that males  
525 may need to be socially ‘primed’ for dispersal. Indeed, some research indicates that nonhuman  
526 primate mothers differentially invest in male offspring (for a review, see Lonsdorf, 2017): by  
527 exhibiting more mutual gazing with sons after birth (Dettmer, Kaburu, Byers et al., 2016), which  
528 may promote social competency (Dettmer, Kaburu, Simpson, et al., 2016), and by increasing  
529 sons’ social networks to include other mothers with offspring (Murray et al., 2014) and non-  
530 matrilineal group members (Timme, 1995). By increasing the complexity of the social  
531 experiences for male offspring, mothers may ‘prime’ males to be more socially savvy, with a  
532 variety of individuals, which can have long-term fitness consequences. Data supporting this  
533 notion have been produced in bottlenose dolphins (e.g., *Tursiops sp.*), where eigenvector  
534 centrality was found to predict survival in males but not females (Stanton & Mann, 2012). On the  
535 other hand, it is also possible that juvenile females were less central in the networks because we  
536 only analyzed peer networks and therefore excluded interactions with adults (and infants).  
537 Juvenile females may bias their social interactions (especially social grooming) to adult females  
538 (Jarrett et al., 2018; Kulik et al., 2015; Widdig et al., 2015) and infants (as they practice  
539 allomothering) in order to form the long-lasting social bonds that enhance individual (Brent et  
540 al., 2017; Silk et al., 2010) and infant survival (Silk et al., 2003). Males may, on the other hand,  
541 bias interactions to other juveniles, especially other males (Hassett, Rupp, & Wallen, 2009) to  
542 form relationships that can be beneficial during dispersal. Although we intentionally examined  
543 peer networks, future studies should investigate overall network positions of developing  
544 primates. In this case, we may see deviations in network integration between males and females,  
545 with females potentially being more integrated into the overall adult network than males.  
546 Similarly, we found that older juveniles were more central in grooming networks, indicating that



547 juveniles have a developmental shift from play to grooming. As primates age, especially females,  
548 they are more likely to focus on grooming interactions to solidify bonds, as play becomes less  
549 and less frequent, which allows for successful integration into the group (Kulik et al., 2015).

550         In experiment 2, following removal from their mothers and the formation of the yearling  
551 group, the predominant factor influencing network position across all three social networks  
552 (social contact, social grooming, and social play) was early social experience. Although  
553 dominance rank predicted the social contact eigenvector centrality, this could still have been  
554 heavily influenced by early social experiences. We have previously demonstrated that early  
555 social experiences predicted dominance rank, with MG outranking UG subjects after group  
556 formation, and the opposite after group relocation (Wooddell et al., 2017a). Therefore, our  
557 results suggest that dominance rank was less important in structuring social networks when in the  
558 absence of the mother. While it could be argued that we would not expect to find a relationship  
559 between social network position and dominance rank following relocation because the  
560 dominance ranks were in constant flux and very unstable (Wooddell et al., 2017a) and therefore  
561 network positions might be unstable too, this was not the case. Time period was not a predictor  
562 (except in the social contact network), indicating that even during a period of stability,  
563 dominance rank was not a predominant predictor of social network position in this population.  
564 Secondly, individuals were stable in their social network position before and after relocation ( $R^2$   
565 ranged from 0.40 to 0.76 across the different social behaviors examined), suggesting that  
566 although dominance ranks changed significantly, network positions did not. These findings  
567 indicate that the early social experiences were crucial in determining network positions, and that  
568 infants from highly complex, MG groups may have a specific advantage in forming social  
569 relationships. The social connections made early in life are shaped by the early social

570 environment (MG or UG), can remain stable in new environments, and can promote the  
571 development of similar social networks later on, even in the absence of the mother (e.g., African  
572 elephants, *Loxodonta africana*: Goldenberg et al., 2016). These stable relationships can be  
573 especially important during times of social stress and instability and can act as a social buffer,  
574 which is an area for future study.

575         In the naturalistic population, social contact and social play eigenvector values were  
576 positively correlated for infants and juveniles, whereas in the peer group, social contact/social  
577 grooming were inversely correlated with social play eigenvector values. We hypothesize that  
578 social play may have been functionally different in the peer group than in the naturalistic group.  
579 In the naturalistic field station, play may have been a primary source of affiliation, as dominance  
580 ranks were primarily governed by maternal rank. In the peer group, while maternal rank did  
581 predict dominance rank (see Wooddell et al., 2017a), this was true primarily only for the MG  
582 subjects (indicating sustained maternal rank inheritance). Dominance ranks between UG-UG and  
583 MG-UG subjects therefore depended on other extrinsic factors aside from maternal rank. Social  
584 play may have functioned as not only an affiliative behavior, but also as a way to assess rivals  
585 and practice skills necessary for fighting (as in yellow-bellied marmots, *Marmota flaviventris*:  
586 Blumstein, Chung, & Smith, 2013; and chimpanzees: *Pan troglodytes*: Paquette, 1994),  
587 especially for UG-UG and MG-UG dyads. In doing so, individuals that were well-connected in  
588 the social contact and social grooming networks were less connected in social play networks, as  
589 social play may have been a precursor to aggressive interactions (Paquette, 1994). Social play  
590 can likely have different social functions depending on the unique sociodynamics of the group.  
591 Play can also have direct fitness outcomes such as preparing males for intrasexual competition

592 for access to females, or in females for forming coalitions to defend resources and maintain the  
593 social hierarchy.

