

1 **Social network analysis of wild chimpanzees provides insights for**  
2 **predicting infectious disease risk**

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## 11 **Summary**

- 12 1. Heterogeneity in host association patterns can alter pathogen transmission and strategies for  
13 control. Great apes are highly social and endangered animals that have experienced  
14 substantial population declines from directly transmitted pathogens; as such, network  
15 approaches to quantify contact heterogeneity could be crucially important for predicting  
16 infection probability and outbreak size following pathogen introduction, especially owing to  
17 challenges in collecting real-time infection data for endangered wildlife.
- 18 2. We present here the first study using network analysis to quantify contact heterogeneity in  
19 wild apes, with applications for predicting community-wide infectious disease risk.  
20 Specifically, within a wild chimpanzee community, we ask how associations between  
21 individuals vary over time, and we identify traits of highly connected individuals that might  
22 contribute disproportionately to pathogen spread.
- 23 3. We used field observations of behavioral encounters in a habituated wild chimpanzee  
24 community in Kibale Forest, Uganda to construct monthly party-level (*i.e.*, subgroup) and  
25 close-contact (*i.e.*,  $\leq 5\text{m}$ ) association networks over a nine-month period.
- 26 4. Network analysis revealed that networks were highly dynamic over time. In particular, estrus  
27 events significantly increased pairwise party associations, suggesting that community-wide  
28 disease outbreaks should be more likely to occur when many females are in estrus.
- 29 5. Bayesian mixed-effects models and permutation tests identified traits of chimpanzees that  
30 were highly connected within the network. Individuals with large families (*i.e.*, mothers and  
31 their juveniles) that range in the core of the community territory and to a lesser extent high-  
32 ranking males were central to association networks, and thus represent the most important  
33 individuals to target for disease intervention strategies.

34 6. Overall, we show striking temporal variation in network structure and traits that predict  
35 association patterns in a wild chimpanzee community. These empirically-derived networks  
36 can inform dynamic models of pathogen transmission and have practical applications for  
37 infectious disease management of endangered wildlife species.

38

39 **Key words**

40 association patterns, infectious disease dynamics, *Pan troglodytes*, pathogen control, wildlife

41 conservation

## 42 **Introduction**

43           Many pathogens spread through host populations via social interactions (Altizer *et al.*  
44 2003); thus, knowledge of a community's social system and contact structure can provide crucial  
45 information for predicting infectious disease outbreaks (*e.g.*, Nunn *et al.* 2008; Drewe 2010;  
46 Griffin & Nunn 2012). Inter-individual contacts that lead to pathogen transmission can be  
47 represented using networks, where each node represents an individual, and edges between nodes  
48 represent interactions that allow for pathogen transmission. Contact networks for humans and  
49 animals are often heterogeneous (*e.g.*, dolphins: Lusseau 2003; humans: Schneeberger *et al.*  
50 2004; marmots: Wey & Blumstein 2010), which violates the common assumption of many basic  
51 epidemiological models that contacts are random and individuals are well mixed (Anderson &  
52 May 1991). Network analysis provides a feasible (albeit data intensive) approach to  
53 mathematically formalize transmission pathways and host contact variation (Newman 2010).  
54 Further, network analysis can identify potential superspreaders, individuals with  
55 disproportionately high contact levels, that could be targeted for vaccination, treatment, or  
56 isolation (Lloyd-Smith *et al.* 2005). Studies of human contact networks often detect  
57 heterogeneity and the presence of superspreaders, which has been extremely influential in our  
58 understanding of transmission dynamics for SARS and HIV/AIDS (Anderson, Gupta & Ng  
59 1990; Lloyd-Smith *et al.* 2005; Meyers *et al.* 2005). Superspreaders have also been identified in  
60 a few wildlife populations (*e.g.*, possums: Porphyre *et al.* 2008; deer mice: Clay *et al.* 2009);  
61 however, network analysis is rarely used to investigate the epidemiology and control of wildlife  
62 diseases (Craft & Caillaud 2011). Here we present the first study to analyze empirical wild  
63 chimpanzee contact networks within a framework of predicting implications for infectious  
64 disease risk.

65           Endangered wild ape populations have recently experienced outbreaks of Ebola, measles  
66   and respiratory viruses, making infectious disease a major threat to their survival (Ryan & Walsh  
67   2011), in part owing to the risk of pathogen spillover from humans to wild apes (Kaur *et al.*  
68   2008; Köndgen *et al.* 2008). Thus, given the push to habituate wild apes for tourism across more  
69   than 15 African sites (Muehlenbein & Ancrenaz 2009), infectious disease risks for apes will  
70   likely continue or escalate. Respiratory diseases in particular have resulted in outbreaks with up  
71   to 25% community-level mortality at several long-term chimpanzee research sites (Ryan &  
72   Walsh 2011). With low birth rates and late reproductive maturity, ape populations can take  
73   decades to recover in size after an outbreak. For example, using mathematical models and a  
74   range of parameters derived from published ape epidemics (*i.e.*, mortality rates of 4-25%), Ryan  
75   and Walsh (2011) estimated that a mountain gorilla population would require 5-32 years to  
76   recover following an outbreak of respiratory disease. In accordance with these predictions, a  
77   Tanzanian chimpanzee community took 15 years to return to its pre-epidemic population size  
78   after a 1987 respiratory disease outbreak (Williams *et al.* 2008).

79           In addition to the detrimental impact that pathogens can have on endangered apes,  
80   obtaining real-time infection data for wildlife is notoriously difficult. Collecting biological  
81   samples often requires risky interventions including darting and possibly anesthetizing immune-  
82   challenged individuals. Furthermore, the speed with which respiratory pathogens typically spread  
83   through ape communities (e.g., with a duration of roughly two weeks to two months: Hanamura  
84   *et al.* 2008; Williams *et al.* 2008; Köndgen *et al.* 2010) can limit researchers' abilities to collect  
85   comprehensive health data during an outbreak. Given these challenges, parameterizing realistic  
86   epidemiological models with association data (*e.g.*, Davis *et al.* 2008; Hamede *et al.* 2011) is  
87   essential for developing strategies to reduce the risk and impact of infectious diseases. An

88 underlying assumption of these models is that network edges truly represent possible pathogen  
89 transmission routes. Indeed, while relatively few wildlife studies have both host infection and  
90 host association data, there is a growing body of evidence that wildlife social networks strongly  
91 predict individual infection status (Otterstatter & Thomson 2007; Leu, Kappeler & Bull 2010;  
92 Bull, Godfrey & Gordon 2012) and that highly connected individuals tend to have greater  
93 parasite burdens than less connected individuals (Corner, Pfeiffer & Morris 2003; Godfrey *et al.*  
94 2009; Leu, Kappeler & Bull 2010; but see: Otterstatter & Thomson 2007).

