Linking parasitism to network centrality and the impact of sampling bias in its interpretation

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Abstract

Group living is beneficial for individuals, but also comes with costs. One such cost is the increased possibility of pathogen transmission because increased numbers or frequencies of social contacts are often associated with increased parasite abundance or diversity. The social structure of a group or population is paramount to patterns of infection and transmission. Yet, for various reasons, studies investigating the social transmission of parasites in animals, especially in primates, have only taken into account parts of the group (e.g., only adults or even only adult females), which is likely to impact the interpretation of any results linking sociality and parasitism. Here, we investigated the relationship between social network centrality and an estimate of gastrointestinal helminth infection intensity in a whole group of Japanese macaques (*Macaca fuscata*). We then tested the impact of omitting parts of the group on this relationship. We aimed to test: (1) whether social network centrality – in terms of the number of partners (degree), frequency of interactions (strength), and level of social integration (eigenvector) – was linked to parasite infection intensity; and, (2) to what extent excluding all or portions of individuals within the group from the analyses might influence the observed relationship. We conducted social network analysis on data collected from one group of Japanese macaques over two months on Koshima Island, Japan, to relate metrics of network centrality to an index of parasite infection intensity (eggs per gram of faeces: EPG). We then ran a series of knock-out simulations to test the effect(s) of accounting only for certain age-sex classes on the observed relationship. General linear mixed models showed that, in the whole network, centrality was positively associated with infection by the examined geohelminths (*Oesophagostomum aculeatum*, *Trichuris trichiura,* and *Strongyloides fuelleborni*). However, in partial networks with only adult females, only juveniles, or random subsets of the group, the strength of this relationship - albeit still generally positive - lost statistical significance. Our study indicates that sampling bias can impact the relationship that is observed between social interaction and parasitism. In addition to supporting earlier results linking geohelminth infection to Japanese macaque social networks, this work introduces important methodological considerations for research into the dynamics of social transmission, with applications to infectious disease epidemiology, population management, and health interventions.

Key words: sociality, social network, geohelminth, Knock-out simulation, sampling bias

Introduction

Living in a group provides many benefits to individuals, but individuals can also face substantial costs (Loehle, 1995). One such cost is increased exposure to parasites and a higher probability of parasite transmission from one individual to another (Altizer et al., 2003; Arneberg et al., 1998; Freeland, 1976; Loehle, 1995). This pattern may arise from higher contact rates between individuals and generally higher local densities of hosts. From the perspective of vectors of parasites, a group of animals is an aggregation of hosts, potentially more attractive than a single host (Altizer et al., 2003; Arneberg, 2002). Even for parasites that are not transmitted through direct contact between hosts, sharing of resources and space, such as food patches, sleeping sites, or home ranges, increases the likelihood that hosts encounter infectious stages of parasites in the environment, which increases the probability of transmission between hosts (Altizer et al., 2003; Müller Klein et al., 2019; Nunn et al., 2015).

Although living in a group may generally mean greater parasite exposure, within a group, individuals exhibit different rates of interacting: social interactions are influenced by kinship ties, dominance ranks, or age, size, and sex assortativity (Kurvers et al. 2014). This creates heterogeneity in contact patterns, leading to differences between potential contacts and actual contacts, thereby influencing each individual's exposure to parasites (Altizer et al. 2003). Thus, the positive relationship that is expected to occur between increased group size and increased parasitism is not always observed (Moller et al., 1993). Accounting for social structure and the role and position of individuals within it therefore helps make sense of how parasites are transmitted within animal groups. Studying the relationship between social interactions and parasite infection is essential for understanding how animal social behaviours might reflect adaptations to infection risk, or conversely how parasites might invade or persist in host populations.

In this endeavour, Social Network Analysis (SNA) is an efficient statistical tool that can analyse groups of individuals as a whole and help make predictions about the spread of infectious diseases (Borgatti, 2005). Social networks reflect the patterns of interactions, associations, or spatial proximity between individuals. SNA can provide information about the whole structure of the network, but also analyse the structural importance of certain nodes (e.g. individuals) and their ties (e.g. interactions) to identify influential individuals within a network (Borgatti et al., 2009). So-called central individuals

have qualitatively or quantitatively greater direct or indirect connections than less central or peripheral individuals. An individual's direct connections can vary in both degree, i.e., the cumulative number of unique interaction partners, and strength, i.e., the frequency with which the individual interacts with its partners. An individual's indirect connections further consider the relative degrees and strengths of those individuals to which it is connected. Central individuals are thus expected to be at once key dispersers of parasites but also at the greatest risk of acquiring parasites from others (Romano et al., 2016). For example, gidgee skinks (*Egernia stokesii*) with high refuge-sharing rates are more likely to be infected by ticks and host a more diverse blood parasite community than less-connected skinks in the same refuge-sharing network (Godfrey et al., 2009). Similarly, female Japanese macaques (*Macaca fuscata yakui*) that are better connected in their grooming networks exhibit more diverse intestinal helminth communities and greater intensity of infection with certain parasite species (MacIntosh et al., 2012).

Factors like sex, social rank, and age can also influence host exposure and susceptibility to parasites. These traits might have an impact on the frequency, quality, and quantity of interactions with social partners and with the environment. For instance, in species where young males disperse from their natal group, males will interact with more numerous and diverse individuals compared with females (Teichroeb et al., 2011). In addition, these traits might be linked to variations in physiological and immunological responses. As a case in point, meta-analyses in vertebrates suggest that greater parasitism is biased toward high-ranking individuals (Habig et al., 2018). This may be linked to stressful social situations - such as the struggle to achieve high dominance status - that trigger the production of glucocorticoids, which is essential in the activation of the immune response (Cain and Cidlowski, 2017).

Concerning age, juveniles may have a higher chance of contracting infectious agents because of their specific activity patterns, which means higher exposure to infection (e.g., greater and more diverse exploration of substrates, heightened reliance on social interactions, etc.) (Sarabian et al., 2018b). Similarly, juveniles are thought to have a less efficient or weaker immune system than adults, which increases their susceptibility to infection. (East et al., 2008; Ebersole et al., 2008; Fallon et al., 2003). Often, though, studies investigating links between sociality and parasitism only include adults, perhaps because conducting research on juveniles is more difficult due to more challenging identification and observation conditions. Previous studies, including those by some of us (Duboscq et al., 2016;

MacIntosh et al., 2012; Romano et al., 2016), are missing juveniles, a key group of individuals, and this may preclude a fuller understanding of infection dynamics. As case in point, although unrelated to infection, a previous study using knockout simulations indicated that juvenile or adolescent baboons can act as bridges between clusters of otherwise weakly connected individuals, thus changing the nature of the networks being observed (Fedurek and Lehmann, 2017).