594         Our study is not without its limitations. First, our highly skewed sex ratios, which were  
595 beyond our control, in nearly every study group limited our ability to draw conclusions about sex  
596 differences. Ideally, we would have a greater number of young females (and adult males) in  
597 order to assess differences between sexes, as males and females have different developmental  
598 trajectories (Barale et al., 2015; Kulik et al., 2015; Widdig et al., 2015) particularly as they  
599 prepare for their sexually dimorphic adult social roles. Although we are limited in drawing  
600 conclusions about sex differences, the greater number of immature male subjects is an  
601 unintentional added benefit, as relatively less is known about juvenile male social networks in  
602 female philopatric species. In addition, although our study was designed to assess the influence  
603 of the mother's presence, we did this by examining groups with mothers and other kin compared  
604 to a peer group without mothers and adult kin. Another way to examine the influence of the  
605 mother, which would provide invaluable information about the *direct* impact of the mother's  
606 presence on network development, would be to focus on constructing social networks in which  
607 the mother is or is not nearby. This could add to the literature depicting the processes by which  
608 infant networks mirror maternal networks. Indeed, previous research has indicated that mothers  
609 can direct their offspring's interactions towards close kin (Berman et al., 1997) or non-  
610 matrilineal group members (Timme, 1995), which can all influence the developmental trajectory  
611 of infants' networks.

612         Dominance rank is a predominant factor in the structuring of adult social networks, and  
613 here, we have also demonstrated substantial similar effects for infants and juveniles. Although  
614 high-ranking immature primates are more central in their affiliative networks, this seems to be

615 primarily present in multigenerational groups in which the mother is present, although the exact  
616 mechanisms behind this process remain unknown. Multigenerational kin support is seen in a  
617 number of long-lived animals, including African elephants (Shannon et al., 2013), orcas (Wright,  
618 Stredulinsky, Ellis, & Ford, 2016), primates (Berman, 1980; Berman et al., 1997), and humans  
619 (Sear, Mace, & McGregor, 2000). There may be a potential evolutionary advantage to having  
620 complex family structures, as large extended families can provide leadership and knowledge that  
621 aid in survival (Sear et al., 2000; Wright et al., 2016), but also possibly, sociality (Shannon et al.,  
622 2013). Furthermore, our findings are also consistent with the human literature showing how the  
623 presence of kin, such as grandmothers, plays a key role for infant rearing and development in  
624 humans (Hawkes et al., 1998), hinting at the intriguing possibility of the evolutionary origin of  
625 family support in the development of social skills. By examining the direct role that mothers and  
626 kin play in shaping social networks, future research will shed light onto the role the mother and  
627 other kin have in the behavioral developmental trajectory of immature offspring, which has long-  
628 term fitness consequences.

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926 **Figure Legends**

927 **Figure 1: Social networks in adults (A), juveniles (B), and infants (C) in a naturalistic**  
928 **population of rhesus macaques**

929 The adult social grooming network (A), juvenile social play network (B) and infant social  
930 play (C) networks in a group of semi-free ranging rhesus macaques. Nodes represent  
931 individuals, while the numbers inside the nodes represent individuals' ordinal ranks, with  
932 1 being the highest-ranking individual. Node sizes are scaled based on eigenvector  
933 centrality with larger nodes representing more socially connected individuals. Lines  
934 between individuals represent interactions among one another. Shapes refer to sex  
935 (squares are males, circles are females). Colors represent matriline, and matriline are  
936 ranked in order of dominance rank: 3 (blue; dominant matriline), 4 (red; intermediate  
937 ranking matriline), and 1 (yellow; lowest-ranking matriline). Notably, the alpha male is  
938 from matriline 1, but is the highest-ranking animal. Across all ages, high-ranking  
939 individuals are more central in their peer social networks.

940 **Figure 2: Relationship between mother and offspring eigenvector centrality**

941 Mothers' eigenvector centrality in the social grooming network predicted offspring's  
942 eigenvector centrality in the peer social play network, specifically for males.

943 **Figure 3: Juvenile male centrality in social networks**

944 High-ranking juvenile rhesus macaques, especially males, were more central in social  
945 play networks.

946 **Figure 4: Infant centrality in social networks**

947 High-ranking infants (<8 months old) were more central in social play networks.

948

949 **Table Legends**

950

951 **Table 1.** Results of the regression models testing whether Elo-rating values, sex, age and the  
952 interaction between sex and Elo-rating significantly predicted adult, juvenile and infant social  
953 contact, social grooming, and social play eigenvector values. Only the results from the best  
954 model are presented.

955

956 **Table 2.** Results of the LMM models testing whether mothers' grooming eigenvector, infant sex,  
957 and their interaction significantly predicted their offspring's play eigenvector. Only the results  
958 from the best model are presented.

959

960 **Table 3.** Results of the LMM models ran to test whether yearling early social experience, Elo-  
961 rating, period (before vs after relocation), sex, and age predicted their eigenvector values. Only  
962 the results from the best model are presented.

963

964 **Supplementary Material:**

965 **Comparison of observed vs randomized networks in rhesus macaques:** All networks  
966 generated from real social data were significantly different from randomized networks.

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