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

J. Rushmore*, D. Caillaudb, L. Matambac, R. M. Stumpfd, S. P. Borgattié, and S. Altizera

a Odum School of Ecology, University of Georgia, Athens, GA 30602, USA
b Section of Integrative Biology, The University of Texas at Austin, Austin, TX 78712, USA
c Department of Mathematics, University of Georgia, Athens, GA 30602, USA
d Department of Anthropology, University of Illinois at Urbana-Champaign, Urbana, IL 61801
e Department of Management, University of Kentucky, Lexington, KY 40506, USA

*Corresponding author: rushmore@uga.edu
Summary

1. Heterogeneity in host association patterns can alter pathogen transmission and strategies for control. Great apes are highly social and endangered animals that have experienced substantial population declines from directly transmitted pathogens; as such, network approaches to quantify contact heterogeneity could be crucially important for predicting infection probability and outbreak size following pathogen introduction, especially owing to challenges in collecting real-time infection data for endangered wildlife.

2. We present here the first study using network analysis to quantify contact heterogeneity in wild apes, with applications for predicting community-wide infectious disease risk. Specifically, within a wild chimpanzee community, we ask how associations between individuals vary over time, and we identify traits of highly connected individuals that might contribute disproportionately to pathogen spread.

3. We used field observations of behavioral encounters in a habituated wild chimpanzee community in Kibale Forest, Uganda to construct monthly party-level (i.e., subgroup) and close-contact (i.e., ≤ 5m) association networks over a nine-month period.

4. Network analysis revealed that networks were highly dynamic over time. In particular, estrus events significantly increased pairwise party associations, suggesting that community-wide disease outbreaks should be more likely to occur when many females are in estrus.

5. Bayesian mixed-effects models and permutation tests identified traits of chimpanzees that were highly connected within the network. Individuals with large families (i.e., mothers and their juveniles) that range in the core of the community territory and to a lesser extent high-ranking males were central to association networks, and thus represent the most important individuals to target for disease intervention strategies.
Overall, we show striking temporal variation in network structure and traits that predict association patterns in a wild chimpanzee community. These empirically-derived networks can inform dynamic models of pathogen transmission and have practical applications for infectious disease management of endangered wildlife species.

**Key words**

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

Many pathogens spread through host populations via social interactions (Altizer et al. 2003); thus, knowledge of a community’s social system and contact structure can provide crucial information for predicting infectious disease outbreaks (e.g., Nunn et al. 2008; Drewe 2010; Griffin & Nunn 2012). Inter-individual contacts that lead to pathogen transmission can be represented using networks, where each node represents an individual, and edges between nodes represent interactions that allow for pathogen transmission. Contact networks for humans and animals are often heterogeneous (e.g., dolphins: Lusseau 2003; humans: Schneeberger et al. 2004; marmots: Wey & Blumstein 2010), which violates the common assumption of many basic epidemiological models that contacts are random and individuals are well mixed (Anderson & May 1991). Network analysis provides a feasible (albeit data intensive) approach to mathematically formalize transmission pathways and host contact variation (Newman 2010). Further, network analysis can identify potential superspreaders, individuals with disproportionately high contact levels, that could be targeted for vaccination, treatment, or isolation (Lloyd-Smith et al. 2005). Studies of human contact networks often detect heterogeneity and the presence of superspreaders, which has been extremely influential in our understanding of transmission dynamics for SARS and HIV/AIDS (Anderson, Gupta & Ng 1990; Lloyd-Smith et al. 2005; Meyers et al. 2005). Superspreaders have also been identified in a few wildlife populations (e.g., possums: Porphyre et al. 2008; deer mice: Clay et al. 2009); however, network analysis is rarely used to investigate the epidemiology and control of wildlife diseases (Craft & Caillaud 2011). Here we present the first study to analyze empirical wild chimpanzee contact networks within a framework of predicting implications for infectious disease risk.
Endangered wild ape populations have recently experienced outbreaks of Ebola, measles and respiratory viruses, making infectious disease a major threat to their survival (Ryan & Walsh 2011), in part owing to the risk of pathogen spillover from humans to wild apes (Kaur et al. 2008; Köndgen et al. 2008). Thus, given the push to habituate wild apes for tourism across more than 15 African sites (Muehlenbein & Ancrenaz 2009), infectious disease risks for apes will likely continue or escalate. Respiratory diseases in particular have resulted in outbreaks with up to 25% community-level mortality at several long-term chimpanzee research sites (Ryan & Walsh 2011). With low birth rates and late reproductive maturity, ape populations can take decades to recover in size after an outbreak. For example, using mathematical models and a range of parameters derived from published ape epidemics (i.e., mortality rates of 4-25%), Ryan and Walsh (2011) estimated that a mountain gorilla population would require 5-32 years to recover following an outbreak of respiratory disease. In accordance with these predictions, a Tanzanian chimpanzee community took 15 years to return to its pre-epidemic population size after a 1987 respiratory disease outbreak (Williams et al. 2008).

