




Gregariousness is associated with parasite species richness in a community of wild chimpanzees

Jessica R. Deere¹ · Kathryn L. Schaber^{2,3} · Steffen Foerster⁴ · Ian C. Gilby⁵ · Joseph T. Feldblum⁶ · Kimberly VanderWaal¹ · Tiffany M. Wolf¹ · Dominic A. Travis¹ · Jane Raphael⁷ · Iddi Lipende⁸ · Deus Mjungu⁹ · Anne E. Pusey⁴ · Elizabeth V. Lonsdorf¹⁰ · Thomas R. Gillespie^{2,3} 

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Abstract

Increased risk of pathogen transmission through proximity and contact is a well-documented cost of sociality. Affiliative social contact, however, is an integral part of primate group life and can benefit health. Despite its importance to the evolution and maintenance of sociality, the tradeoff between costs and benefits of social contact for group-living primate species remains poorly understood. To improve our understanding of this interplay, we used social network analysis to investigate whether contact via association in the same space and/or physical contact measured through grooming were associated with helminth parasite species richness in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). We identified parasite taxa in 381 fecal samples from 36 individuals from the Kasekela community of chimpanzees in Gombe National Park, Tanzania, from November 1, 2006, to October 31, 2012. Over the study period, eight environmentally transmitted helminth taxa were identified. We quantified three network metrics for association and grooming contact, including degree strength, betweenness, and closeness. Our findings suggest that more gregarious individuals—those who spent more time with more individuals in the same space—had higher parasite richness, while the connections in the grooming network were not related to parasite richness. The expected parasite richness in individuals increased by 1.13 taxa (CI: 1.04, 1.22; $p = 0.02$) per one standard deviation increase in degree strength of association contact. The results of this study add to the understanding of the role that different types of social contact play in the parasite richness of group-living social primates.

Significance statement

Parasite infections reveal costs of group living among wild animal populations. We studied the relationship between sociality and parasite transmission by assessing whether variation in social behavior among wild chimpanzees is associated with the number of unique helminth parasites detected in individual fecal samples. Our findings revealed that associating in the same shared space, but not grooming contact, is related to higher parasite richness. These findings improve our understanding of the complex interplay of parasitism and sociality with important implications for parasite transmission patterns in host species with flexible grouping patterns.

Keywords Apes · Contact networks · Fission–fusion social structure · Parasitology · Sociality · Social network analysis

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✉ Thomas R. Gillespie
thomas.gillespie@emory.edu

Extended author information available on the last page of the article

Introduction

Sociality has complex consequences for the health and reproduction of individuals within social groups (Nunn et al. 2015). These effects are often context-specific and variable over time and space. For example, strong social bonds and social integration can have beneficial effects on immune function and neuroendocrine mechanisms (Seeman and McEwen 1996) and can ultimately increase life expectancy and reproductive success (Holt-Lunstad et al. 2010; Ostner

and Schülke 2018; Thompson 2019). However, the potential benefits of social contact may be outweighed by increased risk of parasite transmission, which itself is determined by social structure, demography, and transmission dynamics of the pathogen (Altizer et al. 2003; Griffin and Nunn 2012; Romano et al. 2016). For example, prevalence of parasites generally increases with group size, as has been shown in birds and African bovids (Tella 2002; Ezenwa 2004), but social network structure can mediate within-group variation in infection risk (e.g., giraffe: VanderWaal et al. 2014). Understanding which behaviors relate to parasite infection risk requires knowledge of the factors that mediate exposure and transmission of parasites between hosts.

The dynamics of infectious diseases are often difficult to quantify in wild social groups due to the invasive sampling methods required, the need for continuous monitoring of known individuals, and the acute nature of many infections that would require frequent sampling to detect. Theoretical modeling can provide insights into the causes and consequences of disease transmission within and between social groups (Griffin and Nunn 2012; Romano et al. 2016; Rushmore et al. 2017; Wolf et al. 2019), but requires numerous assumptions about processes that are often poorly understood. Macroparasites, such as gastrointestinal helminths, are relatively more accessible for empirical research than other pathogens because they can be quantified noninvasively in fecal samples collected from individually identified hosts, allowing a continuous assessment of infection status and variation in infection across time and space. Helminth parasites are ubiquitous and often cause chronic, sublethal infections in their hosts. However, evidence suggests that such infections can cause subtle disease, which may influence behavior (Ghai et al. 2015), have negative consequences on reproductive output (Ilmonen et al. 2000; Schwanz 2008a, b; Hillegass et al. 2010), increase susceptibility to other pathogens (Ezenwa et al. 2010), and decrease host survival (Nguyen et al. 2015), thereby shifting life history tradeoffs (Schwanz 2008b).