More generally, problems of missing data in social networks are well known. Missing nodes (Davis et al., 2018; Gilbertson et al., 2021; Kossinets, 2006; Smith and Moody, 2013), especially missing central nodes (Smith et al., 2017), produce measurement bias in social network centrality because network data are relational and hence one data point (node, edge, etc) is not independent of another. Although many network measures can be estimated with incomplete information and can be robust to missing individuals (Borgatti et al., 2006), it is important to assess the impact on precision, accuracy, and bias created by subsampling networks or by carrying analyses with partial networks (Silk, 2018; Silk et al., 2015). This impact can be assessed via comparing, correlating, or regressing original whole-group network measures with newly calculated partial network measures. At present, we are starting to better understand the effects of using partial or subsampled networks on network measures (Smith et al. 2017; Silk et al. 2015), but we have scarce knowledge about the influence that such measurement bias has on the conclusions we might draw concerning the relationship between network characteristics and other social or ecological processes (but see Silk et al. 2015 or Herrera et al. 2021). Assessing measurement bias can thus inform us about how best to carry out our observations or even how we might correct for sampling bias when data have already been collected (Hoppitt and Farine, 2018; Silk et al., 2015; Smith et al., 2017). It is thus meaningful to assess how including (or excluding) juveniles or any other often-missing subgroup(s), or even individuals at random, might affect our interpretation of the relationship between infection and social network centrality, which is the target of this study.

Japanese macaques and their gastrointestinal parasites comprise a well-suited system for studying pathogen transmission in wildlife (MacIntosh, 2014). Japanese macaque populations are generally stable and distributed throughout Japan and have been subject to a long history of research, which provides a firm foundation regarding their ecology and social structure. Japanese macaques are mainly terrestrial, enabling direct observation of social behaviour and sampling for parasitological analyses. Japanese

macaques are also infected by numerous gastrointestinal nematode parasites, including various geohelminths, which are amenable to study through faecal sampling. Helminths are commonly found in mammals (Stephens et al., 2017) and can impact host health and fitness by imposing nutritional constraints and other physiological conditions that can reduce host fitness, and in some cases may directly cause mortality (Hillegass et al., 2010).

There are three known geohelminths in Japanese macaques: *Oesophagostomum aculeatum* (Strongylida), *Strongyloides fuelleborni* (Rhabditida), and *Trichuris trichiura* (Trichocephalida) (Gotoh, 2000). These parasites are transmitted through contact with contaminated substrates, though while *O. aculeatum* and *T. trichiura* use the faecal-oral pathway, *S. fuelleborni* infects hosts percutaneously. Voided with faeces, the eggs of *O.aculeatem* and *S. Fuelleborni* hatch and develop into infectious third-stage larvae in the environment. *S. Fuelleborni* exhibits a heterogonic life cycle whereby some larvae continue to develop in the external environment and persist as free-living adults, mating and reproducing opportunistically. Others (females only) become parasitic in a host. In contrast, the eggs of *T. trichiura* become embryonated but do not hatch until they have been ingested by a suitable host. Each can thus be transmitted between hosts that share environmental resources, even if separated in time (Modrý et al., 2018).

The presented study examined gastrointestinal nematode parasites infecting Japanese macaques on Koshima island, Japan, to test two hypotheses: (1) whether social network centrality, as measured by the number of partners (degree), frequency of interactions (strength), and social integration (eigenvector) observed across individuals, was linked to an estimate of intestinal parasite infection intensity (eggs per gram of faeces, EPG); and, (2) analyses based on a partial network produced different results. We made two predictions. First, we predicted a positive association between an individual's social network centrality and its gastrointestinal nematode parasite infection intensity (estimated via faecal egg counts), as was found previously in Japanese macaques (MacIntosh et al., 2012). We chose multiple network metrics because, in theory, each may be associated with a different aspect of transmission or may be more or less instrumental to the process (MacIntosh et al. 2012; Duboscq et al. 2016; Tiddi et al. 2019). Second, we predicted that taking into account only partial networks would lead to divergent results concerning the network-infection link. Partial networks examined included a juvenile-only network,

because of their high rates of infection (MacIntosh et al., 2010), an adult female-only network, because of their core role in macaque society and their prominence in previous studies of this nature, and a series of random subsets of the network. We do not make more precise predictions here as we cannot *a priori* predict with confidence the effects of missing individuals on network measures.

Methods

Ethical Statement

The research presented here complied with the Guidelines for the Care and Use of Nonhuman Primates established by the Primate Research Institute of Kyoto University (KUPRI), to the legal requirements of Japan, and to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates. Permissions were acquired from the Field Research Committee of KUPRI, the Cooperative Research Program of the Wildlife Research Center of Kyoto University, and the City of Kushima's Agency for Cultural Affairs.

Study site and subjects

This research was conducted on Koshima island, a 0.35km^2 island located in the Sea of Hyūga in Miyazaki Prefecture, Japan (31°27′N, 131°22′E). The island is inhabited by two groups of macaques and some solitary males. The home ranges of the two groups only overlap at their edges, and macaques were never observed in proximity during the observation period. The study group, the "main" group, inhabits the western part of the island, including a sandy beach, a range of forest, and a rim of rocky beach. Provisioning and behavioural observations of Koshima macaques started in 1952, and demographic, ecological, behavioural, and life-history data are available since then (Watanabe, 2008). Previous studies on this island identified four nematode parasites infecting Koshima macaques (Gotoh, 2000; Horii et al., 1982). The study group is currently provisioned with approximately 3 kg of wheat twice weekly. At the time of the study, the main group had 47 stable group members and 5 solitary roaming males that ranged in proximity to the group on an irregular basis. The group included 20 adult females (≥5 years old), 8 adult males (≥5 yo) (including the 5 solitary males), 13 juvenile females

182 (between 1 and 4 yo), and 11 juvenile males (between 1 and 4 yo). Because the population has been
183 monitored for decades, we have the exact age of each individual in the population.
184
185 Behavioural Data Collection
186 The observation team - including ZX, AC-N, EM-M - observed the macaques for 88 days over 3
187 months from March to June 2017. All individuals could be identified reliably based on a combination
188 of facial and other physical characteristics (such as facial tattoos, scars, limps, coat colour, etc.), and
189 allowed researchers to approach within 5m, facilitating observation and faecal sample collection. We
190 carried out 20-minute focal animal observations, recording behavioural activities of the focal individual
191 (including resting, feeding, locomotion, playing, giving and receiving grooming, and self-grooming) at
192 30-second intervals. At the same scan point, we also recorded the identity of each individual within 1m
193 of, or in body contact with, the focal animal. Agonistic interactions of all individuals in the group were
194 recorded *ad libitum*. To assess the dominance hierarchy, we used all agonistic interactions recorded by
195 the observation team between November 2016 and June 2017. We observed every individual in the
196 group, including two infants that were born in 2016, every day in a pseudorandomized order, updated
197 daily. We avoided repeating observations of the same individual on the same day, and we balanced
198 observations between individuals as much as possible across days and times of day (e.g., early and late
199 morning, early and late afternoon).
200 Data were collected either on paper or using a tablet (Panasonic Tough-pad, with the application
201 PRIM8 (McDonald and Johnson, 2014)). A multi-observer reliability test based on Fleiss' Kappa index
202 (Fleiss and Cohen, 1973) indicated a good match between observers for proximity records, including
203 the identities of all subjects involved (Kappa = 0.815). In total, we conducted 547 focal observations
204 recording 22,066 focal scans, or 183.3 hours of focal observations, with a mean ± SD of 10.7 ± 6.6 focal
205 follows per individual (or 11.2 ± 0.8 per individual without 4 rarely seen solitary roaming males).
206 Supplementary material 1 (SP1) summarizes the attributes of and data from the study subjects.
207