In addition to the detrimental impact that pathogens can have on endangered apes, obtaining real-time infection data for wildlife is notoriously difficult. Collecting biological samples often requires risky interventions including darting and possibly anesthetizing immune-challenged individuals. Furthermore, the speed with which respiratory pathogens typically spread through ape communities (e.g., with a duration of roughly two weeks to two months: Hanamura et al. 2008; Williams et al. 2008; Köndgen et al. 2010) can limit researchers’ abilities to collect comprehensive health data during an outbreak. Given these challenges, parameterizing realistic epidemiological models with association data (e.g., Davis et al. 2008; Hamede et al. 2011) is essential for developing strategies to reduce the risk and impact of infectious diseases. An
underlying assumption of these models is that network edges truly represent possible pathogen transmission routes. Indeed, while relatively few wildlife studies have both host infection and host association data, there is a growing body of evidence that wildlife social networks strongly predict individual infection status (Otterstatter & Thomson 2007; Leu, Kappeler & Bull 2010; Bull, Godfrey & Gordon 2012) and that highly connected individuals tend to have greater parasite burdens than less connected individuals (Corner, Pfeiffer & Morris 2003; Godfrey et al. 2009; Leu, Kappeler & Bull 2010; but see: Otterstatter & Thomson 2007).

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

In this study, we use network analysis to examine association patterns among individuals in a community of wild chimpanzees at Kibale National Park, Uganda. In particular, we quantify how association patterns that represent potential pathogen transmission routes vary over time, in
response to factors such as fruit availability or the number of estrous females. We also examine individual traits that contribute to high levels of association, and predict that high-ranking males and estrous females will have disproportionately high levels of association with community members owing to increased rates of grooming and mating (e.g., Goodall 1986; Emery Thompson & Wrangham 2008). Importantly, investigating the dynamics and drivers of contact variation in wild apes is a necessary step for simulating pathogen spread and evaluating the success of much needed disease intervention strategies for this highly threatened primate clade.

Materials and Methods

Study site and population

We studied the habituated wild Kanyawara chimpanzee community at Kibale National Park (0°34′N, 30°21′E) in Uganda. The site is dominated by moist deciduous forest interspersed with secondary forest, grassland, and swamp (Chapman & Wrangham 1993). Weather data for the site were provided by C. Chapman. Further details on the ecology of Kibale are discussed in Struhsaker (1997). The Kanywara chimpanzee community occupies roughly 37.8 km² of forest (Wilson, Hauser & Wrangham 2001), and during the time of the study the community included 48 chimpanzees with 12 adult males (aged > 14), 14 adult females (aged > 13), 9 immature males and 6 immature females (aged between 5-14 and 5-13 respectively; hereafter referred to as juveniles), and 7 dependent offspring (aged ≤ 4). For additional information on the Kanyawara community, see Supporting Information (Appendix S1).