95         Great ape societies are highly structured and complex. Chimpanzees in particular live in  
96 permanent social groups termed communities, and have a fission-fusion social structure,  
97 whereby individuals within the community frequently break off into subgroups, called parties,  
98 that vary in size and composition (Goodall 1986). A chimpanzee mother and her offspring travel  
99 together in a family unit, and sociality can vary greatly among adult females (Boesch & Boesch-  
100 Achermann 2000). In fact, Goodall (1986) noted that eastern chimpanzee females ranging in the  
101 core of the community's territory encountered other individuals on a daily or weekly basis,  
102 whereas females ranging on the periphery of the territory might encounter community members  
103 only a few times per year. Compared to females, males follow a linear dominance hierarchy  
104 (Muller & Wrangham 2004) and tend to be more gregarious (Gilby & Wrangham 2008).  
105 Additionally, other studies showed that party size tends to increase when females are in estrus or  
106 when ripe fruits are available (*e.g.*, Wrangham 2000; Anderson *et al.* 2002; Itoh & Nishida  
107 2007).

108         In this study, we use network analysis to examine association patterns among individuals  
109 in a community of wild chimpanzees at Kibale National Park, Uganda. In particular, we quantify  
110 how association patterns that represent potential pathogen transmission routes vary over time, in

111 response to factors such as fruit availability or the number of estrous females. We also examine  
112 individual traits that contribute to high levels of association, and predict that high-ranking males  
113 and estrous females will have disproportionately high levels of association with community  
114 members owing to increased rates of grooming and mating (*e.g.*, Goodall 1986; Emery  
115 Thompson & Wrangham 2008). Importantly, investigating the dynamics and drivers of contact  
116 variation in wild apes is a necessary step for simulating pathogen spread and evaluating the  
117 success of much needed disease intervention strategies for this highly threatened primate clade.

118

## 119 **Materials and Methods**

### 120 *Study site and population*

121 We studied the habituated wild Kanyawara chimpanzee community at Kibale National  
122 Park (0°34'N, 30°21'E) in Uganda. The site is dominated by moist deciduous forest interspersed  
123 with secondary forest, grassland, and swamp (Chapman & Wrangham 1993). Weather data for  
124 the site were provided by C. Chapman. Further details on the ecology of Kibale are discussed in  
125 Struhsaker (1997). The Kanyawara chimpanzee community occupies roughly 37.8 km<sup>2</sup> of forest  
126 (Wilson, Hauser & Wrangham 2001), and during the time of the study the community included  
127 48 chimpanzees with 12 adult males (aged > 14), 14 adult females (aged > 13), 9 immature  
128 males and 6 immature females (aged between 5-14 and 5-13 respectively; hereafter referred to as  
129 juveniles), and 7 dependent offspring (aged ≤ 4). For additional information on the Kanyawara  
130 community, see Supporting Information (Appendix S1).

131

### 132 *Data collection*

133 We collected data on chimpanzee association patterns over nine months between Dec  
134 2009-Aug 2010 for 4-6 days per week between 6:00am and 7:30pm. Each morning, we randomly  
135 selected a focal chimpanzee from a party (typically at a nest site) to follow for 10 hours. Every  
136 15 min, we scanned the focal individual's party and recorded the identity of all party members  
137 based on individuals within a 50m radius, a common criterion for estimating chimpanzee party  
138 sizes (Clark & Wrangham 1994). As an index for assessing patterns of close association within  
139 parties, at the same 15-min intervals, we also recorded pairs of individuals that were within 5m  
140 of each other, which is a measure that commonly contributes to identifying close associations  
141 among primates (*e.g.*, Gilby & Wrangham 2008). We limited our focal follows and party  
142 composition data to chimpanzees greater than 4 years of age (*i.e.*, excluding dependent offspring,  
143 which remain in close contact with their mothers); we also excluded two adult females and a  
144 juvenile male on the periphery of the community who were observed only twice during the  
145 study. Our total sample size was 37 individuals (12 adult males, 12 adult females, 7 juvenile  
146 males, and 6 juvenile females). We recorded days when parous females had maximal sexual  
147 swellings and noted ripe fruit species on which focal animals foraged.

148

#### 149 *Estimating association indices*

150 We calculated monthly pairwise association indices between individuals at two spatial scales:  
151 (i) party-level association indices were based on the frequency of monthly co-occurrence in the  
152 same party, and (ii) close contact association indices (*i.e.*, within-party and overall 5m-  
153 associations, described below) were based on the frequency with which two individuals were  
154 seen within 5m of each other during a given month. We examined associations at the party-level  
155 as a proxy for the transmission of pathogens spread by non-close contact (*e.g.*, via fomites,



156 aerosol transmission, or fecal-oral routes). To estimate party-level associations, we calculated a  
157 monthly ‘twice weight index’ (Cairns & Schwager 1987), hereafter referred to as a monthly  
158 party association index (PAI), from party membership scans. This parameter calculates the ratio  
159 of scans in which chimpanzees A and B were observed in the same party relative to the total  
160 number of scans in which either A or B was observed in any party as follows:

$$161 \quad \text{PAI}_{AB} = S_{AB}/(S_A + S_B + S_{AB}) \quad (1)$$

162 where  $S_{AB}$  represents the number of scans where A and B were observed in the same party,  $S_A$   
163 represents scans where A was observed in a party without B, and  $S_B$  represents scans where B  
164 was observed in a party without A. PAIs and subsequent indices described below could range  
165 from 0 (*i.e.*, individuals in a pair were never observed associating in the given month) to 1 (*i.e.*,  
166 individuals in a pair were observed to be associating during 100% of the observations for the  
167 given month).