Social data analysis

Dominance

To compute the dominance rank of all individuals, we used the Elo-rating method (Neumann and Kulik, 2014), which reflects an individual's success in agonistic interactions relative to all other members (Albers and de Vries, 2001; Neumann et al., 2011). Elo-rating is based on a sequence of agonistic interactions ordered in time. Each individual is seeded with an arbitrary rating of 1000. This rating is then updated after each agonistic interaction with a clear outcome. The rating increases/decreases based on the outcome of the interaction (won or lost), the previous ratings of both opponents, and a determined factor, k (here k = 100 (Neumann et al., 2011)). In our analyses, we aggregated all data and calculated the Elo-rating scores for all individuals at the end of the observation period.

Social network centrality

We constructed an undirected proximity network based on recorded 1m (close) proximity. The parasites of our interest are transmitted through resource sharing. However, we currently lack well-tested methods to collect data that can link behavioural exactly to infection processes. Instead, we decided to collect spatial proximity data as a proxy of resource-sharing potential, and use it to construct contact networks that were found to be related to infection in previous studies (MacIntosh et al. 2012). Even though spatial proximity is different from resource sharing, it is reasonable to consider that frequency of being observed in proximity is related to the frequency of sharing resources. So, in this study, we assumed that the transmission of parasites is linked with space sharing, which is reflected in patterns of spatial proximity among individuals within a network. Furthermore, we decided to construct a network based on aggregated data over the whole study period (3 months). Given the pattern of infection of the parasite under study (from 2 to 6 weeks based on livestock data (Anderson, 1992)), networks based on shorter periods may better match the time lag between infection and detection, but would not reflect robustly the actual connections between individuals.

We built a symmetrical matrix of undirected social proximities, in which dyadic proximity data were scaled by the number of scans collected from each individual of the corresponding dyad. The

236 proximity matrix was then analysed with the package "igraph" (Csardi and Nepusz, 2006) in R
237 Statistical Software v.4.0.5 (R Development Core Team, 2021). For each individual, we computed: (1)
238 degree (how many partners an individual had); (2) strength (how many times an individual was in
239 proximity with others); and, (3) eigenvector centrality (the sum of the centralities of an individual's
240 neighbours; high centrality can be achieved by having either a large degree or being connected to
241 associates with a high degree (or both) (Farine and Whitehead, 2015)).
242
243 Parasite Collection and Analysis
244 We opportunistically collected between 1 and 4 fresh faecal samples from each individual (3.5±1.6)
245 during observations whenever a clearly identified individual was seen defecating. We put the entire
246 faeces into a sealable plastic bag and then into a cooler bag with ice until we brought all samples to the
247 lab for processing. Within 12h of collection, we weighed and homogenized about 1-2 grams of faeces
248 into 3.5ml of a sodium acetate-acetic acid-formaldehyde (SAF) solution for the preservation of parasite
249 eggs and larvae. After the fieldwork period, we sent all samples to Kyoto University's Primate Research
250 Institute, where we conducted the further analysis.
251 We processed all parasitological samples following previous work with Japanese macaque
252 parasites using a modified formalin-ethyl acetate sedimentation protocol to concentrate helminth eggs
253 from faeces (MacIntosh et al., 2010). We added 5 drops of Triton X-100 to the faecal mixture before
254 filtration to better isolate eggs from other components of faeces. To filter samples, we used a 330µm
255 Saran™ mesh (Asahi Kasei, Japan). To reduce the amount of formaldehyde consumed in the process,
256 we used saline instead of formaldehyde for all intermediate washing steps during concentration. For all
257 centrifugation steps, we spun our samples at 3000 rpm for 5 minutes.
258 After processing, we again suspended the retained faecal pellet in SAF and stored it at room
259 temperature until analysis. For parasitological examination, we used a volumetric method based on
260 McMaster microscopy to estimate the intensity of parasitic infection in each individual through
261 counting the number of eggs observed per gram of faecal sediment (EPG) (Modrý et al., 2018). We
262 drew aliquots from the faecal suspension, kept homogeneous during reading using a magnetic stirrer,
263 and viewed them in a McMaster chamber with a 10x objective lens. Parasite eggs were identified by

their specific morphology and size (Modrý et al., 2018). We repeated this procedure five times per sample and used the mean count to calculate EPG from each sample based on the amount of sediment viewed per volume of suspension, with the following formula: $EPG = \frac{\frac{total\ number\ of\ eggs}{number\ of\ chambers}}{\frac{W_{sediment}}{V_{solution}} \times V_{chamb}}$

In the formula, *total number of eggs* reflects the number of eggs the examiner counted in all chambers. The *number of chambers* refers to the number of chambers examined in the sample (here, 5). $W_{sediment}$ refers to the weight of the faecal pellet after filtration, and $V_{solution}$ refers to the volume of solution that was used to dilute the sample (in this case, between 10ml and 50ml depending on the thickness of the faecal suspension, which significantly affects viewing). $V_{chamber}$ refers to the volume of suspension contained in each counting chamber (0.15ml for a single McMaster chamber). EPG is a standard index of parasite infection intensity. Although it is not always indicative of true worm infection intensity (Gillespie, 2006; Modrý et al., 2018), numerous studies have found significant correlations between EPG and the number of reproductive female worms infecting a given host (Bont et al., 2002; Mohammed et al., 2016). The method is commonly used to measure domestic animal health and in wildlife parasitology, particularly in cases where parasite population estimation is needed but it is neither advisable nor possible to sample individuals via other - more invasive or destructive - means.

Statistical Analyses

All statistical analyses were conducted using R v4.0.5 (R Development Core Team, 2021). We built a dataset that included one line for each parasite species in each faecal sample of each individual as the unit of analysis, i.e., three times (three parasite species) the number of faecal samples analysed. In addition, each sample was associated with an individual and all of its attributes, including its centrality measures (degree, strength, and eigenvector), Elo-rating, sex, and age, along with the sample's collection date. EPG was used as the response variable in the statistical models described below.