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

Estimating association indices

We calculated monthly pairwise association indices between individuals at two spatial scales: (i) party-level association indices were based on the frequency of monthly co-occurrence in the same party, and (ii) close contact association indices (i.e., within-party and overall 5m-associations, described below) were based on the frequency with which two individuals were seen within 5m of each other during a given month. We examined associations at the party-level as a proxy for the transmission of pathogens spread by non-close contact (e.g., via fomites,
aerosol transmission, or fecal-oral routes). To estimate party-level associations, we calculated a monthly ‘twice weight index’ (Cairns & Schwager 1987), hereafter referred to as a monthly party association index (PAI), from party membership scans. This parameter calculates the ratio of scans in which chimpanzees A and B were observed in the same party relative to the total number of scans in which either A or B was observed in any party as follows:

\[
PAI_{AB} = \frac{S_{AB}}{S_A + S_B + S_{AB}}
\]  

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

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

\[
WPAI_{AB} = \frac{S_{AB5}}{S_{AB}}
\]  

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

\[
5mAI = PAI_{AB} \times WPAI_{AB}
\]
Thus, this index estimates the overall proportion of time that individuals A and B were within a 5m distance.

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

**Visualizing networks**

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

**Individual trait data**

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

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

Monthly changes in network density

To compare PAIs and 5mAIs over time, we calculated monthly network density as the sum of the network’s observed edge weights divided by the sum of the maximum possible edge weights (Hanneman & Riddle 2005). To examine how stable party and 5m-networks were over
time, we assessed correlations between monthly association index matrices using a quadratic assignment procedure (see Appendix S3 for details) in UCI\textsc{net} version 6.343 (Borgatti, Everett & Freeman 2002).

\textit{Analyses of pairwise associations}

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

We also included two key parameters that could affect associations over time. First, we included a parameter for the number of parous estrous females observed during each month, as males prefer mating with parous over nulliparous females (Muller, Thompson & Wrangham 2006). Additionally, research at some sites shows that increased fruit availability is linked to larger parties (\textit{e.g.}, Wrangham 2000). We did not have fruit abundance data; however, we
included parameters for the monthly presence/absence of preferred ripe fruit species (*Mimusops bagshawei*, *Pseudospondias microcarpa*, *Uvariopsis congensis*) (Wrangham *et al.* 1996) according to our focal data (as eating of preferred fruits is strongly associated with fruit availability for Kanyawara chimpanzees: Wrangham *et al.* 1991), along with a parameter for the mean daily rainfall from two months prior, which we considered to be a proxy for current fruit availability.

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

**Individual traits associated with network centrality**

To identify individual traits associated with increased contact, we used UCINET to calculate three weighted network centrality measures for each chimpanzee: degree, eigenvector, and flow-betweenness. Weighted degree centrality (hereafter referred to as degree) for each node is the sum of the node’s edge weights (Newman 2010). Eigenvector centrality is based on an individual’s connectedness and the connectedness of an individual’s associates, where an individual with high eigenvector centrality is connected to well-connected associates (Newman 2010). Lastly, flow-betweenness centrality is defined as the proportion of times an individual lies
along the shortest path between pairs in the network (Freeman, Borgatti & White 1991). Previous theoretical and empirical work in human and wildlife systems has shown that individuals with high degree, eigenvector, or flow-betweenness centrality are more likely to contract and transmit pathogens than individuals with low centrality (e.g., Corner, Pfeiffer & Morris 2003; Salathé et al. 2010).

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

Results

Association patterns and social network descriptions

On average, each chimpanzee was followed as a focal subject for 27.79 (± 3.6) hours (Fig. S1), comprising a total of 1028 focal observation hours and 4114 15-min scans for all individuals combined. Our analysis included 306,212 pairwise party associations and 14,673 pairwise 5m-associations over the nine month period. When averaged across months and
individuals, randomly selected chimpanzee pairs were observed associating at the party-level approximately 26% of the time (mean PAI: 0.255, range: 0.0-1.0, SE: 0.003) and at the 5m-level 4% of the time (mean 5mAI: 0.041, range: 0.0-1.0, SE: 0.001). Three parous females came into estrous at different points in the study; the number of estrous females per month was low (range: 0-2) owing to a high proportion of lactating females in the study population.