168 Close-contact interactions were examined as a proxy for pathogens requiring direct contact or  
169 respiratory droplets to spread. As one close-contact measure, within-party association indices  
170 (WPAI) represent the proportion of scans in which chimpanzees A and B were observed within  
171 5m of each other, given that they were within the same party:

$$172 \quad \text{WPAI}_{AB} = (S_{AB5}/S_{AB}) \quad (2)$$

173 where  $S_{AB5}$  represents the number of scans where A and B were observed within 5m of each  
174 other. To examine which individuals were most central to the 5m-networks, we calculated an  
175 overall 5m-association index (5mAI), which incorporated the probabilities that individuals A and  
176 B would be both within the same party and within 5m of each other:

$$177 \quad 5\text{mAI} = \text{PAI}_{AB} * \text{WPAI}_{AB} \quad (3)$$

178 Thus, this index estimates the overall proportion of time that individuals A and B were within a  
179 5m distance.

180 To examine host interactions at a temporal scale that reflects the transmission biology of  
181 real-world pathogens, we analyzed association patterns at both two-week and monthly intervals,  
182 as respiratory diseases common to chimpanzees and humans have infectious periods that range  
183 from a few days to one month (*e.g.*, influenza: 2-3 days, measles: 6-7 days, chicken pox: 10-11  
184 days, *Streptococcus spp.* (Ekdahl *et al.* 1997): 14-30 days) (reviewed in: Anderson & May 1991,  
185 Table 3.1) and published reports of wild chimpanzee respiratory illnesses suggest that epidemic  
186 durations often range from roughly two weeks to two months (Hanamura *et al.* 2008; Williams *et*  
187 *al.* 2008; Köndgen *et al.* 2010). Because associations across both time steps were significantly  
188 correlated for both PAIs and 5mAIs (Table S1, Supporting Information), and other results were  
189 robust across both time steps, we present results for monthly associations in the main text (see  
190 Tables S2 and S3 for two-week time step results).

191

### 192 *Visualizing networks*

193 We constructed monthly party and 5m-association networks in R version 2.15.1 (R Core  
194 Development Team 2010) with the igraph package version 0.5.5-4 (Csardi & Nepusz 2006).  
195 Party and 5m-network edges were weighted according to the monthly pairwise PAIs and 5mAIs  
196 respectively, such that pairs with higher association indices had thicker edges.

197

### 198 *Individual trait data*

199 In all analyses, we categorized chimpanzees based on their age, sex, dominance rank,  
200 family size (Table S4), and for pairwise analyses, whether two individuals were related to each

201 other. Chimpanzee rank, based on dominance interactions for adult males, was categorized such  
202 that high-, medium-, and low-ranking adult males respectively occupied the rank categories of  
203 Male 1 (M1, N = 5), Male 2 (M2, N = 4), and Male 3 (M3, N = 3). By grouping individuals in  
204 this way, all males stayed within their respective rank categories throughout the study period,  
205 despite minor reshuffling in the linear hierarchy. Female chimpanzees rarely show dominance  
206 interactions; however, females occupying and foraging in the core area of the territory (at  
207 Kanyawara) tend to be higher ranking than those occupying the peripheral areas (Kahlenberg,  
208 Emery Thompson & Wrangham 2008). Thus, we assigned core-area adult females and their  
209 juvenile offspring to rank categories Female 1 (F1, N = 6) and Juvenile 1 (J1, N = 9), and edge-  
210 ranging adult females and their offspring to Female 2 (F2, N = 6) and Juvenile 2 (J2, N = 4).  
211 Additional details on rank categorization are in Appendix S2 and Table S4.

212         Lastly, we defined a family unit as a mother and her non-infant offspring, such that an  
213 individual's family size was the total number of non-infant chimpanzees in this family unit. In  
214 one unique case, a young adult male and his juvenile sibling were considered a family unit  
215 (Table S4), as their mother was deceased. Chimpanzees who traveled without a family unit (*e.g.*,  
216 adult males, females with infants only) were assigned a family size of one. We considered  
217 mother-offspring pairs and maternal siblings to be related, based on long-term records from the  
218 field site.

219

#### 220 *Monthly changes in network density*

221         To compare PAIs and 5mAIs over time, we calculated monthly network density as the  
222 sum of the network's observed edge weights divided by the sum of the maximum possible edge  
223 weights (Hanneman & Riddle 2005). To examine how stable party and 5m-networks were over

224 time, we assessed correlations between monthly association index matrices using a quadratic  
225 assignment procedure (see Appendix S3 for details) in UCINET version 6.343 (Borgatti, Everett  
226 & Freeman 2002).

227

### 228 *Analyses of pairwise associations*

229 To examine how social factors (*e.g.*, rank status) and ecological factors (*e.g.*, fruit  
230 availability) affect temporal pairwise associations at party and 5m-levels, we fit two models (for  
231 PAI and WPAI data, respectively) to Bayesian logistic mixed-effects models using a Markov  
232 chain Monte Carlo (MCMC) framework. We tested for significant relationships between  
233 monthly pairwise associations and the following predictor variables: age (adult-adult, adult-  
234 juvenile, juvenile-juvenile), sex/estrus (*i.e.*, pairwise combinations of males, non-estrous  
235 females, and estrous females, *Note*: parous females were categorized as estrous during months in  
236 which they were observed to be in estrus; nulliparous females were never categorized as estrous),  
237 relatedness (related, unrelated), difference in family size (range: 0-3), and difference in rank  
238 category (scored as 1/0 where a pair in the same rank category scored a 0 and a pair in different  
239 ranks scored a 1). Because we expected mothers and their juveniles to associate frequently, for  
240 this analysis we collapsed the adult female and juvenile ranks into FJ1 (core-ranging individuals)  
241 and FJ2 (edge-ranging individuals).

242 We also included two key parameters that could affect associations over time. First, we  
243 included a parameter for the number of parous estrous females observed during each month, as  
244 males prefer mating with parous over nulliparous females (Muller, Thompson & Wrangham  
245 2006). Additionally, research at some sites shows that increased fruit availability is linked to  
246 larger parties (*e.g.*, Wrangham 2000). We did not have fruit abundance data; however, we

247 included parameters for the monthly presence/absence of preferred ripe fruit species (*Mimusops*  
248 *bagshawei*, *Pseudospondias microcarpa*, *Uvariopsis congensis*) (Wrangham *et al.* 1996)  
249 according to our focal data (as eating of preferred fruits is strongly associated with fruit  
250 availability for Kanyawara chimpanzees: Wrangham *et al.* 1991), along with a parameter for the  
251 mean daily rainfall from two months prior, which we considered to be a proxy for current fruit  
252 availability.

253 To account for autocorrelation from repeated measures, we assessed model fit with  
254 random effects of chimpanzee ID, chimpanzee pair, and month. One difficulty with including a  
255 random effect for individual ID was that an individual could appear interchangeably as  
256 individual A or individual B in the observed pairwise associations described in equations 1-3.  
257 This interchangeability was due to the fact that the associations were not directed, meaning they  
258 did not have a specific ‘sender’ and ‘receiver.’ We resolved this issue by using the multi-  
259 membership modeling capabilities of the MCMCglmm package (Hadfield 2010) in R. Additional  
260 analysis details are in Appendix S3; R code is available upon request.