Despite the relative ease with which intestinal helminthiasis can be assessed, understanding the mechanisms that mediate variation in infection status within and between social groups is challenging. As helminth life cycles generally involve the environment or other organisms (Anderson 2000), ecological factors such as rainfall, temperature, and vegetation cover can directly mediate changes in group-wide parasite prevalence (Larsen and Roepstorff 1999; Vitazkova and Wade 2007; Hernandez et al. 2013; Young et al. 2013). In addition, infection with environmentally transmitted parasites can be mediated by social interactions, both indirectly and directly (Ezenwa 2004; Vanderwaal et al. 2016). Uninfected individuals may be exposed to parasites shed by infectious individuals with which they share the same space (Gear et al. 2013) or become infected through synchronous

exposure to a contaminated environment. Additionally, infection may occur through direct social contact (Hernandez and Sukhdeo 1995; Otterstatter and Thomson 2007), because infective parasite stages can adhere to body parts, such as lice attaching to apes (Reed et al. 2007). Recent evidence suggests that direct contact (e.g., grooming), rather than shared space use alone, can be a primary driver of gastrointestinal parasite infection risk among brown spider monkeys (Rimbach et al. 2015). A study of Japanese macaques also suggests that centrality in grooming networks is positively related to increased infection risk (MacIntosh et al. 2012). While these findings provide insight into the possible effects of contact networks on parasite transmission, patterns are likely to vary across study systems depending on parasite taxa, mode of infection, and patterns of infection risk relating to host ecology and behavior.

Chimpanzee social structure is characterized by high fission–fusion dynamics in which the size and composition of subgroups, known as parties, varies throughout the day due to a combination of factors such as food abundance and distribution, the presence of estrous females, and social relationships (Nishida 1968; Goodall 1986; Boesch and Boesch-Achermann 2000). Chimpanzee parties provide the opportunity to noninvasively study the influence of social contact on patterns of parasitism. Similar to spider monkeys (Rimbach et al. 2015), the high fission–fusion dynamics of chimpanzees (Nishida 1968; Goodall 1986; Boesch and Boesch-Achermann 2000) results in individual variation in the extent of shared space use with others. Where space use overlaps, individuals can engage in variable levels of social contact through grooming (Foerster et al. 2015). In contrast to arboreal spider monkeys, chimpanzees are more terrestrial and should be more likely to encounter infective stages in the environment (i.e., soil). Thus, our goal was to assess whether variation in social behavior among wild chimpanzees (*Pan troglodytes schweinfurthii*) is associated with parasite species richness (hereafter, parasite richness), the number of unique helminth parasite species detected in individual fecal samples. Parasite richness is commonly used as an indicator of disease risk and immune status in primates (Ezenwa 2004; Muehlenbein 2006; Nunn and Altizer 2006; Benavides et al. 2012; MacIntosh et al. 2012; Rimbach et al. 2015). We predicted that contact measured through grooming (hereafter, grooming contact) would have smaller additive influences on individual differences in parasite richness compared to contact measured through party-level association, referred to hereafter as association contact.

We utilized social network analysis (SNA), a method of mapping and measuring contact patterns within a group of individuals (Martínez-López et al. 2009), to examine how social contact influences parasite richness in a wild chimpanzee population. Network centrality metrics are used in SNA to calculate the importance of individual nodes for

transmission as well as potential transmission pathways among nodes within the network (Martínez-López et al. 2009). We used three metrics previously shown to be relevant for parasite transmission (MacIntosh et al. 2012; Godfrey 2013; Gómez et al. 2013; Rimbach et al. 2015): degree strength, betweenness, and closeness. Degree is a measure of the total number of connections that the focal node has in the network (Martínez-López et al. 2009) and degree strength is the summed weight (i.e., frequency or duration) of all adjacent connections for each individual in the network. Betweenness is a measure of the number of times a node is along the shortest path between two other nodes (Martínez-López et al. 2009); nodes with high betweenness may mediate the flow of disease through the network. Closeness is an estimation of how closely connected a node is to all other nodes in the network (Martínez-López et al. 2009) and measures how many steps are required to access every other individual from a given individual. Degree strength is a local metric that represents direct connections with immediate surrounding, local nodes (Silk et al. 2017). In contrast, betweenness and closeness are global metrics that account for indirect, global connections (Silk et al. 2017). We hypothesized that individuals with high centrality values (i.e., degree strength, betweenness, and closeness) would have high exposure to many parasites, and thus have higher parasite richness. Furthermore, because the different metrics lie on a spectrum from local to global, we expected that their relationship with richness may vary.