Testing for associations between network centrality and parasite infection intensity

Considering that all parasites of interest are transmitted via contact with contaminated substrates, we decided to include EPG from different parasite species in one model. In doing so, we accept the

limitation that we are not testing for specific associations related to each parasite type, assuming instead that similar mechanisms may drive links between social behaviour and infection, should such links exist. We modelled EPG as zero-inflated and overdispersed count data. Parasites typically exhibit an aggregated distribution across their hosts that is best approximated by a negative binomial distribution (Crofton, 1971; Poulin, 2007; Shaw et al., 1998). We confirmed that our EPG distribution indeed followed a negative binomial distribution using the "*fitdistr"* function from the R package "MASS" (Venables and Ripley, 2002). We then built generalized linear mixed models with a negative binomial error structure using the "glmmTMB" package (Brooks et al., 2017). The three centrality measures we investigated were related to each other in our data (Pearson's Correlation of degree and strength: $r = 0.49$, $p < 0.001$; degree and eigenvector: $r = 0.33$, $p = 0.018$; strength and eigenvector: $r = 0.76$, $p < 0.001$). Moreover, eigenvector centrality itself is derivative of degree and strength. Thus, including these metrics in the same model would violate the assumption of data independence (Webber et al., 2020). Therefore, we constructed one model for each one of them. Age, sex, and Elo-rating score were set as control fixed effects as they are known to affect EPG but are not factors of interest here. Since EPG can vary considerably across parasite species, and since there are only three species in this study, we also included parasite species as a control fixed effect. EPG can vary considerably over time and sample to sample within an individual (Wood et al., 2013). To account for such effects, we collected multiple faecal samples per individual and set the individual ID and date of sample collection as random effects in the models.

Table 1. Outline of the factors included in the GLMMs in this study. We constructed one model for each of the three network metrics: Degree, Strength and Eigenvector.

Fixed effects	Random effects
Network metric	Individual ID
Age	Collection Date
Sex (Male against Female)	
Elo-rating score	
Parasite species (*S. fuelleborni* or *T. trichiura* against *O. aculeatum*)	

The model residuals showed heteroscedasticity and overdispersion, so we added a zero-inflation term to account for the substantial number of zeros in the EPG data (124 instances or 24% of the 517 total data points). The zero-inflated models showed better residual distributions and significantly lower AIC compared with standard negative binomial models (for the degree models, AIC of the zero-inflated model is 7268.8 while AIC of the simple model is 7727.0; for the strength models, AIC is 7254.5 compared with 7718.0; for the eigenvector centrality models, AIC is 7260.7 compared with 7722.1). We also assessed whether other assumptions of the models were met, such as lack of multicollinearity (variance inflation factor < 3) and overly influential cases (Cook's distance < 4/N). Lastly, we conducted likelihood ratio tests (LRT) to evaluate the statistical strength of our models against an informed null model containing only the control factors age, sex, Elo-rating, and parasite species, including all random effects.

Testing the effect of knockout simulations on the relationship between centrality and parasite infection intensity

To have a point of comparison with previous studies and to gain insight into the influence of only examining certain age-sex classes on the relationship between centrality and infection intensity, we ran two more analyses. We first constructed partial social networks including only (1) adult females (20, or 38.5% of the group), which mimics what was done in previous studies, or (2) juveniles (28, or 53.8% of the group). To compare the network metrics from original and partial networks, we calculated Pearson's correlation coefficients between the original and partial network metrics. Then, we built models with the same structure as those described above but with network metrics calculated from partial networks. These models went through all the checks as previously described.

Removing individuals from the network itself might already affect social network structure and thus change the observed result. In a second step, therefore, we conducted randomized knock-out simulations: we randomly removed 5%, 10%, 25%, and 50% of individuals from the network, re-calculated the network metrics, and re-integrated them into the models for calculation over 1000 iterations. After each simulation, the model parameters of interest (here estimates and confidence intervals) were saved and the results were compared with the results from the original models. We chose

342 those percentages because they represent biologically relevant cases of missing individuals during data
343 collection or within a study design, like solitary roaming males or peripheral females (e.g., <10% of the
344 group), or when taking into account only certain age-sex classes, here adult females or juveniles,
345 effectively removing everyone else (e.g., >25% of the group, depending on group composition and
346 demography).

347 Knock-out simulations not only disrupt the network structure and change the centrality metrics
348 calculated, but they also reduce the number of individuals included in the model, reducing sample size
349 and possibly statistical power. We thus tested whether the results produced with partial networks reflect
350 disrupted network structure or simply a generic statistical power issue. We first sub-sampled data as
351 before (i.e. adult female-only data or juvenile-only data), but instead of re-constructing the network and
352 re-calculating metrics, we ran the statistical models while retaining the centrality metrics from the whole
353 network. We also ran randomized knock-out simulations in which we randomly removed 5%, 10%, 25%
354 or 50% of individuals over 1000 iterations and re-ran these statistical models as well, again retaining
355 the network metrics from the whole network.