261

### 262 *Individual traits associated with network centrality*

263 To identify individual traits associated with increased contact, we used UCINET to  
264 calculate three weighted network centrality measures for each chimpanzee: degree, eigenvector,  
265 and flow-betweenness. Weighted degree centrality (hereafter referred to as degree) for each node  
266 is the sum of the node’s edge weights (Newman 2010). Eigenvector centrality is based on an  
267 individual’s connectedness and the connectedness of an individual’s associates, where an  
268 individual with high eigenvector centrality is connected to well-connected associates (Newman  
269 2010). Lastly, flow-betweenness centrality is defined as the proportion of times an individual lies

270 along the shortest path between pairs in the network (Freeman, Borgatti & White 1991). Previous  
271 theoretical and empirical work in human and wildlife systems has shown that individuals with  
272 high degree, eigenvector, or flow-betweenness centrality are more likely to contract and transmit  
273 pathogens than individuals with low centrality (*e.g.*, Corner, Pfeiffer & Morris 2003; Salathé *et*  
274 *al.* 2010).

275 Using node-level permutation-based regressions, we fit individual centrality data in R  
276 with 30,000 permutations per test to investigate relationships between each centrality measure  
277 and the following predictor variables: rank, estrous-status, family size, continuous age, and sex  
278 (while controlling for month effects). We controlled for sampling effort across individuals by  
279 weighting the model variance structure according to the number of scans in which each  
280 individual was a focal subject. To account for comparisons of three centrality measures, we  
281 applied a Bonferroni correction and considered relationships where  $P < 0.017$  (*i.e.*,  $P < 0.05/3$ ) to  
282 be significant. Age and sex were excluded from the final models because they were confounded  
283 with rank (which was already separated by age and sex groups), explained less than one percent  
284 of the variation (as determined by adjusted  $R^2$ ), and were never significant after Bonferroni  
285 correction. Additional analysis details are in Appendix S3.

286

## 287 **Results**

### 288 *Association patterns and social network descriptions*

289 On average, each chimpanzee was followed as a focal subject for 27.79 ( $\pm$  3.6) hours  
290 (Fig. S1), comprising a total of 1028 focal observation hours and 4114 15-min scans for all  
291 individuals combined. Our analysis included 306,212 pairwise party associations and 14,673  
292 pairwise 5m-associations over the nine month period. When averaged across months and

293 individuals, randomly selected chimpanzee pairs were observed associating at the party-level  
294 approximately 26% of the time (mean PAI: 0.255, range: 0.0-1.0, SE: 0.003) and at the 5m-level  
295 4% of the time (mean 5mAI: 0.041, range: 0.0-1.0, SE: 0.001). Three parous females came into  
296 estrous at different points in the study; the number of estrous females per month was low (range:  
297 0-2) owing to a high proportion of lactating females in the study population.

298 Monthly party networks were dynamic over time (Figs 1-2, S2-S3) and network density  
299 ranged from 0.14 (Jan) to 0.42 (Apr). Party networks for consecutive months were highly  
300 correlated (Fig. S3), but correlation coefficients decayed as the time lag increased, indicating that  
301 party networks were locally stable within 2-3 month periods but were dynamic on a longer time  
302 scale. The 5m-network density ranged from 0.03 (Mar) to 0.06 (Jan) (Figs 2, S4). There was no  
303 significant relationship between monthly party network density and monthly 5m-network density  
304 ( $R^2 = 0.17$ ,  $P = 0.270$ ; Fig. 2 inset). Variance-to-mean ratios of total edge weights per individual  
305 (*i.e.*, weighted degree centrality) for party and 5m-networks were relatively low across months  
306 (party network: 3.52, 5m-network: 0.73; Fig. S5), and while monthly party networks were  
307 significantly more aggregated than 5m-networks ( $t_{8,3} = 4.38$ ,  $P = 0.002$ ), degree distributions  
308 indicated that networks were not highly aggregated at either scale (Figs S6-S7).

309

### 310 *Effects of social and ecological factors on pairwise associations*

311 The number of estrous females in a given month significantly increased pairwise  
312 associations at the party-level, where for each additional estrous female, the odds of a pair  
313 associating were roughly twice as high (Table 1, Fig. 3). There was a significant interaction  
314 between the number of estrous females and age, such that adult-adult pairs experienced the  
315 largest increase in associations as the number of females in estrus increased. Similarly, of all the

316 pairwise sex combinations, pairs that included one estrous female associated the most frequently.  
317 The odds of related pairs being in a party together were over 20 times greater than the odds for  
318 unrelated pairs, and chimpanzees were significantly more likely to associate with individuals of  
319 their own rank category. Family size difference negatively affected association indices,  
320 indicating that individuals with large families (*i.e.*, 3-4 members, Table S4) tended to associate  
321 with other large families, and individuals without family units tended to associate with each  
322 other (Table 1).

323         The final model for pairwise party associations included random effects of chimpanzee  
324 ID and pair ID. Month was not included as a fixed or random effect, as the number of estrous  
325 females per month was a better predictor of monthly pairwise associations than month per se,  
326 based on the relative deviance information criterion, DIC ( $\Delta$  DIC > 50). Rainfall lag and fruit  
327 availability parameters were removed because their exclusion increased model fit (rainfall:  $\Delta$   
328 DIC > 30, fruit:  $\Delta$  DIC > 20, see Appendix 4 for discussion of fruit availability and network  
329 structure). The final model had  $R^2$  values that ranged from 0.32-0.58 for the amount of variation  
330 explained in each of the monthly networks, with the exception of August ( $R^2 = 0.07$ ; Fig. S8).

331         Results for 5mAIs were similar to the party-level results, although several variables in the  
332 5m-model were significant in some but not all months (Table S5). A major difference between  
333 these two levels of association was that pairs including an estrous female were often less likely to  
334 associate within 5m (as compared to pairs including an estrous female being more likely to  
335 associate at the party-level). As a second key difference, month was included as a fixed effect  
336 variable that interacted with every other fixed effect variable (age, sex/estrus, relatedness, family  
337 size difference, rank category difference), allowing the coefficients of these variables to vary for  
338 each monthly network (Table S5). While more challenging to interpret, this final model fitted the



339 data much better than the model including month as a random (and hence, additive) effect ( $\Delta$   
340 DIC > 100), or excluding month and including the number of estrous females to describe  
341 monthly change ( $\Delta$  DIC > 350). This indicates that the number of estrous females was not as  
342 good of a predictor for 5m-associations as it was for party associations. The incorporation of  
343 month as a fixed effect precluded testing temporal variables (*i.e.*, fruit availability, rainfall, and  
344 number of estrous females per month). Monthly  $R^2$  values for the final 5m-association model  
345 ranged between 0.18-0.53 (mean: 0.34; Fig. S8).