Methods

Study site

This study investigated parasite richness in contact networks among chimpanzees at Gombe National Park (GNP) (4° 40' S, 29° 38' E), Kigoma District, Tanzania. The park was established in 1968 and is a small (35 km²) forest reserve located on a narrow strip of land between Lake Tanganyika and a rift escarpment that rises from the lakeshore (Pusey et al. 2008). We studied 39 (26 females, 13 males) sexually mature chimpanzees (ranging in age from 12 to 51 years) of the Kasekela study community, who are habituated to humans and are individually identifiable to researchers (Goodall 1986; Wilson 2012). We followed the precedent of previous studies (Goodall 1986; Wallis 2002; Lonsdorf et al. 2011) and divided years into quartile seasons to control for seasonal fluctuations in climate based on rainfall: early wet (November–February), late wet (March–April), early dry (May–July), and late dry (August–October). Seasonality has important implications for chimpanzee behavior and health (e.g., body mass: Pusey et al. 2005; activity budget: Lodwick et al. 2004; party size: Murray et al. 2006;

disease transmission and surveillance: Lonsdorf et al. 2011; Wolf et al. 2019). Our analyses focused on a 6-year period (November 1, 2006,–October 31, 2012). While in the field, researchers follow guidelines to reduce the human-induced disease risk to the chimpanzees (Collins 2003; Gilardi et al. 2015). These include maintaining a minimum viewing distance of 7.5 m and undergoing a quarantine period after arrival to the park.

Behavioral data

As part of ongoing long-term behavioral studies, Tanzanian field research staff conducted full-day focal follows on chimpanzees of the Kasekela community. During these follows, researchers targeted one individual for an entire day and recorded which chimpanzees were present in the focal chimpanzee's party every 15 min. A party was defined as any individual that was present in the group composition scans, which means that the individual was visible to the observer and, presumably, the chimpanzees. Researchers also recorded the direction (giving or receiving), start time, and end time of all grooming bouts involving the focal individual (Wilson 2012). When collecting chimpanzee party and grooming data, researchers recorded the time of arrival and departure of all individuals in the focal group. It was not possible to record data blindly because our study involved focal animals in the field. This study utilized behavioral data collected from 2006 to 2012, when simultaneous parasite data were available, to calculate individual network metrics. Researchers observed individuals an average of 218 ± 154 (mean \pm standard deviation (SD)) hours each season.

We assessed social network metrics for contact measures that quantify the strength of association (i.e., edge weights) among individuals (i.e., nodes). We calculated two indices based on undirected contact networks: (1) association contact, defined as party-level association to estimate shared space use and the potential for environmental transmission of parasites and (2) grooming contact, defined as grooming interactions to estimate the potential for direct transmission of parasites. For association contact, we calculated a Dyadic Association Index (DAI) (Cairns and Schwager 1987). The DAI calculates the proportion of 15-min interval focal follows of two individuals in which they were together in the same party, or:

$$\text{DAI} = \frac{P_{AB}}{P_A + P_B - P_{AB}}$$

where P_{AB} is the number of parties containing both A and B, P_A is the number of parties containing A, and P_B is the number of parties containing B (Gilby and Wrangham 2008). We generated DAI matrices by season across approximately 6 years for all sexually mature individuals for which pairwise association data were available.

For grooming contact, we calculated the grooming rate, defined as the proportion of time two individuals spent grooming with each other when they were both in the same party and one of them was the focal (Machanda et al. 2013; Foerster et al. 2015), or:

$$\text{grooming rate} = \frac{G_{AB}}{F_{AB}}$$

where G_{AB} is time spent grooming when either A or B was the recipient and F_{AB} is time together when A or B was the focal individual and the other was present in the party. We calculated grooming rates of focal individual grooming for each season. Similar to association contact, we analyzed grooming networks by season from years 2006–2012.

We conducted all network analyses and plots using the *igraph* package (Csárdi and Nepusz 2006) in R version 4.0.2 (R Core Team 2020). For each individual in each season, we calculated three metrics: degree strength, betweenness, and closeness. Rather than estimating each metric based on whether or not individuals were associated with every other group member (i.e., yes or no) in a given time period, we weighted all metrics based on the respective network measures (DAI or grooming rate).