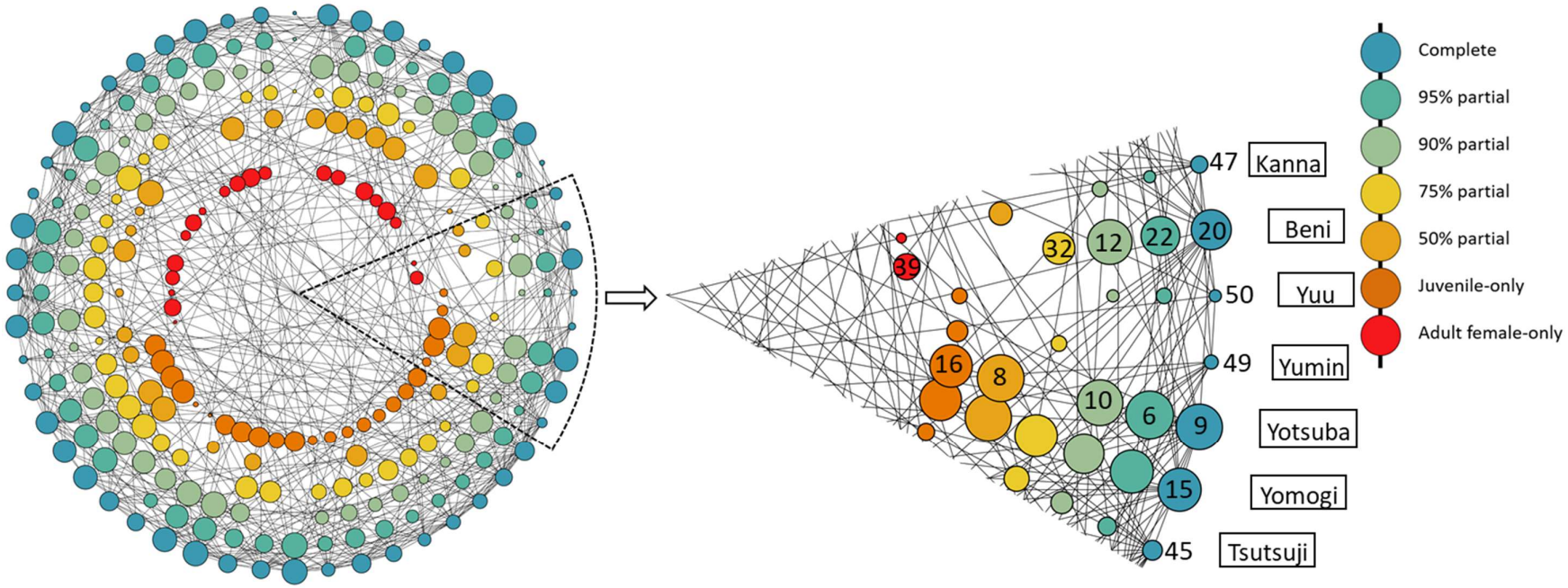

Figure 1: Network graph representing differences in each individual's eigenvector centrality in whole networks versus partial networks. All the edges are based on the whole network (i.e., the outer, blue nodes). Node size represents the eigenvector centrality rank of each individual in the network; larger nodes have a higher eigenvector centrality rank. To make nodes comparable across networks, we also removed the rank values that each node held in the whole network when removing them from the partial networks so that changes in node size remain consistent across networks even when fewer individuals are included. The right side of the graph represents an enlarged version of one corner of this network. As shown in the graph, node size and the number inside the node represent the corresponding rank in the network. When individuals were removed from the network, eigenvector centrality ranks changed dramatically

Results

Social network metrics

Descriptive results are tabulated in Table 2.

Table 2. Summary of network metrics from whole or partial networks in this study.

	Whole group (mean±SD)	Adult female-only (mean±SD)	Juvenile-only (mean±SD)
Degree	13.80±5.48	13.75±4.22	15.33±4.93
Strength	0.44±0.21	0.55±0.20	0.43±0.16
Eigenvector	0.32±0.29	0.39±0.32	0.33±0.32

Parasitological results

We observed four nematode parasites infecting our subjects during the study period: *Oesophagostomum aculeatum*, *Strongyloides fuelleborni*, *Trichuris trichiura* and *Streptopharagus pigmentatus*. Concerning the geohelminths only, *O. aculeatum*, *S. fuelleborni* and *T. trichiura* – which were the focus of this study – most of the individuals were infected by all parasites. Juveniles showed the highest average EPG compared to the average group-level EPG and that of adult females only (Table 3).

Table 3. Summary of prevalence and infection intensity (EPG) of three geohelminths examined in this study.

		O. aculeatum	*T.trichiura*	*S.fuelleborni.*
Full group data	Prevalence	100%	90%	90%
	Average EPG	1380.72±863.28	775.09±989.16	3080.10±3776.99
Adult females only	Prevalence	100%	90%	85%
	Average EPG	1172.38±578.25	345.21±383.47	682.33±918.725
Juveniles only	Prevalence	100%	96%	100%
	Average EPG	1736.90±975.41	1282.26±1195.90	5827.03±3811.14

Network-infection relationship

Whole networks

Likelihood ratio tests demonstrated that the models with strength and eigenvector centrality as fixed effects, but not with degree centrality, had higher explanatory value than their respective informed null models (Table 4).

Strength and eigenvector centralities were positively related to infection intensity, such that more central individuals had higher EPG of intestinal nematodes (Table 4). Age was negatively related to infection: the younger the individual the more likely it was to show high EPG. Sex and dominance rank were overall not related to infection intensity (Figure 2).

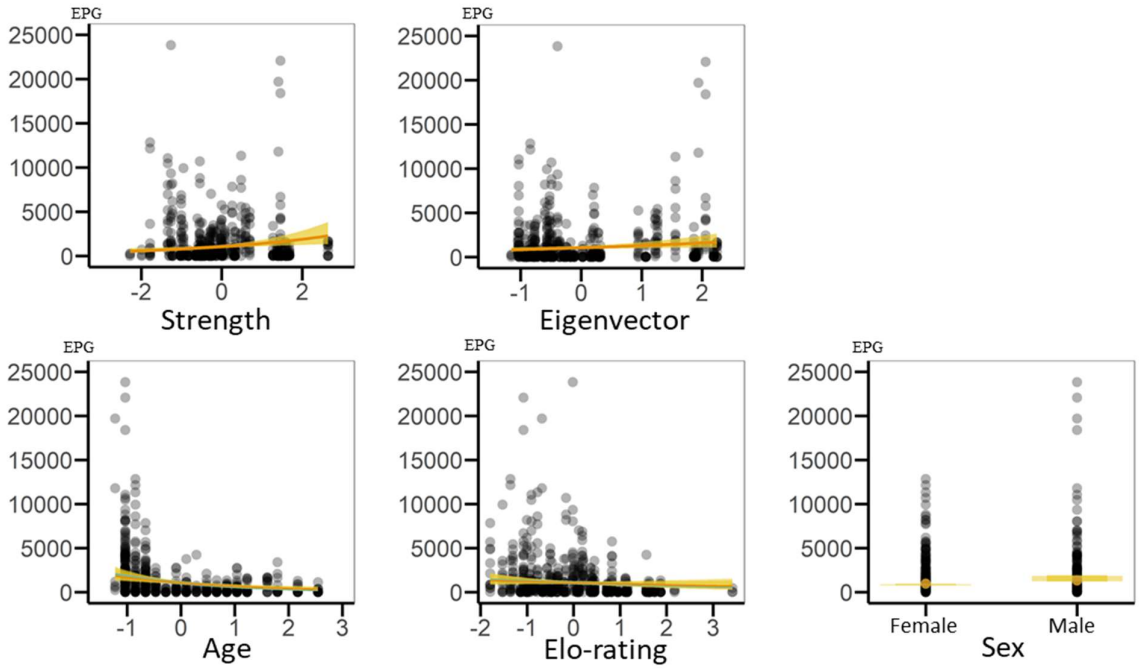

Figure 2: Regression plots representing results of GLMMs based on the whole network. All fixed factors are scaled and centred. Since we constructed one model for each network metric, the regression plots representing shared factors (age, Elo-rating, and sex) show lines from each of the models in different colours.

Table 4. Results of GLMMs testing for variation in geohelminth infection intensity (EPG) among Japanese macaques on Koshima island. LRT are likelihood ratio tests, shown with Chi-square χ^2 tests, degrees of freedom (d.f.) and p-values (p). Results of models that fail to outperform the null model are presented in SP3. Estimates (β) are given with standard errors (SE) and p-values (p). Variance is given with standard deviation (SD). Results in bold are statistically significant ($p < 0.05$).