346

#### 347 *Predictors of individual centrality*

348 Family size and dominance rank were the most important predictors for individual centrality  
349 at both the party and 5m-levels after controlling for the month of observation (Table 2; Figs 4,  
350 S9). Adult females and juveniles with large families (*i.e.*, 3-4 members) had significantly higher  
351 degree and eigenvector centrality; however, family size was not an important predictor for an  
352 individual's flow-betweenness centrality. This indicates that chimpanzees with large families had  
353 more edges and associated with other well-connected individuals, but were not more likely than  
354 random to connect two other individuals in the community.

355 Regarding rank, in both the party and 5m-association networks edge-ranging females and  
356 juveniles (F2 and J2) had significantly lower degree and eigenvector centrality than all other  
357 ranks in both party and 5m-networks (with the exception that J2 did not have significantly lower  
358 degree centrality than low-ranking males in 5m-networks after Bonferroni correction; Figs 4, S9;  
359 Table S6). F2 and J2 also had significantly lower flow-betweenness centrality in party networks  
360 than high- and medium-ranking males. Altogether, these results indicate that edge-ranging adult  
361 females and juveniles were less connected to others and had fewer well-connected associates

362 than all other ranks. They were also less likely than adult males to connect two random  
363 individuals in the party networks.

364 In 5m networks, high-ranking males (M1) had significantly higher degree centrality than  
365 low-ranking males (M3) (Figs 4, S9; Table S6). Additionally, there was a strong trend ( $P < 0.05$ )  
366 for M1 to have higher eigenvector centrality than M3 in 5m-networks and higher flow-  
367 betweenness than core-ranging adult females and juveniles (F1, J1) in party networks; however,  
368 these differences were not significant after Bonferroni correction. Thus, while edge-ranging  
369 females and juveniles were nearly always the least central to the community, the relationship  
370 between high-ranking males and centrality was weaker and less consistent, with high-ranking  
371 males being significantly more central than other community members (*e.g.*, M3, F2, J2) for  
372 some but not all centrality measures (Figs 4, S9; Table S6). Lastly, estrous status was never  
373 significantly related to centrality in party or 5m-networks (Table 2).

374

## 375 **Discussion**

### 376 *Association patterns and insights for disease transmission*

377 Our results demonstrate inter-individual and temporal variation in association patterns of  
378 wild chimpanzees, which should have profound effects on pathogen transmission dynamics. A  
379 main advantage of network analysis over more traditional connectivity measures, such as party  
380 size, is that network analysis explicitly quantifies how connectivity varies in relation to  
381 demographic and behavioral traits, and among individuals in a community. Degree distributions  
382 demonstrated that neither party nor 5m-networks were highly aggregated (*i.e.*, most individuals  
383 had moderate centrality as opposed to a few superspreaders accounting for a majority of  
384 contacts); yet certain types of individuals had significantly higher association rates than others.

385           Adult females and juveniles with large families (*i.e.*, 3-4 family members) were  
386 significantly more central than expected by chance in both party and 5m-networks, and  
387 individuals in core-ranging families were significantly more central than those in edge-ranging  
388 families. Additionally, chimpanzees associated more frequently with related individuals and  
389 individuals that had similar family sizes. Thus, it seems that core-ranging chimpanzees with  
390 large families associated frequently with family members and also formed what Goodall (1986)  
391 referred to as “nursing parties,” where mothers and juveniles of different family units socialize  
392 together. Edge-ranging families on the other hand, were nearly always the least central. In fact,  
393 the average degree centrality between a core-ranging adult female with a large family and an  
394 edge-ranging adult female without any juvenile offspring differed roughly by a factor of 2 in  
395 party networks and 2.5 in 5m-networks. Thus, individuals from edge-ranging families were the  
396 least likely to contribute to or be affected by disease transmission from a community-level  
397 perspective (although peripheral individuals could be exposed to pathogens from other  
398 communities or human settlements that overlap with forest edges).

399           Among core-ranging individuals, the average centrality of an adult female chimpanzee  
400 with three juveniles was roughly 2.5 degrees higher than that of an adult female with no  
401 juveniles. Previous wildlife network studies have demonstrated that even small differences in  
402 centrality can be linked to key differences in individual infection status. For example, a study  
403 examining parasites in gidgee skinks (*Egernia stokesii*) determined that while network centrality  
404 was an effective predictor of parasite burden, the average difference in centrality between skinks  
405 with and without ticks was only ~ 0.35 degrees (Godfrey *et al.* 2009). Thus, while we recognize  
406 that the magnitude of centrality metrics (which are dependent on network size and system-  
407 specific association definitions) should not be directly compared across systems, the significant

408 increase we observed in chimpanzee centrality due to family size (even if modest in magnitude)  
409 could have a crucial impact on individual infection status.

410         While not as consistently central as core-ranging individuals with large families, high-  
411 ranking males also had high centrality. Past work on the same study community showed that  
412 high-ranking males tend to have increased levels of immunosuppressing testosterone (Muller &  
413 Wrangham 2004), and work in a nearby chimpanzee community (Ngogo) recently demonstrated  
414 that high-ranking males had both increased testosterone levels and greater helminth burdens  
415 (Muehlenbein & Watts 2010). Thus, in combination with the well-established  
416 immunosuppressive effects of sex hormones, their moderately central location in the network  
417 should make high-ranking males susceptible to contracting and transmitting a variety of  
418 pathogens. Similarly, there is evidence in West African chimpanzees (Taï Forest) that young  
419 juveniles maintain respiratory diseases in the community through play or close contact (Kuehl *et*  
420 *al.* 2008), a dynamic that has been demonstrated among human children for various childhood  
421 diseases (*e.g.*, Fine & Clarkson 1982). Taken altogether, we expect core-ranging adult female  
422 and juvenile chimpanzees with large families and to a lesser extent high-ranking males should  
423 play an important role in pathogen transmission.

424         Contrary to our predictions, estrous females were not significantly more central than  
425 expected by chance in party or 5m-networks. This is surprising considering that among party  
426 networks, pairs including estrous females had higher levels of association and estrous females  
427 significantly increased association patterns across the community. Because a majority of adult  
428 females in our study community were nursing infants, the sample size for estrous females was  
429 limited ( $N = 3$ ). Furthermore, one estrous female was frequently absent from the community and  
430 was presumed to be engaging in consortships, in which a mating pair travels away from the

431 community (Goodall 1986). In future studies of centrality with larger samples of estrous females,  
432 it may be necessary to develop networks that span shorter time frames (*i.e.*, the length of  
433 maximal swelling, or roughly one week), as examining longer time steps includes intervals when  
434 the female does not have an estrous swelling and is potentially experiencing lower centrality.