Monthly party networks were dynamic over time (Figs 1-2, S2-S3) and network density ranged from 0.14 (Jan) to 0.42 (Apr). Party networks for consecutive months were highly correlated (Fig. S3), but correlation coefficients decayed as the time lag increased, indicating that party networks were locally stable within 2-3 month periods but were dynamic on a longer time scale. The 5m-network density ranged from 0.03 (Mar) to 0.06 (Jan) (Figs 2, S4). There was no significant relationship between monthly party network density and monthly 5m-network density ($R^2 = 0.17, P = 0.270$; Fig. 2 inset). Variance-to-mean ratios of total edge weights per individual (i.e., weighted degree centrality) for party and 5m-networks were relatively low across months (party network: 3.52, 5m-network: 0.73; Fig. S5), and while monthly party networks were significantly more aggregated than 5m-networks ($t_{8.3} = 4.38, P = 0.002$), degree distributions indicated that networks were not highly aggregated at either scale (Figs S6-S7).

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

The number of estrous females in a given month significantly increased pairwise associations at the party-level, where for each additional estrous female, the odds of a pair associating were roughly twice as high (Table 1, Fig. 3). There was a significant interaction between the number of estrous females and age, such that adult-adult pairs experienced the largest increase in associations as the number of females in estrus increased. Similarly, of all the
pairwise sex combinations, pairs that included one estrous female associated the most frequently. The odds of related pairs being in a party together were over 20 times greater than the odds for unrelated pairs, and chimpanzees were significantly more likely to associate with individuals of their own rank category. Family size difference negatively affected association indices, indicating that individuals with large families (i.e., 3-4 members, Table S4) tended to associate with other large families, and individuals without family units tended to associate with each other (Table 1).

The final model for pairwise party associations included random effects of chimpanzee ID and pair ID. Month was not included as a fixed or random effect, as the number of estrous females per month was a better predictor of monthly pairwise associations than month per se, based on the relative deviance information criterion, DIC (ΔDIC > 50). Rainfall lag and fruit availability parameters were removed because their exclusion increased model fit (rainfall: ΔDIC > 30, fruit: ΔDIC > 20, see Appendix 4 for discussion of fruit availability and network structure). The final model had R² values that ranged from 0.32-0.58 for the amount of variation explained in each of the monthly networks, with the exception of August (R² = 0.07; Fig. S8).

Results for 5mAIs were similar to the party-level results, although several variables in the 5m-model were significant in some but not all months (Table S5). A major difference between these two levels of association was that pairs including an estrous female were often less likely to associate within 5m (as compared to pairs including an estrous female being more likely to associate at the party-level). As a second key difference, month was included as a fixed effect variable that interacted with every other fixed effect variable (age, sex/estrus, relatedness, family size difference, rank category difference), allowing the coefficients of these variables to vary for each monthly network (Table S5). While more challenging to interpret, this final model fitted the
data much better than the model including month as a random (and hence, additive) effect ($\Delta$ DIC $> 100$), or excluding month and including the number of estrous females to describe monthly change ($\Delta$ DIC $> 350$). This indicates that the number of estrous females was not as good of a predictor for 5m-associations as it was for party associations. The incorporation of month as a fixed effect precluded testing temporal variables (i.e., fruit availability, rainfall, and number of estrous females per month). Monthly $R^2$ values for the final 5m-association model ranged between 0.18-0.53 (mean: 0.34; Fig. S8).