Centrality metric of focus	*Degree*	*Strength*	*Eigenvector*
LRT against null (χ^2; d.f.; p)	1.940; 2; 0.379	16.491; 2; <0.001	10.238; 2; 0.006
Fixed effects		*Estimate β* ± SE [p]	
Intercept	/	6.88 ± 0.12 [<0.001]	6.89 ± 0.13 [<0.001]
Centrality metric	/	**0.29 ± 0.09 [0.003]**	**0.21 ± 0.09 [0.025]**
Age	/	**-0.53 ± 0.13 [<0.001]**	**-0.45 ± 0.13 [<0.001]**
Sex (male)*	/	0.34 ± 0.21 [0.110]	0.29 ± 0.22 [0.199]
Elo-rating	/	-0.16 ± 0.11 [0.152]	-0.13 ± 0.12 [0.286]
Species (Stro)**	/	**0.65 ± 0.13 [<0.001]**	**0.65 ± 0.13 [<0.001]**
Species (Tri)***	/	**-0.67 ± 0.12 [<0.001]**	**-0.67 ± 0.12 [<0.001]**
Random effects		*Variance ± SD*	
Collection Date	/	0.02 ± 0.13	0.02 ± 0.14
Individual ID	/	0.24 ±0.49	0.26 ±0.51

* *Sex (male) is the effect of sex male against female*
** *Species (Stro) is the effect of parasite species S. fuelleborni* against *O. aculeatum*
*** *Species (Tri) is the effect of parasite species T. trichiura* against *O. aculeatum*

Female- and juvenile-only networks

When comparing measures calculated from partial versus whole networks, in both female-only and juvenile-only networks, partial-network measures were strongly to moderately correlated with the original whole-group-network measures (females: $r_{degree} = 0.79$, $p < 0.001$, $r_{strength} = 0.38$, $p < 0.001$, $r_{eigenvector} = 0.63$, $p < 0.001$; juveniles: $r_{degree} = 0.90$, $p < 0.001$, $r_{strength} = 0.61$, $p < 0.001$, $r_{eigenvector} = 0.57$, $p < 0.001$).

Using data from adult females only, likelihood ratio tests demonstrated that the models with strength, but not those with eigenvector centrality or degree centrality as main predictors, had higher

explanatory value than their respective informed null models (Table 5). Neither age nor rank was related to nematode infection intensity (SP 2).

Using data from juveniles only, likelihood ratio tests demonstrated that none of the models had a higher explanatory value than their respective informed null models (Table 6).

Using data from adult females only or juveniles only but maintaining the network metrics from the whole network, the model results are similar to those with re-calculated network metrics (SP 6, SP 7).

Table 5. Results of GLMMs testing for variation in geohelminth infection intensity (EPG) among adult female Japanese macaques on Koshima island. LRT are likelihood ratio tests, here with χ^2 tests, degrees of freedom (d.f.) and p-values (p). Results of models that fail to outperform the null model are presented in SP4. Estimates (β) are given with standard errors (SE) and p-values (p). Results in bold are statistically significant ($p < 0.05$).

Centrality metric of focus	*Degree*	*Strength*	*Eigenvector*
LRT against null (χ^2; d.f.; p)	3.616; 2; 0.164	**7.424; 2; 0.024**	4.214; 2; 0.122
Fixed effects		*Estimate β ± SE [p]*	
Intercept	/	6.76 ± 0.13 [<0.001]	/
Centrality metric	/	**0.32 ± 0.12 [0.006]**	/
Age	/	-0.09 ± 0.13 [0.477]	/
Elo-rating	/	-0.06 ± 0.13 [0.622]	/
Species (Stro)**	/	**-1.00 ± 0.29 [<0.001]**	/
Species (Tri)***	/	**-1.16 ± 0.18 [<0.001]**	/
Random effects		*Variance ± SD*	
Collection Date	/	0.00 ± 0.00	/
Individual ID	/	0.15 ± 0.39	/

** *Species (Stro) is the effect of parasite species S. fuelleborni* against *O. aculeatum*
*** *Species (Tri) is the effect of parasite species T. trichiura* against *O. aculeatum*

Table 6. Results of GLMMs testing for variation in geohelminth infection intensity (EPG) among juvenile Japanese macaques on Koshima island. LRT are likelihood ratio tests, here with χ^2 tests, degrees of freedom (d.f.) and p-values (p). None of these models significantly outperformed its respective informed null model. Results of models that fail to outperform the null model are presented in SP5.

Centrality metric of focus	*Degree*	*Strength*	*Eigenvector*
LRT against null (χ^2; d.f.; p)	0.120; 2; 0.942	2.491; 2; 0.288	1.643; 2; 0.440

Random partial networks

Random removals of individuals comprising 5, 10, 25, and 50% of the group, following which networks were reconstructed with remaining individuals, all led rapidly to a decrease in the strength of the observed relationship between infection and centrality (Table 7, SP 8); i.e., the observed relationship estimates approached zero and did not reach statistical significance. These results do not appear to be caused by loss of statistical power, because the majority of results from models in which knockouts were conducted but original, whole-network metrics were retained were much closer to the original results obtained with all individuals present (SP 9, SP 10). Thus, the loss of association between centrality and infection stems in our study from omitting individuals before the construction of the networks rather than from the loss of statistical power.

Table 7: Results of 1000 random removals of individuals (% given in the first column) run with observed network data and used to (re)model the relationship between network centrality (here strength or eigenvector) and infection intensity. The heading "Number of model results equivalent to observed" indicates the number of simulation model results out of 1000 simulations that gave a positive estimate for the relationship between centrality and EPG within a 95% confidence interval excluding zero (see text for details).