435         While often overlooked in epidemiological analysis, temporal changes in behavioral  
436 interactions can affect the outbreak timing (Altizer *et al.* 2006), as demonstrated by peaks in  
437 measles transmission in children during school sessions (Fine & Clarkson 1982) or by phocine  
438 distemper outbreaks coinciding with the haul-out behavior of seals (Swinton *et al.* 1998).  
439 Chimpanzee pairs were twice as likely to associate and party networks were denser when  
440 females were in estrus, suggesting that estrous events represent times of high vulnerability to  
441 infectious disease outbreaks. This result confirms findings from long-term field studies showing  
442 that chimpanzee party size increases with the number of estrous females (*e.g.*, Wrangham 2000).  
443 Notably, there was no significant relationship between party and 5m-network density, and the  
444 number of estrous females did not significantly affect 5m-level associations. Thus, our network  
445 analyses suggest that the potential risk of outbreaks from pathogens that require very close  
446 contact for transmission might not increase with estrous events.

447

#### 448 *Implications for conservation and infectious disease management*

449         Epidemiological modeling studies in humans have shown that targeting central  
450 individuals for control efforts is significantly more effective in mitigating disease than applying  
451 control efforts randomly (Lloyd-Smith *et al.* 2005; Salathé *et al.* 2010). In a handful of cases,  
452 vaccination has been used to reduce the impact of emergent epidemics in endangered wildlife  
453 populations (gorilla measles and chimpanzee polio: Woodford, Butynski & Karesh 2002;

454 Ethiopian wolf rabies: Haydon *et al.* 2006). Given the detrimental impacts of pathogens on great  
455 ape communities (e.g., Bermejo *et al.* 2006; Caillaud *et al.* 2006; Köndgen *et al.* 2008), some  
456 wildlife biologists have called for vaccinating great apes prophylactically for high-risk pathogens  
457 (Ryan & Walsh 2011). To effectively plan control strategies and minimize human interference,  
458 network models can indicate the minimum number of well-connected individuals that should be  
459 vaccinated to reduce outbreak sizes (as per: Salathé *et al.* 2010). Importantly, using coarser  
460 connectivity metrics such as party size or group membership to parameterize infectious disease  
461 models would only capture a fraction of the contact heterogeneity observed in the networks  
462 described here. Our next steps include using Susceptible-Infected-Recovered (SIR) bond  
463 percolation models (Newman 2002; Meyers 2007) to simulate the transmission of various  
464 pathogen types (*e.g.*, respiratory pathogens, STDs) on the observed monthly chimpanzee  
465 networks to assess the effectiveness of different intervention strategies in mitigating epidemics  
466 (such as targeting core-ranging individuals with large families for vaccination). This work is  
467 already underway with results from these simulations showing that respiratory infections starting  
468 in core-ranging adult females and juveniles with large families are likely to generate significantly  
469 larger outbreaks than infections starting in other individuals (J. Rushmore, unpublished data).

470 Our findings are limited by examining a single chimpanzee community, and we  
471 recognize the need for similar analyses at additional field sites to provide a more comprehensive  
472 framework for designing disease management plans. Notably, the association data necessary for  
473 network analyses are likely available in long-term databases for many habituated wild ape  
474 communities. We encourage additional researchers to analyze such association data with a focus  
475 on potential pathogen transmission routes. In conclusion, our findings demonstrate temporal and  
476 inter-individual variation in association patterns for a wild chimpanzee community, and highlight

477 how such behavioral variation could be incorporated into the development of disease  
478 management strategies for an endangered wildlife population.

479

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673

674

675 **Tables**

676 **Table 1.** Effect of social factors on pairwise associations in party networks. The posterior  
 677 mean, 95% credible interval, *P*-value based on MCMC sampling, and odds ratios (OR)  
 678 are shown for fixed effect parameters. Bolded relationships are significant at *P* < 0.05.  
 679 Sex/estrus and age categories are abbreviated as follows: age (adult: adult, AA; adult:  
 680 juvenile, AJ; juvenile: juvenile, JJ), sex/estrus (pairwise combinations of male (M),  
 681 female in estrus (Fe) and female not in estrus (F)).

Factor	Posterior Mean	95% CI	<i>P</i>	OR
<b>Intercept</b>	-3.58	(-4.90, -2.22)	<b>&lt;0.001</b>	
<b>Related</b>	3.01	(2.63, 3.39)	<b>&lt;0.001</b>	20.20
Sex (M:F)	0.73	(-0.11, 1.57)	0.087	2.07
Sex (M:M)	1.30	(-0.38, 2.92)	0.119	3.67
<b>Sex (F:Fe)</b>	1.76	(1.24, 2.28)	<b>&lt;0.001</b>	5.83
<b>Sex (M:Fe)</b>	2.67	(1.72, 3.65)	<b>&lt;0.001</b>	14.44
<b>Difference in family size</b>	-0.13	(-0.20, -0.06)	<b>&lt;0.001</b>	0.88
<b>Difference in rank</b>	-1.04	(-1.21, -0.86)	<b>&lt;0.001</b>	0.35
Age (AJ)	0.69	(-0.23, 1.55)	0.125	1.99
Age (JJ)	1.16	(-0.59, 2.92)	0.191	3.18
<b>Number (#) of estrous females</b>	0.98	(0.84, 1.12)	<b>&lt;0.001</b>	2.65
<b># of estrous females:Age (AJ)</b>	-0.22	(-0.40, -0.02)	<b>0.025</b>	2.14
<b># of estrous females:Age (JJ)</b>	-0.44	(-0.72, -0.16)	<b>0.003</b>	1.70

682 **Table 2.** Effect of social factors on party and 5m-association network centrality measures. Coefficients ( $\beta$ ) and  $P$ -values are presented.  
683  $P$ -values for rank post-hoc significance tests are in Table S6. Coefficients and  $P$ -values for month parameters are presented in Table  
684 S7. Bolded values indicate significant relationships after Bonferroni correction.  $R^2$  values are shown for each test.