Predictors of individual centrality

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

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

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

Discussion

Association patterns and insights for disease transmission

Our results demonstrate inter-individual and temporal variation in association patterns of
wild chimpanzees, which should have profound effects on pathogen transmission dynamics. A
main advantage of network analysis over more traditional connectivity measures, such as party
size, is that network analysis explicitly quantifies how connectivity varies in relation to
demographic and behavioral traits, and among individuals in a community. Degree distributions
demonstrated that neither party nor 5m-networks were highly aggregated (i.e., most individuals
had moderate centrality as opposed to a few superspreaders accounting for a majority of
contacts); yet certain types of individuals had significantly higher association rates than others.
Adult females and juveniles with large families (i.e., 3-4 family members) were significantly more central than expected by chance in both party and 5m-networks, and individuals in core-ranging families were significantly more central than those in edge-ranging families. Additionally, chimpanzees associated more frequently with related individuals and individuals that had similar family sizes. Thus, it seems that core-ranging chimpanzees with large families associated frequently with family members and also formed what Goodall (1986) referred to as “nursing parties,” where mothers and juveniles of different family units socialize together. Edge-ranging families on the other hand, were nearly always the least central. In fact, the average degree centrality between a core-ranging adult female with a large family and an edge-ranging adult female without any juvenile offspring differed roughly by a factor of 2 in party networks and 2.5 in 5m-networks. Thus, individuals from edge-ranging families were the least likely to contribute to or be affected by disease transmission from a community-level perspective (although peripheral individuals could be exposed to pathogens from other communities or human settlements that overlap with forest edges).

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

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

Contrary to our predictions, estrous females were not significantly more central than expected by chance in party or 5m-networks. This is surprising considering that among party networks, pairs including estrous females had higher levels of association and estrous females significantly increased association patterns across the community. Because a majority of adult females in our study community were nursing infants, the sample size for estrous females was limited (N = 3). Furthermore, one estrous female was frequently absent from the community and was presumed to be engaging in consortships, in which a mating pair travels away from the
community (Goodall 1986). In future studies of centrality with larger samples of estrous females, it may be necessary to develop networks that span shorter time frames (i.e., the length of maximal swelling, or roughly one week), as examining longer time steps includes intervals when the female does not have an estrous swelling and is potentially experiencing lower centrality.

While often overlooked in epidemiological analysis, temporal changes in behavioral interactions can affect the outbreak timing (Altizer et al. 2006), as demonstrated by peaks in measles transmission in children during school sessions (Fine & Clarkson 1982) or by phocine distemper outbreaks coinciding with the haul-out behavior of seals (Swinton et al. 1998).

Chimpanzee pairs were twice as likely to associate and party networks were denser when females were in estrus, suggesting that estrous events represent times of high vulnerability to infectious disease outbreaks. This result confirms findings from long-term field studies showing that chimpanzee party size increases with the number of estrous females (e.g., Wrangham 2000). Notably, there was no significant relationship between party and 5m-network density, and the number of estrous females did not significantly affect 5m-level associations. Thus, our network analyses suggest that the potential risk of outbreaks from pathogens that require very close contact for transmission might not increase with estrous events.

Implications for conservation and infectious disease management

Epidemiological modeling studies in humans have shown that targeting central individuals for control efforts is significantly more effective in mitigating disease than applying control efforts randomly (Lloyd-Smith et al. 2005; Salathé et al. 2010). In a handful of cases, vaccination has been used to reduce the impact of emergent epidemics in endangered wildlife populations (gorilla measles and chimpanzee polio: Woodford, Butynski & Karesh 2002;
Ethiopian wolf rabies: Haydon et al. 2006). Given the detrimental impacts of pathogens on great
ape communities (e.g., Bermejo et al. 2006; Caillaud et al. 2006; Köndgen et al. 2008), some
wildlife biologists have called for vaccinating great apes prophylactically for high-risk pathogens
(Ryan & Walsh 2011). To effectively plan control strategies and minimize human interference,
network models can indicate the minimum number of well-connected individuals that should be
vaccinated to reduce outbreak sizes (as per: Salathé et al. 2010). Importantly, using coarser
connectivity metrics such as party size or group membership to parameterize infectious disease
models would only capture a fraction of the contact heterogeneity observed in the networks
described here. Our next steps include using Susceptible-Infected-Recovered (SIR) bond
percolation models (Newman 2002; Meyers 2007) to simulate the transmission of various
pathogen types (e.g., respiratory pathogens, STDs) on the observed monthly chimpanzee
networks to assess the effectiveness of different intervention strategies in mitigating epidemics
(such as targeting core-ranging individuals with large families for vaccination). This work is
already underway with results from these simulations showing that respiratory infections starting
in core-ranging adult females and juveniles with large families are likely to generate significantly
larger outbreaks than infections starting in other individuals (J. Rushmore, unpublished data).