Fecal sample collection and processing

During the study period, we screened a total of 381 freshly voided fecal samples. Field researchers collected an average of 2.5 ± 1.5 (mean \pm SD) from each individual per season (range: 1–7). Researchers added feces to Para-Pak® containers (Meridian Bioscience, Cleveland, OH) prefilled with 15 ml of 10% formalin fixative, up to a pre-marked fill line. Care was taken to avoid collecting soil, foliage, or standing water contaminants. Researchers sealed sample tubes with Parafilm® (Pechiney Plastic Packaging, Chicago, IL), shook tubes thoroughly, and then stored tubes until lab processing. We recovered helminth eggs and larvae via sodium nitrate floatation and fecal sedimentation as described in Gillespie (2006). If needed, we added one drop of Lugol's iodine solution to aid in identification. We identified parasites on the basis of egg or larvae coloration, shape, contents, and size. Researchers measured representatives of each taxon to the nearest 0.1 μm with an ocular micrometer at $\times 400$ magnification and photographed for later examination.

Over the study period, we identified a total of eight helminth taxa known to be environmentally transmitted (see Table 1 for prevalence across taxa): *Ascaris* sp., *Necator* sp., *Oesophagostomum* sp., *Strongyloides fulleborni*, *Trichostrongylus* sp., and *Trichuris* sp. An additional species of recovered nematode, *Probstymayria gombensis*, has an unknown transmission pathway but larvae present in feces are likely infective (File et al. 1976). An unknown strongyle

Table 1 Mean seasonal prevalence of intestinal helminth taxa recorded from sexually mature chimpanzees in Gombe National Park, Tanzania, from November 1, 2006, to October 31, 2012

Parasite taxon	Prevalence (%)
<i>Oesophagostomum</i>	95.8
<i>Strongyloides</i>	53.3
<i>Necator</i>	36.5
<i>Probstymayria</i>	13.4
<i>Trichostrongylus</i>	12.3
<i>Trichuris</i>	8.4
Unknown strongyle	6.0
<i>Ascaris</i>	4.7

was also included in the count of environmentally transmitted helminths. We included helminths known to be environmentally transmitted because they have the potential to be transmitted through social contact as well. We excluded one unknown egg because of the uncertain nature of identification, as well as three taxa that are known to require intermediate hosts for transmission: *Physaloptera*, *Mammomonogamus*, and an unknown fluke.

Statistical analysis

We conducted all analyses in R version 4.0.2 (R Core Team 2020). We aggregated parasite presence/absence data per individual per season by counting presence of a parasite taxon in any sample collected during a given season as an infection with that taxon for the length of the season. We assessed the relationship between individual seasonal parasite richness and social contact using generalized linear mixed models in the *glmmTMB* package (Brooks et al. 2017), with a Conway-Maxwell-Poisson distribution and log-link function (Brooks et al. 2019). Before models were fit, we conducted an exploratory analysis to check model assumptions and find the best-fit distribution. We detected under-dispersion in Poisson and negative binomial models, so we used a Conway-Maxwell-Poisson distribution (Brooks et al. 2019), which can handle both overdispersion and under-dispersion (Lynch et al. 2014). Allowing for zero-inflation improved the fit of the models; thus, we included a zero-inflation term in all final models. All models included a network metric (i.e., degree strength, betweenness, or closeness) for each network (association and grooming), age (in years), sex, and season (i.e., early wet, late wet, early dry, or late dry) as fixed effects. The number of fecal samples collected from a given individual in a given season was also included as a fixed effect to control for the influence of sample size on accumulative parasite richness. Additionally, the total time (in minutes) each individual was observed each season was included as a fixed effect to control for uneven

season lengths. Chimpanzee ID was included as a random effect to control for repeated and uneven sampling among individuals. All numeric variables were scaled (also known as z-scoring) across the entire dataset by taking the difference from the mean and dividing by the standard deviation. Each metric was included one at a time alongside the above predictors. Models 1–3 represent degree strength, betweenness, and closeness based on association and grooming contact.