685

	Party association networks, N=294						5m association networks, N=294					
	Degree		Eigenvector		Flow-betweenness		Degree		Eigenvector		Flow-betweenness	
	$\beta$	$P$	$\beta$	$P$	$\beta$	$P$	$\beta$	$P$	$\beta$	$P$	$\beta$	$P$
Intercept	17.36	<b>&lt;0.001</b>	0.17	0.269	33.41	0.058	1.35	0.096	0.13	0.324	35.52	0.109
Rank: M2	-1.43	0.108	-0.03	0.052	-1.41	0.212	-0.23	0.153	-0.04	0.085	-0.75	0.449
Rank: M3	-1.54	0.112	-0.02	0.078	-2.11	0.135	-0.65	<b>0.004</b>	-0.05	0.028	-0.15	0.496
Rank: F1	-1.19	0.150	-0.01	0.230	-3.51	0.023	-0.18	0.209	-0.02	0.271	-5.08	0.163
Rank: J1	-0.82	0.253	0.00	0.389	-3.74	0.019	-0.28	0.112	-0.02	0.221	-3.49	0.255
Rank: F2	-5.30	<b>&lt;0.001</b>	-0.09	<b>&lt;0.001</b>	-6.91	<b>&lt;0.001</b>	-1.20	<b>&lt;0.001</b>	-0.12	<b>&lt;0.001</b>	-7.43	0.074
Rank: J2	-4.47	<b>&lt;0.001</b>	-0.08	<b>&lt;0.001</b>	-5.82	<b>0.002</b>	-1.13	<b>&lt;0.001</b>	-0.13	<b>&lt;0.001</b>	1.57	0.389
Estrus	0.85	0.324	0.01	0.404	0.24	0.443	0.30	0.204	0.05	0.102	3.72	0.272
Family size	0.73	<b>0.008</b>	0.01	<b>&lt;0.001</b>	0.57	0.114	0.18	<b>0.001</b>	0.02	<b>0.001</b>	-0.50	0.356
$R^2$	0.618	<b>&lt;0.001</b>	0.347	<b>&lt;0.001</b>	0.195	<b>&lt;0.001</b>	0.406	<b>&lt;0.001</b>	0.251	<b>&lt;0.001</b>	0.037	0.835

686 **Figure Legends**

687 **Figure 1.** Monthly party association networks for a month with a) no estrous females (Jan), b) one estrous female (Jun), and c) two  
688 estrous females (Aug). Nodes (circles) represent individual chimpanzees ( $N = 37$ ) and edges (lines) represent observed associations,  
689 where edge thickness corresponds to the pairwise party association indices (PAIs). All networks are displayed with identical layouts  
690 and only edges with PAIs  $> 0.35$  are shown. Dark red nodes have at least one edge above the PAI cutoff whereas light red nodes do  
691 not have any edges above the PAI cutoff. All nine monthly party association networks are shown in Fig. S2.

692

693 **Figure 2.** Density of monthly party networks (blue solid line) and 5m-networks (red dashed line) with standard error bars. The inset  
694 shows that there is no significant relationship between monthly party network density and monthly 5m-network density (Spearman  
695 Rank Test:  $\rho = -0.4$ ,  $P = 0.291$ ). Circled numbers show the number of estrous females in each month.

696

697 **Figure 3.** Estimated effect of estrous events on pairwise party associations. Model estimates of average association indices are shown  
698 for the three age-pair combinations with 95% credible intervals. The x-axis shows the number of females in estrus for a given month.  
699 Age combinations of adult-adult, adult-juvenile, and juvenile-juvenile pairs are represented by squares, circles, and triangles

700 respectively. Figure estimates were calculated from the MCMC posterior distributions, while holding the presented parameters  
701 constant and allowing all other parameters to range across their possible values.

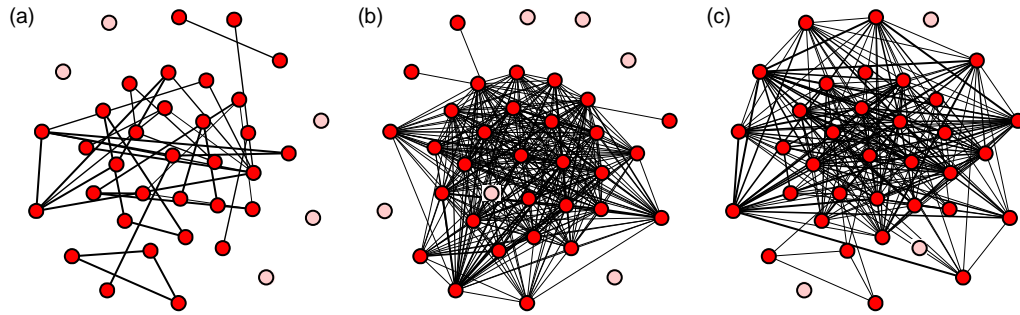
702

703 **Figure 4.**

704 Estimated effects of rank and family size on average degree for (a) party and (b) 5m-networks. There was a significant positive  
705 relationship between an individual's family size and degree centrality. Black, white, and cross-symbol circles represent model  
706 estimates for individuals with family sizes of one, three, and four members respectively (by definition of family unit, adult male ranks  
707 are only presented with a family size of one). Letters on plots show which rank categories were significantly different (where overlap  
708 in letters between two rank categories indicates no significant difference after Bonferroni correction), after controlling for family size  
709 and estrus.