Our findings are limited by examining a single chimpanzee community, and we
recognize the need for similar analyses at additional field sites to provide a more comprehensive
framework for designing disease management plans. Notably, the association data necessary for
network analyses are likely available in long-term databases for many habituated wild ape
communities. We encourage additional researchers to analyze such association data with a focus
on potential pathogen transmission routes. In conclusion, our findings demonstrate temporal and
inter-individual variation in association patterns for a wild chimpanzee community, and highlight
how such behavioral variation could be incorporated into the development of disease management strategies for an endangered wildlife population.

Acknowledgements

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Table 1. Effect of social factors on pairwise associations in party networks. The posterior mean, 95% credible interval, \(P\)-value based on MCMC sampling, and odds ratios (OR) are shown for fixed effect parameters. Bolded relationships are significant at \(P < 0.05\).

Sex/estrus and age categories are abbreviated as follows: age (adult: adult, AA; adult: juvenile, AJ; juvenile: juvenile, JJ), sex/estrus (pairwise combinations of male (M), female in estrus (Fe) and female not in estrus (F)).

<table>
<thead>
<tr>
<th>Factor</th>
<th>Posterior Mean</th>
<th>95% CI</th>
<th>(P)</th>
<th>OR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-3.58</td>
<td>(-4.90, -2.22)</td>
<td>(&lt;0.001)</td>
<td></td>
</tr>
<tr>
<td>Related</td>
<td>3.01</td>
<td>(2.63, 3.39)</td>
<td>(&lt;0.001)</td>
<td>20.20</td>
</tr>
<tr>
<td>Sex (M:F)</td>
<td>0.73</td>
<td>(-0.11, 1.57)</td>
<td>0.087</td>
<td>2.07</td>
</tr>
<tr>
<td>Sex (M:M)</td>
<td>1.30</td>
<td>(-0.38, 2.92)</td>
<td>0.119</td>
<td>3.67</td>
</tr>
<tr>
<td>Sex (F:Fe)</td>
<td>1.76</td>
<td>(1.24, 2.28)</td>
<td>(&lt;0.001)</td>
<td>5.83</td>
</tr>
<tr>
<td>Sex (M:Fe)</td>
<td>2.67</td>
<td>(1.72, 3.65)</td>
<td>(&lt;0.001)</td>
<td>14.44</td>
</tr>
<tr>
<td>Difference in family size</td>
<td>-0.13</td>
<td>(-0.20, -0.06)</td>
<td>(&lt;0.001)</td>
<td>0.88</td>
</tr>
<tr>
<td>Difference in rank</td>
<td>-1.04</td>
<td>(-1.21, -0.86)</td>
<td>(&lt;0.001)</td>
<td>0.35</td>
</tr>
<tr>
<td>Age (AJ)</td>
<td>0.69</td>
<td>(-0.23, 1.55)</td>
<td>0.125</td>
<td>1.99</td>
</tr>
<tr>
<td>Age (JJ)</td>
<td>1.16</td>
<td>(-0.59, 2.92)</td>
<td>0.191</td>
<td>3.18</td>
</tr>
<tr>
<td>Number (#) of estrous females</td>
<td>0.98</td>
<td>(0.84, 1.12)</td>
<td>(&lt;0.001)</td>
<td>2.65</td>
</tr>
<tr>
<td># of estrous females:Age (AJ)</td>
<td>-0.22</td>
<td>(-0.40, -0.02)</td>
<td>(0.025)</td>
<td>2.14</td>
</tr>
<tr>
<td># of estrous females:Age (JJ)</td>
<td>-0.44</td>
<td>(-0.72, -0.16)</td>
<td>(0.003)</td>
<td>1.70</td>
</tr>
</tbody>
</table>
Table 2. Effect of social factors on party and 5m-association network centrality measures. Coefficients (β) and P-values are presented. P-values for rank post-hoc significance tests are in Table S6. Coefficients and P-values for month parameters are presented in Table S7. Bolded values indicate significant relationships after Bonferroni correction. R² values are shown for each test.