Centrality measure	Percentage of individuals removed	Number of model results equivalent to observed
Degree	5%	98.0%
	10%	96.6%
	25%	95.4%
	50%	95.9%
Strength	5%	3.2%
	10%	4.2%
	25%	3.9%
	50%	4.7%
Eigenvector	5%	12.6%
	10%	7.1%
	25%	3.8%
	50%	5.3%

449 **Discussion**

450 Studies have shown repeatedly that increased sociality is linked to increased parasitism (Godfrey,
451 2013; Nunn, 2012; Rushmore et al., 2017; White et al., 2017), constituting a major cost of group living.
452 However, not all kinds of social investment are equivalent in terms of parasite transmission: sometimes
453 it is having a lot of social partners, or living in a big group, that leads to increased infection (Böhm et
454 al., 2009), while at other times specific properties of an individual's position within a network may
455 mediate this relationship. Our results reflect the latter case, in that we showed positive correlations
456 between geohelminth infection intensity and two out of three social network centrality measures
457 examined (strength and eigenvector centrality but not degree) in a Japanese macaque group. In brief,
458 the frequency with which individuals were in proximity to one another and their further social
459 integration, but not the number of individuals with which they shared proximity, were positively
460 associated with infection intensity of geohelminths. Moreover, we demonstrated that the choice of
461 animals within a study group (i.e., sampling bias) can impact the relationship that is observed between
462 network centrality and parasitism, a fact that is often neglected or ignored in wildlife studies. Partial
463 networks – e.g., those including only a subset of the group like adult females or juveniles – yielded
464 divergent results compared to those analyses that included the whole-group network, to the point where
465 statistical relationships originally observed between network centrality and infection intensity
466 disappeared. From an epidemiological perspective, every individual can be responsible for the
467 transmission of a pathogen, so neglecting them in the analysis may affect the reliability of the data. From
468 a social network perspective, neglecting individuals can dramatically change the network structure and
469 affect the metrics calculated (Kossinets, 2006; Silk, 2018; Silk et al., 2015; Smith and Moody, 2013;
470 Smith et al., 2017). Thus, sampling bias can lead to misdirected conclusions about the relationships
471 between sociality and parasitism, or any other network process, for that matter.

472 The overall positive association we observed between geohelminth infection intensity and both
473 network strength and eigenvector centrality partially aligns with the results of previous work in a
474 different population of Japanese macaques (MacIntosh et al., 2012). In this previous study and our own,
475 not all network metrics were linked to infection intensity, but both investigations now suggest that
476 eigenvector centrality, whether in grooming or proximity networks, is associated with nematode

477 parasitism in Japanese macaques. Our results also align with a recent meta-analysis of studies
478 investigating parasites in host social networks, wherein strength and eigenvector centrality showed
479 stronger associations with parasitism than did any of betweenness, closeness, or degree centrality
480 (Briard and Ezenwa, 2021). It therefore seems important to consider what these various centrality
481 measures represent in terms of host socio-biology, and in terms of social or ecological processes.

482 Degree centrality represents how many others an individual has been in proximity with, regardless
483 of duration. We observed no relationship between degree and geohelminth infection, here or previously
484 (MacIntosh et al., 2012). There are some reasons not to expect such an association, for example, because
485 even individuals with the same degree might spend very different amounts of time in proximity to other
486 individuals (in our studied group, adult males have very high degree centrality with comparatively low
487 strength). This led to groups of individuals that had high centrality scores but lacked the actual between-
488 individual connections that facilitate parasite infection, leading to a mismatch between centrality and
489 infection. Furthermore, degree centrality may not be a good predictor of proximity to the individuals
490 most likely to transmit infections, i.e., associations with many uninfected or lightly infected individuals
491 may dilute infection risk (Otterstatter and Thomson, 2007; Powell et al., 2020; VanderWaal et al., 2013).
492 Another consideration is the type of parasite under investigation. For example, it was demonstrated
493 previously in the same group of Japanese macaques that degree centrality may at times be positively
494 associated with estimates of louse infestation (Duboscq et al., 2016). Lice are parasites that can transmit
495 directly between individuals over short time scales and can subsequently colonize the new host relatively
496 quickly. In that sense, degree centrality reflects an immediate risk (Borgatti, 2005), but this is not the
497 dominant mode of transmission for geohelminths.

498 In our study, strength centrality represents how frequently individuals were in proximity to others
499 during observations. For the parasites under consideration here, the eggs or larvae are voided in faeces,
500 meaning that there is a time-lag between infection of one host and transmission to the next host through
501 the environment. Geohelminths also do not replicate within a host, meaning that EPG reflects the
502 cumulative acquisition of each parasite over time. Even though the dilution effect mentioned about
503 degree might also be true for strength, strength might be more likely to be associated with infection
504 intensity than degree: the more often a macaque remains in proximity to others, the more resources it is

505 likely to share with others and thus the more likely it is to encounter infectious stages of parasites in the
506 environment. Such social individuals, particularly those that have spatiotemporal associations with other
507 heavily infected individuals, would experience greater risk encountering, accumulating, and
508 transmitting parasites.

509 Lastly among the centrality measures we investigated, eigenvector centrality depends on both an
510 individual's strength and degree, as well as that of their associates. This measure thus represents
511 neighbourhood effects, where direct neighbours but also neighbours of neighbours can affect one's own
512 centrality. Since geohelminths produce chronic infections and individuals rarely if ever become fully
513 resistant, repeated exposure can lead to continuous reinfection with the same parasite. In such cases,
514 eigenvector centrality may be a critical long-term risk factor for repeated parasite exposure (Borgatti,
515 2005). Its relationship with geohelminths might thus suggest general trends for well-connected
516 individuals and their associates to encounter parasites at similar rates through increased interactions or
517 use of shared space.

518 Having observed a positive association between the social network and geohelminth infection, we
519 then tested the impact of sampling bias on these results, by including/excluding certain age-sex classes
520 from the analysis. Numerous studies have focused on specific age-sex classes rather than the whole
521 social group (Hamilton et al., 2020; Roberts and Roberts, 2020; Sandel et al., 2021; Webber et al., 2016).
522 Through targeted removal of network subsets and subsequent reanalysis, the simulations we conducted
523 demonstrated that the original relationship observed using the whole group network becomes
524 insignificant in most cases (except strength for the adult female model). In all cases, the direction of the
525 centrality-infection link remained positive.

526 This contrasts somewhat with a previous study that did find a significantly positive relationship
527 between geohelminth infection and network centrality when only considering adult females in the
528 network (MacIntosh et al., 2012). However, note that this previous study was conducted over a period
529 of 16 months and therefore had access to a much larger data set. In the present study, the adult female
530 network was still more predictive of infection than the juvenile network, albeit less so than the full
531 network. Moreover, the estimates linking centrality metrics to infection intensity are higher in adult-

532 female models compared with the whole group models (SP 3, SP 4), so this lack of statistical
533 significance may be the result of lower statistical power rather than lack of biological effect.

534 It may also be relevant to note that, in our study as in previous work with Japanese macaques
535 (MacIntosh et al., 2010), juveniles exhibited higher infection intensities than adults. Furthermore,
536 among juveniles, younger juveniles and males shed more parasite eggs than did older juveniles and
537 females (SP 5). These results concur with the general findings that young animals and males are
538 disproportionately infected by parasites (Habig and Archie, 2015; Hinney et al., 2011; Khan et al., 2010).
539 Hypotheses explaining this difference include age/sex-associated hormonal profiles (Roberts et al.,
540 2001), variable levels of immunity (East et al., 2008; Ebersole et al., 2008; Fallon et al., 2003; Roberts
541 et al., 2001), different probabilities of exposure to contaminated items (Sarabian et al., 2018a; Sarabian
542 et al., 2018b), and differing social positions within the group (Cords et al., 2010; Grassi, 2002; Liao et
543 al., 2018). Considering the different and often higher infection intensities in juveniles, as in adult males,
544 neglecting them as study subjects means the analysis is based on a biased dataset, which could lead to
545 different results or weaker observed effects. Moreover, because individuals, as connected nodes, are not
546 independent of one another, excluding them from the network fundamentally changes its overall
547 structure (Fedurek and Lehmann, 2017).