We performed model diagnostics on all models in the *DHARMA* (Hartig 2020) and *performance* (Lüdtke et al. 2020) packages. The final models showed no evidence of over- or under-dispersion, and there were no significant problems detected in the model predictions versus standardized residuals. As grooming contact is nested within association contact (if chimpanzees groom one another, they are also together in the same party), we checked covariates for multicollinearity. Season showed moderate collinearity in the strength and closeness models (variance inflation factors = 5.48 and 5.99, respectively), but remained in the models because there was little change in coefficients when they were removed. We saw no other issues with multicollinearity in any of the models. We provided model diagnostic plots in the supplemental information. Additionally, since males and females can differ in their level of gregariousness (Murray et al. 2007), we checked for significance of an interaction term between sex and network metrics. We also checked for significance of an interaction term between season and network metrics. These terms were not significant and were not used in any of the final models. The non-independence of social network data violates assumptions of GLMMs; therefore, we based *p*-values on a permutation-based approach where the observed slope coefficients were compared with 1000 coefficients derived from randomized richness networks (i.e., networks in which the richness for individuals was randomized), to ensure that our empirical observations differed significantly from what would be expected if the

identity of infected individuals was random (Farine 2017; Weiss et al. 2020). *P*-values were calculated as the proportion of permutations where the observed slope coefficients were more extreme than the random slope coefficients. To confirm 1000 was a sufficient number of randomizations, we randomly subsampled from the distribution (from 100 to 1000 subsamples) and confirmed that the mean and distribution of the coefficients were stable by iteration 1000. These permuted *p*-values were used to determine significance.

Data availability

The datasets generated and analyzed during the current study are included in the supplemental information. The R scripts used in the current study are available from the corresponding author on request.

Results

Seasonal prevalence of helminths varied by taxa, ranging from 4.7 to 95.8% (Table 1). Overall, parasite richness was variable across seasons and ranged from zero to six taxa per individual across the study period, with a mean (\pm SD) of 2.3 ± 1.1 ($N=381$). Richness was fairly consistent across seasons, with a mean (\pm SD) richness of 2.7 ± 1.2 in the early wet ($N=93$), 1.9 ± 0.9 in the late wet ($N=86$), 2.1 ± 1.0 in the early dry ($N=97$), and 2.5 ± 1.0 in the late dry ($N=105$) seasons. Figure 1 depicts example networks of association (Fig. 1a) and grooming (Fig. 1b) contact during the late dry season (August–October) of 2008, when parasite richness ranged from 0 to 6 taxa per individual. Figure 2 exhibits example networks of association (Fig. 2a) and grooming (Fig. 2b) contact during the late wet season (March–April) of 2008, when parasite richness was less variable (and lower), ranging from 1 to 4 taxa per individual.

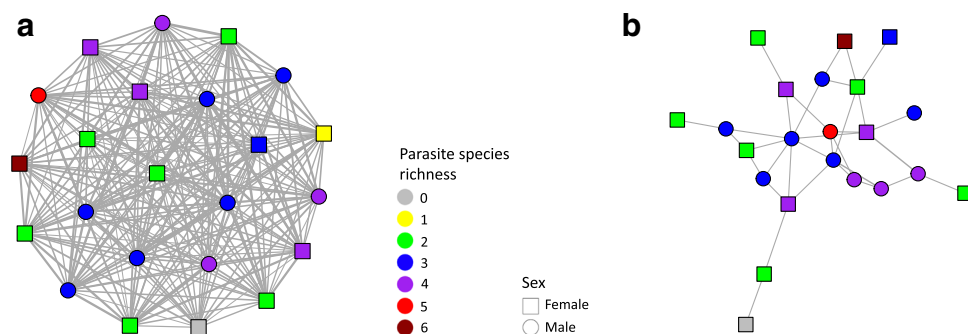


Fig. 1 **a** Association contact and **b** grooming contact network plots during a season with variable parasite species richness (0–6). Networks represent the late dry season (August–October) of 2008 for sexually mature chimpanzees of the Kasakela community in Gombe

National Park, Tanzania. Each node (depicted as male or female) represents an individual chimpanzee. The nodes are colored by parasite species richness. The thicker the edges, the stronger the connection between chimpanzees