<table>
<thead>
<tr>
<th></th>
<th>Party association networks, N=294</th>
<th>5m association networks, N=294</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Degree</td>
<td>Eigenvector</td>
</tr>
<tr>
<td></td>
<td>β</td>
<td>P</td>
</tr>
<tr>
<td>Intercept</td>
<td>17.36</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Rank: M2</td>
<td>-1.43</td>
<td>0.108</td>
</tr>
<tr>
<td>Rank: M3</td>
<td>-1.54</td>
<td>0.112</td>
</tr>
<tr>
<td>Rank: F1</td>
<td>-1.19</td>
<td>0.150</td>
</tr>
<tr>
<td>Rank: J1</td>
<td>-0.82</td>
<td>0.253</td>
</tr>
<tr>
<td>Rank: J2</td>
<td>-5.30</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Estrus</td>
<td>-4.47</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Family size</td>
<td>0.85</td>
<td>0.324</td>
</tr>
<tr>
<td>R²</td>
<td>0.618</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Figure Legends

Figure 1. Monthly party association networks for a month with a) no estrous females (Jan), b) one estrous female (Jun), and c) two estrous females (Aug). Nodes (circles) represent individual chimpanzees (N = 37) and edges (lines) represent observed associations, where edge thickness corresponds to the pairwise party association indices (PAIs). All networks are displayed with identical layouts 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 not have any edges above the PAI cutoff. All nine monthly party association networks are shown in Fig. S2.

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

Figure 3. Estimated effect of estrous events on pairwise party associations. Model estimates of average association indices are shown for the three age-pair combinations with 95% credible intervals. The x-axis shows the number of females in estrus for a given month. Age combinations of adult-adult, adult-juvenile, and juvenile-juvenile pairs are represented by squares, circles, and triangles.
respectively. Figure estimates were calculated from the MCMC posterior distributions, while holding the presented parameters constant and allowing all other parameters to range across their possible values.

Figure 4.

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

Figure 1.
Figure 3.
Figure 4.
Supporting Information

The following Supporting Information is available for this article online:

Appendix S1: Additional information on the Kanyawara chimpanzee community
Appendix S2: Rank categorization of study subjects
Appendix S3: Supplementary information on statistical analyses
Appendix S4: Discussion of how fruit availability or presence of sick chimpanzees might affect network structure

Table S1. Stability of networks across two-week to month time steps
Table S2. Effect of social factors on pairwise associations (PAIs) in party networks using two-week time steps
Table S3. Effect of social factors on party and 5m-association network centrality measures using two-week time steps
Table S4. Individual trait data for study subjects (N = 37)
Table S5. Effect of social factors on within-party association indices (WPAIs) with best-fit model using monthly time steps
Table S6. P-values for post-hoc tests of rank and centrality in party and 5m-association networks
Table S7. Effect of social factors on party and 5m-association network centrality measures (full table)

Figure S1. Histogram of observation effort across individuals
Figure S2. Monthly party association networks
Figure S3. Stability of party association networks over time
Figure S4. Monthly 5m association networks
Figure S5. Overall degree distributions of all individuals (N = 37) across all study months

Figure S6. Degree distributions for all individuals (N = 37) broken down by month

Figure S7. Degree distributions for observed individuals broken down by month

Figure S8. Goodness of fit for monthly party and within-party association models

Figure S9. Estimated effects of rank and family size on centrality measures