548 As presented in our study, the network metrics calculated from both the adult female-only network
549 and the juvenile-only network are rather well correlated with those calculated from the whole network,
550 though the correlation is not perfect and such changes had a dramatic effect on the relationship originally
551 observed between sociality and parasitism. Among these correlations, degree and strength from the
552 juvenile-only network were closer to those from the whole network than were the same measures from
553 the adult female-only network. In contrast, eigenvector centralities from the adult female-only network
554 were closer to those in the whole network than were eigenvector centralities from the juvenile-only
555 network. These differences might stem from the fact that, in the studied group, the number of juveniles
556 was higher than the number of adult females, and we know that degree and strength are usually greatly
557 influenced by the number of individuals present. Moreover, including juveniles may significantly
558 increase the number of contacts for females, because each female may have multiple offspring. However,

559 each juvenile is likely to interact only with a small number of adults, i.e., adult female kin, so the
560 inclusion of adults would not add many more contacts to each juvenile's network.

561 Unlike strength and degree, eigenvector centrality represents the position of an individual within
562 its whole network of connections and is a relative value, so it may not depend as much on group size
563 (Griffin and Nunn, 2012). Since females are known to form the core of Japanese macaque groups
564 (Yamagiwa and Hill, 1998), it may be that their patterns of interaction dominate the emergent social
565 network structure, such that properties of female networks linked to social integration (as in eigenvector
566 centrality) do not change as much with the inclusion/exclusion of other subgroups. If so, links between
567 centrality and infection in female macaques may be robust to sampling bias, whereas networks of
568 juveniles, which are likely to vary substantially with and without the inclusion of their maternal adult
569 kin, may not be. An alternative explanation for our results is that we cannot exclude the possibility that
570 our study period was simply too short to detect a significant relationship between centrality and infection
571 in subsets of the group, particularly in females where only one network metric is found related to
572 infection. As shown by Perreault (2010), the number of observed interactions between nodes can
573 dramatically affect the observed network. That notwithstanding, our study does show that not
574 considering all subsets of individuals constituting a group and its social network can limit our ability to
575 detect real relationships between sociality and parasitism.

576 Taking this idea a step further, we also conducted a series of random knock-out simulations in
577 which certain percentages of individuals were removed at random from the observed social network.
578 Removing 5% of individuals from the group at random impacted the results, and the strength of the
579 relationship between centrality and infection dramatically decreased in approximately 90% of the
580 subsequent models. Similar results were found when randomly removing 10%, 25%, or 50% of
581 individuals: fewer than 6% of models contained significant positive associations between centrality and
582 infection. It is worth mentioning that results from partial networks but with centrality metrics from
583 whole networks retained are much closer to the actual results from observed networks. These results
584 showed that it is the disrupted network structure rather than any effect of low statistical power that
585 largely dismantled the centrality-infection link.

586 Our results corroborate simulation and empirical studies demonstrating that missing nodes can
587 produce (more or less significant) measurement bias (Kossinets, 2006; Silk, 2018; Silk et al., 2015;
588 Smith and Moody, 2013; Smith et al., 2017). Other studies investigated the effect of random missing
589 nodes or targeted node removal, and not surprisingly, showed that targeted removal of more central
590 individuals had the strongest effect on network measures (Smith and Moody, 2013; Smith et al., 2017).
591 Moreover, as the proportion of individuals excluded increases, the probability that one or more central
592 nodes are excluded also increases (Silk, 2018; Silk et al., 2015; Smith et al., 2017). It is notable that, in
593 our study, random removals of individuals impacted the results even more than did targeted removals
594 of subsets of individuals, suggesting that, while the full network is always preferred, including complete
595 subsets might be important. Ultimately, however, whether individuals are omitted intentionally or
596 accidentally, our results highlight the potential impacts of partial networks on the conclusions drawn.
597 Despite our results and the conclusions drawn from them, we do not intend to devalue the results
598 of previous studies solely on these grounds. Partial networks can still provide robust network metrics,
599 providing that there is little imbalance as to who gets excluded (Borgatti et al., 2006; Silk et al., 2015).
600 In our study, we focused only on excluding broad categories of individuals or used pseudo-random
601 knock-outs, and we did not control for the specific social characteristics of the removed individuals. It
602 is further possible that excluding particular individuals – super-spreaders, keystone individuals, policing
603 individuals, alpha individuals – would have a much larger effect on the processes that occur on social
604 networks than would excluding individuals with a less influential role. For instance, knocking out
605 policers in a social group of pigtailed macaques greatly destabilized the structure of several social
606 networks, setting the stage for reduced group cohesion (Flack et al., 2006). This is also reminiscent on
607 the one hand of work investigating the effect of targeting specific individuals for health interventions or
608 information transmission: depending on which individual is targeted, information has a greater
609 likelihood to spread in the community (e.g. Kim et al., 2015), and on the other hand, of work looking at
610 the spread of an infectious disease or a parasite depending on which individual gets it first (e.g. Romano
611 et al., 2016). Knowing the characteristics of individuals that play important roles in the sociality-
612 parasitism relationship can help practitioners develop strategies for disease control (Romano et al., 2016;
613 Rushmore et al., 2014) and captive population management (McCowan et al., 2008) for examples.

In conclusion, our study confirmed that social network centrality is positively related to geohelminth infection in Japanese macaques, but at the same time brought to light some nuances to that relationship. Studying a partial network showed different results compared with the whole-group network model, leading to different conclusions. A bit of caution and increasing research effort is therefore warranted in future studies.

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Conflict of interest disclosure

The authors declare they have no conflict of interest relating to the content of this article.

Author contributions

ZX: Conceptualization; Data curation; Formal analysis; Writing – original draft.

AJJM: Conceptualization; Methodology; Project administration; Supervision; Writing – review and editing.

AC-N: Methodology; Investigation.

EM-M: Methodology; Investigation.

TS: Resources.

JD: Methodology; Supervision; Formal analysis; Writing – review and editing.

Data, script and code availability

The dataset (SP 1) and scripts are available on Git repository:

"https://github.com/XuZhihong-cn/Network_Centrality_analysis_and_KO-simulation"

The Supplementary information is available on Biorxiv:

"https://www.biorxiv.org/content/10.1101/2021.06.07.447302v1.supplementary-material"

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