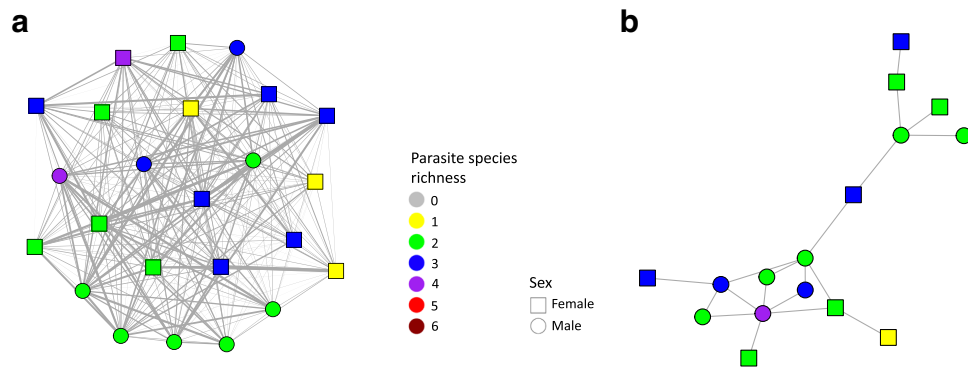


Fig. 2 **a** Association contact and **b** grooming contact network plots during a season with less variable parasite species richness (1–4). Networks represent the late wet season (March–April) of 2008 for sexually mature chimpanzees of the Kasakela community in Gombe

National Park, Tanzania. Each node (depicted as male or female) represents an individual chimpanzee. The nodes are colored by parasite species richness. The thicker the edges, the stronger the connection between chimpanzees

We assessed whether association contact measured by shared environmental exposure of individuals within a party or contact measured by grooming was associated with gastrointestinal parasite richness. Degree strength from association contact was significantly associated with parasite richness (Table 2). An individual’s parasite richness increased by 1.13 taxa (CI: 1.039, 1.218;

$p = 0.017$) per one standard deviation change in degree strength of association contact. After accounting for party-level association, grooming did not significantly explain additional variation in richness (Table 2). Betweenness and closeness did not play a significant role in the relationship between parasite richness and contact networks (Tables 3 and 4).

Table 2 Results of generalized linear mixed model examining degree strength as a predictor of parasite species richness in contact networks of sexually mature chimpanzees in Gombe National Park, Tanzania. An asterisk indicates a significant p -value (<0.05)

Fixed effect	Effect estimate	Exp (effect estimate) (confidence interval)	Permuted p
Association contact	0.118	1.125 (1.039, 1.218)	0.017*
Grooming contact	-0.045	0.956 (0.909, 1.004)	0.052
Age	-0.074	0.928 (0.866, 0.995)	0.002*
Sample size	0.114	1.184 (1.134, 1.235)	0.000*
Time observed	-0.001	0.999 (0.920, 1.084)	0.485
Sex			
Female	Ref	Ref	Ref
Male	0.087	1.090 (0.937, 1.268)	0.059
Season			
Early wet	Ref	Ref	Ref
Late wet	0.115	1.121 (0.927, 1.356)	0.156
Early dry	0.099	1.104 (0.924, 1.319)	0.187
Late dry	0.110	1.117 (0.979, 1.274)	0.087

Table 3 Results of generalized linear mixed model examining betweenness as a predictor of parasite species richness in contact networks of sexually mature chimpanzees in Gombe National Park, Tanzania. An asterisk indicates a significant p -value (<0.05)

Fixed effect	Effect estimate	Exp (effect estimate) (confidence interval)	Permuted p
Association contact	-0.027	0.973 (0.925, 1.024)	0.174
Grooming contact	-0.004	0.996 (0.955, 1.039)	0.462
Age	-0.074	0.929 (0.866, 0.995)	0.002*
Sample size	0.171	1.186 (1.135, 1.239)	0.000*
Time observed	0.071	1.073 (1.000, 1.152)	0.061
Sex			
Female	Ref	Ref	Ref
Male	0.062	1.064 (0.916, 1.236)	0.132
Season			
Early wet	Ref	Ref	Ref
Late wet	0.055	1.056 (0.878, 1.272)	0.315
Early dry	0.012	1.011 (0.851, 1.202)	0.466
Late dry	0.150	1.161 (1.020, 1.322)	0.031*

Table 4 Results of generalized linear mixed model examining closeness as a predictor of parasite species richness in contact networks of sexually mature chimpanzees in Gombe National Park, Tanzania. An asterisk indicates a significant p -value (<0.05)

Fixed effect	Effect estimate	Exp (effect estimate) (confidence interval)	Permuted p
Association contact	-0.012	0.989 (0.934, 1.046)	0.324
Grooming contact	0.019	1.020 (0.980, 1.060)	0.194
Age	-0.079	0.924 (0.862, 0.991)	0.002*
Sample size	0.172	1.187 (1.137, 1.240)	0.000*
Time observed	0.071	1.073 (0.999, 1.154)	0.065
Sex			
Female	Ref	Ref	Ref
Male	0.059	1.060 (0.913, 1.232)	0.141
Season			
Early wet	Ref	Ref	Ref
Late wet	0.073	1.076 (0.879, 1.316)	0.258
Early dry	0.005	1.005 (0.845, 1.196)	0.482
Late dry	0.140	1.151 (1.008, 1.314)	0.041*