710 **Figures**

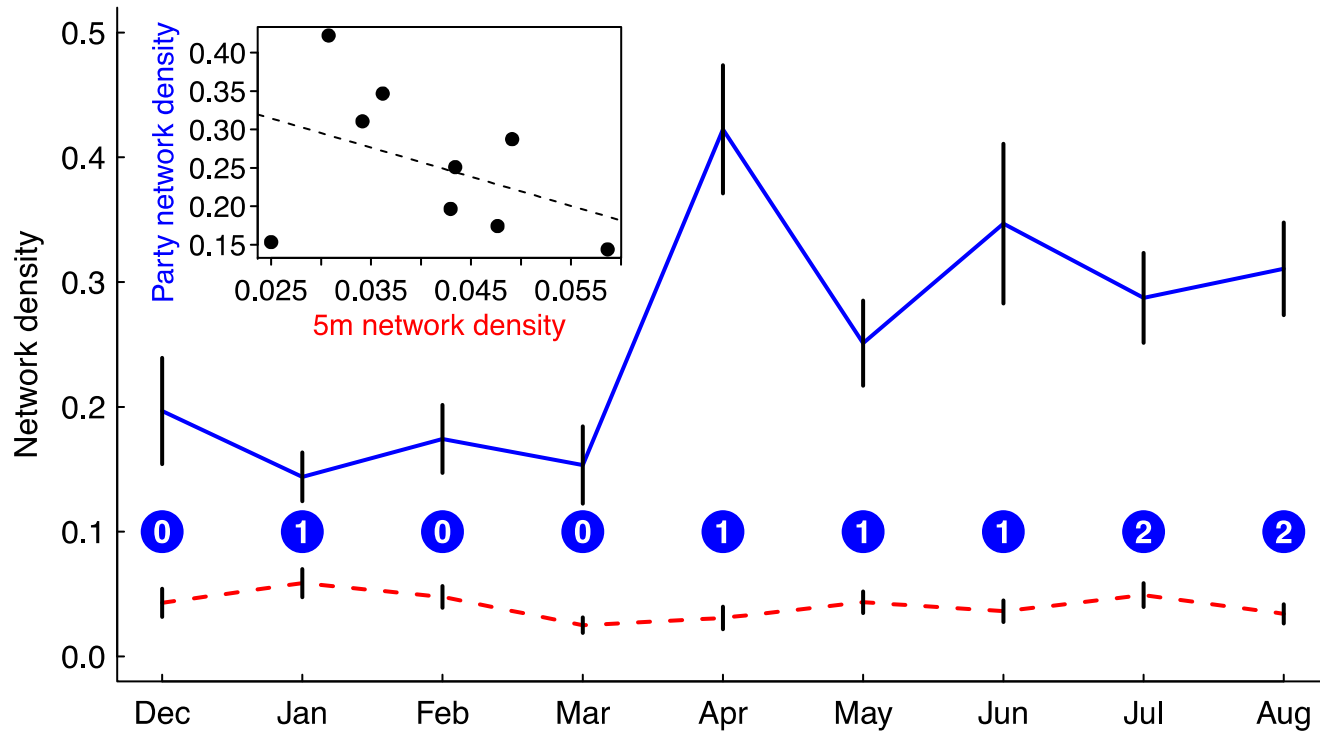
711 **Figure 1.**



712

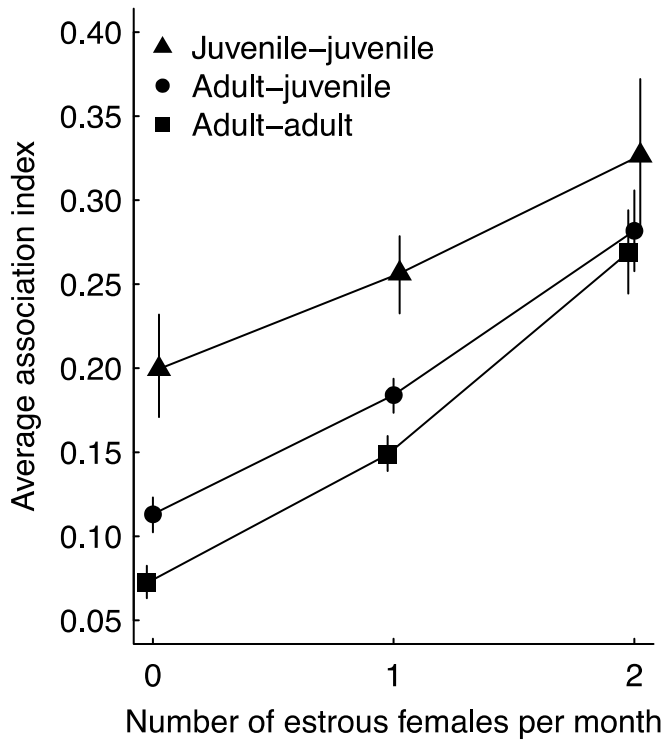


713 **Figure 2.**



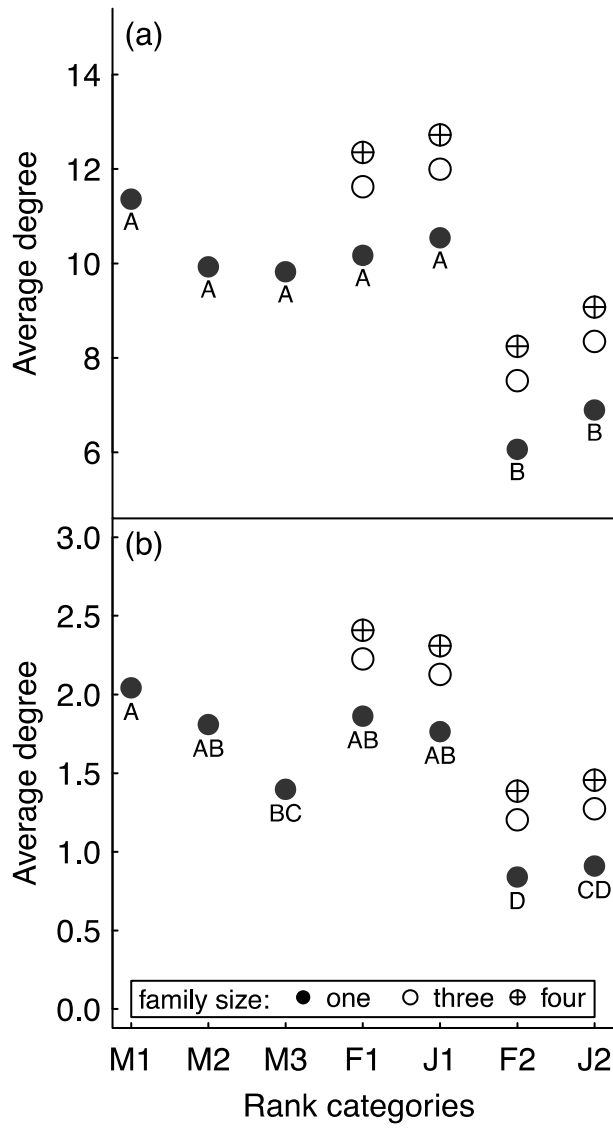
714

715 **Figure 3.**



716

717 **Figure 4.**



718

719 **Supporting Information**

720 The following Supporting Information is available for this article online:

721 Appendix S1: Additional information on the Kanyawara chimpanzee community

722 Appendix S2: Rank categorization of study subjects

723 Appendix S3: Supplementary information on statistical analyses

724 Appendix S4: Discussion of how fruit availability or presence of sick chimpanzees might  
725 affect network structure

726 Table S1. Stability of networks across two-week to month time steps

727 Table S2. Effect of social factors on pairwise associations (PAIs) in party networks using  
728 two-week time steps

729 Table S3. Effect of social factors on party and 5m-association network centrality  
730 measures using two-week time steps

731 Table S4. Individual trait data for study subjects (N = 37)

732 Table S5. Effect of social factors on within-party association indices (WPAIs) with best-  
733 fit model using monthly time steps

734 Table S6. P-values for post-hoc tests of rank and centrality in party and 5m-association  
735 networks

736 Table S7. Effect of social factors on party and 5m-association network centrality  
737 measures (full table)

738 Figure S1. Histogram of observation effort across individuals

739 Figure S2. Monthly party association networks

740 Figure S3. Stability of party association networks over time

741 Figure S4. Monthly 5m association networks

- 742 Figure S5. Overall degree distributions of all individuals ( $N = 37$ ) across all study months
- 743 Figure S6. Degree distributions for all individuals ( $N = 37$ ) broken down by month
- 744 Figure S7. Degree distributions for observed individuals broken down by month
- 745 Figure S8. Goodness of fit for monthly party and within-party association models
- 746 Figure S9. Estimated effects of rank and family size on centrality measures