Original Article

The "strength of weak ties" and helminth parasitism in giraffe social networks

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The so-called "strength of weak ties" is a central concept in social network theory, especially for understanding how information and diseases are transmitted through socially structured populations. In general, weak ties occur in networks where relatively few individuals are responsible for maintaining linkages between groups of individuals that would otherwise be poorly connected. This common structural motif can be seen in the social networks of species with fission–fusion social organization, such as giraffe (*Giraffa camelopardalis*). Giraffe social networks are characterized by social cliques in which individuals associate more with members of their own social clique than with those outside their clique. Individuals involved in weak, between-clique social interactions are hypothesized to serve as bridges by which an infection may enter a clique and, hence, may experience higher infection risk. Here, we address this and other hypotheses explaining helminth infection patterns in wild giraffe, exploring the relative roles of the social network and ranging behavior in determining infection risk. We show that infection risk is more influenced by weak ties with individuals outside one's clique than by repeated contact with a core set of associates. Even when controlling for age and home range size, individuals who engaged in more between-clique associations, that is, those with multiple weak ties, were more likely to be infected with gastrointestinal helminth parasites. Our results suggest that diverse social interactions with giraffe from multiple cliques may increase exposure to pathogens. The importance of weak ties in pathogen transmission has only rarely been empirically demonstrated in wildlife.

Key words: **African ecosystems, animal behavior, centrality, contact rates, disease ecology, epidemiology, parasite transmission, ranging behavior, social network analysis, social structure, wildlife.**

INTRODUCTION

High rates of pathogen transmission within social groups are often considered an important cost of sociality (Alexander 1974; Hoogland 1979; Brown and Brown 1986; Earley and Dugatkin 2010; Patterson and Ruckstuhl 2013). Positive correlations between parasitism and group size indicate that high rates of interaction among group members can create opportunities for pathogen transmission (Freeland 1976; Coté and Poulin 1995; Patterson and Ruckstuhl 2013). Most studies of sociality–parasitism trade-offs relate parasitism to group size (Hoogland 1979; Coté and Poulin 1995; Ezenwa 2004; Patterson and Ruckstuhl 2013), mating system, or individual group membership status (Porteous and Pankhurst 1998; Gompper 2004). Group-level metrics commonly used to study sociality–parasitism trade-offs, such as group size or population density, usually assume homogenous interactions among all group members (Wey et al. 2008), which often fail to detect pathogen-related costs in species exhibiting fission–fusion social dynamics where groups frequently shift in size and membership (Ezenwa 2004). Furthermore, the potential role of contact outside one's social group in spreading pathogens is also neglected.

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Social network metrics, in contrast, characterize individual variation in sociality and provide a more useful approach than group-level metrics to understanding pathogen-related costs of sociality in species that lack clearly defined social units (Godfrey 2013). Network analysis is also an effective tool for comparing the likelihood of acquiring infection through repeated contact with a specific set of individuals (analogous to within-group contact) versus intermittent contact with individuals outside one's core group (so-called "weak ties") (Granovetter 1973). The "strength of weak ties" concept has long been recognized as important for maintaining social cohesion in human and primate societies, and widespread diffusion of information within structured populations relies on weak ties (Granovetter 1973; Ramos-Fernández et al. 2006). Models of infectious disease transmission suggest that connections between communities are critical for disease spread (Salathé and Jones 2010; Nunn et al. 2015), and individuals involved in weak ties may serve as gatekeepers for infection within a social group. However, the "strength of weak ties" in increasing infection risk has not been explored to our knowledge, and there is little to no empirical evidence demonstrating this pattern in wildlife.