In all three models, age was negatively associated with parasite richness. The expected parasite richness in individuals decreased by 0.93 taxa (CI: 0.866, 0.995; $p=0.002$) per one standard deviation change in age in the models that included degree strength and betweenness (Tables 2 and 3) and by 0.92 taxa (CI: 0.862, 0.991; $p=0.002$) in the model that included closeness (Table 4). Sample size was positively associated with parasite richness in all three models (Tables 2, 3, and 4). In models that included betweenness and closeness, late dry season was a significant predictor of parasite richness when compared to the early wet (the reference group). The expected parasite richness in late dry season versus early wet season increased by 1.16 taxa (CI: 1.020, 1.322; $p=0.031$) and 1.51 taxa (CI: 1.008, 1.314; $p=0.041$) in the models that included betweenness and closeness, respectively (Tables 3 and 4).

Discussion

We utilized a social network approach to examine the role that social behavior plays in parasite richness among the Kasekela community of chimpanzees in GNP across a 6-year period. Our results suggest that the two levels of

contact we examined—association and grooming—differ with respect to their impact on parasite richness depending on the network metric assessed. Our prediction—that grooming contact would have smaller additive influences on individual differences in parasite richness compared to association contact—was partly supported by the findings of this study. Network metrics lie along a spectrum from local to global, with the former accounting for the immediately surrounding nodes of a given node and the latter accounting for indirect connections among nodes and the structure of the whole network (Silk et al. 2017). Degree strength, a local metric, played a significant role in explaining the association between parasite richness and association contact, but betweenness and closeness did not, indicating that network metrics that account for immediate surrounding, local nodes, may be better suited for analyzing parasite richness and social contact rather than those accounting for indirect, global connections.

The degree strength of an individual's ties in the association network was positively associated with parasite richness, while the individuals that were more central in the grooming network did not have increased parasite richness. Therefore, the more gregarious individuals were more likely to be infected with helminth parasites. Gregariousness is associated with both costs and benefits of sociality in group living animals (Ostner and Schülke 2018; Thompson 2019), and parasitism is often one of the costs of gregariousness (Côté and Poulin 1995; Patterson and Ruckstuhl 2013) across species, including African bovids (Ezenwa 2004) and fish (Benmansour and Ben Hassine 1998).

Degree strength is a local metric that accounts for immediately neighboring nodes and provides information about the extent to which two individuals share the same environmental space at the same point in time. Local metrics often play a less important role than global metrics in understanding the spread of directly transmitted infections (Silk et al. 2017); however, degree strength is important in this study of environmentally transmitted gastrointestinal parasites, indicating that sharing environmental space is more important for increasing parasite richness than grooming contact. Therefore, when the environment plays an important role in transmission, rather than pathogens that require direct contact among individuals (e.g., simian immunodeficiency virus (Keele et al. 2009)), strength is a good predictor of parasitism. Other infectious agents that are directly transmitted or have a more complex life cycle (e.g., include an intermediate host) may not result in the same dynamics found in the models presented here. Future studies of parasites with different life cycles and of other primates and wildlife living sympatrically with chimpanzees may provide additional information about transmission dynamics in this system.

Betweenness and closeness both account for global connections among individuals, and neither was significantly

related to parasite richness. Global metrics utilize information on all nodes within the network, thus reflect both direct and indirect relationships (Wey et al. 2008). Betweenness measures the importance of individuals in connecting different parts of the network, making it valuable to explain an individual's role in the spread of infection (Silk et al. 2017). Similarly, closeness is important for reflecting an individual's ability to quickly spread infection to the entire group (Dallas et al. 2019). However, the global metrics assessed here were not associated with parasite richness, which could indicate that they do not capture the importance of shared environmental space. Global metrics measure a node's role in propagation of a pathogen through the network; therefore, individual parasites may propagate through the network, while richness does not. While parasite richness is often used as an indicator of disease risk and immune status in primates (Ezenwa 2004; Muehlenbein 2006; Nunn and Altizer 2006; Benavides et al. 2012; MacIntosh et al. 2012; Rimbach et al. 2015), parasite richness does not completely equate to disease risk (Johnson et al. 2013). Therefore, where global metrics might adequately measure a node's role in propagation of a particular pathogen through the network, they might not describe the same relationship for parasite richness, which is likely related to variation in exposure to parasite-infective stages within parasite richness. Furthermore, parasite richness for one individual might not encompass the same parasites as richness for another individual. Additionally, the high fission–fusion dynamics of chimpanzees leads to variation in how individuals use their space, both in dyadic associations and individual gregariousness, which could lead to inconsistencies in the effects of global metrics.

Studies of the impact of age on disease risk in primates have yielded mixed results (Nunn and Altizer 2006; Cooper et al. 2012), which could be a result of not accounting for variability in social contact. While older individuals could have higher parasite richness due to the accumulation of parasites over time (Nunn and Altizer 2006), older individuals often have increased immunity to parasites (Woolhouse 1998; De Nys et al. 2013), and thus, the relationship between age and richness can be negative, as was the pattern observed here. A study in chacma baboons found a positive relationship between age and parasites before sexual maturity and a negative effect after (Benavides et al. 2012), which supports the finding in this study of sexually mature chimpanzees (all greater than 12 years of age).

Our finding that there was no significant relationship between grooming contact and parasite richness could be limited by our dataset since the grooming data used here were focal grooming and not all-occurrence grooming. However, we do expect focal grooming to be representative of total grooming. In addition, the fact that the grooming data represent only a small subset of all the grooming that is occurring

adds justification for the benefit of utilizing grooming rates rather than grooming time. Another limitation in the current study is the potential bias introduced by uneven sampling size. Sample size was positively associated with parasite richness in all of the models; however, we controlled for the effect of sample size by including it as a variable in the models.

After accounting for shared space use, contact via grooming did not significantly explain additional variation in richness; thus, grooming appears not to be costly in relation to parasite transmission. We found that sharing space with other infected individuals is more costly with regard to increasing parasite richness than physical contact via grooming. Chimpanzees form subgroups, and therefore share space with other individuals, according to a combination of factors that may have a variety of benefits, such as gathering due to female sexual state, the presence of fruiting trees, and/or according to social relationships with other individuals (Goodall 1986; Matsumoto-Oda et al. 1998). Here, we have identified potential costs of gregariousness in terms of increased parasite richness. However, grooming—which also has demonstrable benefits, including social bonding, ectoparasite removal, and other social and health-related benefits (Langergraber et al. 2007; Akinyi et al. 2013; Crockford et al. 2013)—did not significantly increase those costs. As this study primarily focused on gastrointestinal parasites with a fairly simple life cycle, patterns of parasitism and chimpanzee sociality may be quite different when considering parasites with a more complex life cycle (e.g., those with intermediate hosts) or primarily relying on direct transmission (e.g., those lacking an environmental stage). Thus, further research incorporating parasites with different transmission patterns and host species with flexible grouping patterns may provide more insights into the costs of sociality.

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Declarations

Ethics approval All animal use was approved by the Tanzania Commission for Science and Technology, Tanzania Wildlife Research Institute, and Tanzania National Parks Association. This research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

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Authors and Affiliations

Jessica R. Deere¹ · Kathryn L. Schaber^{2,3} · Steffen Foerster⁴ · Ian C. Gilby⁵ · Joseph T. Feldblum⁶ · Kimberly VanderWaal¹ · Tiffany M. Wolf¹ · Dominic A. Travis¹ · Jane Raphael⁷ · Iddi Lipende⁸ · Deus Mjungu⁹ · Anne E. Pusey⁴ · Elizabeth V. Lonsdorf¹⁰ · Thomas R. Gillespie^{2,3} 

¹ Department of Veterinary Population Medicine, College of Veterinary Medicine, University of Minnesota, St. Paul, MN, USA

² Department of Environmental Sciences and Program in Population Biology, Ecology, and Evolutionary Biology, Emory University, Atlanta, GA, USA

³ Department of Environmental Health, Rollins School of Public Health, Emory University, Atlanta, GA, USA

⁴ Department of Evolutionary Anthropology, Duke University, Durham, NC, USA

⁵ School of Human Evolution and Social Change, and Institute of Human Origins, Arizona State University, Tempe, AZ, USA

⁶ Department of Anthropology, and Society of Fellows, University of Michigan, Ann Arbor, MI, USA

⁷ Tanzanian National Park Authority, Arusha, Tanzania

⁸ Tanzania Wildlife Research Institute, Arusha, Tanzania

⁹ Gombe Stream Research Center, The Jane Goodall Institute, Kigoma, Tanzania

¹⁰ Department of Psychology, Franklin and Marshall College, Lancaster, PA, USA