Direct contact among individuals is often not required for the transmission of environmentally transmitted pathogens, and social networks have been shown to influence infection patterns for such pathogens (Fenner et al. 2011; VanderWaal et al. 2013). Transmission of many gastrointestinal parasites, for example, relies on the ingestion of parasite eggs or larvae from fecal-contaminated water and forage (Kilani et al. 2010). Thus, shared space use, whether concurrently or disjointly, may be the primary factor mediating transmission opportunities. Similarly, the importance of intraspecific contact patterns may be masked for pathogens that can infect multiple host species. Because intraspecific contact patterns only capture one dimension of potential transmission routes for multi-host or environmentally transmitted pathogens, other aspects of behavioral ecology may better correlate with exposure risk, such as home range size (Ortiz-Pelaez et al. 2010; Devevey and Brisson 2012). Individuals with larger home ranges, all else being equal, may experience increased intra- and interspecific transmission simply by being exposed to a greater diversity of individuals and environments (Ezenwa 2003). However, this pattern may be more complicated if territorial behavior leads to more intense range use or spatial separation of social groups (Ezenwa 2004; Nunn and Dokey 2006; Nunn et al. 2011). The influence of social contact on pathogen transmission has only rarely been directly contrasted with that of space use and ranging behavior. Some studies find that the social network is more predictive of pathogen transmission patterns than measures of spatial proximity or home range overlap (Bull et al. 2012; Blyton et al. 2014; VanderWaal et al. 2014a), whereas others find the opposite relationship (Chiyo et al. 2014), though the latter did not use a social network approach.

This study contributes to the growing body of research examining the utility of networks in predicting individual infection risk (Otterstatter and Thomson 2007; Hamede et al. 2009; Craft and Caillaud 2011; Fenner et al. 2011; Porphyre et al. 2011; Godfrey 2013; VanderWaal et al. 2013; VanderWaal et al. 2014a). Here, we address multiple hypotheses explaining infection patterns of parasitism in wild giraffe (*Giraffa camelopardalis*) by gastrointestinal helminths. Although helminth prevalence in giraffe is low compared with sympatric ungulate species (VanderWaal et al. 2014b), presumably because foraging on tall vegetation minimizes exposure to helminth eggs and larvae (Apio et al. 2006), giraffe may be exposed to fecal-contaminated water or vegetation when drinking and occasionally feeding on forage <1 m from the ground (Young and Isbell 1991). We focus on helminths with no intermediate hosts and environmental transmission via the fecal–oral route (Kilani et al. 2010). We first compare the impact of social interaction and ranging behavior on helminth parasitism and then explore the relative roles of contact within and between social cliques in mediating an individual's risk of infection by helminths, where a clique is defined as a set of individuals that associated frequently with one another and more rarely with nonmembers (VanderWaal et al. 2014c). We hypothesize that individuals involved in weak, between-clique social interactions experience higher infection risk as a result of exposure to a greater diversity of conspecifics.

MATERIALS AND METHODS

Study area and population

This study was conducted at Ol Pejeta Conservancy (OPC), a 364 km² semiarid savanna woodland ecosystem located in Laikipia, Kenya (0°N, 36°56′E), from 21 January to 2 August 2011. All giraffe ($N = 212$) within OPC were recognized using individually unique spot patterns on their necks. Immigration and emigration were relatively negligible for this population because OPC is enclosed by a perimeter fence except for a few narrow gaps. Indeed, in the last 5 months of the study, only 2 new adults were discovered, which likely immigrated into the population. Disappearances could usually be attributed to death rather than emigration. Of the 3 adults that disappeared during the study period, all were observed in very poor condition prior to disappearing and 2 of their carcasses were discovered shortly after. Of 16 calves born at least 1 month before the end of the study period, only 50% survived to 1 month. First-month survivorship was probably overestimated, as some calves likely died before being observed. Given survival to the age of 1 month, the probability of survival to 2 months was 87.5%. Calves that reached 2 months of age had a very high likelihood of survival. Giraffe were aged according to height estimates and age-associated behaviors (Langman 1977; Pratt and Anderson 1979; Fennessy 2004; VanderWaal et al. 2014c). Animals were considered juveniles if they were <1.5 years, subadult from 1.5 to 4 years, and adult at >4 years. At the conclusion of the study, OPC's giraffe population consisted of 160 adults (82 females, 78 males), 20 subadults (8 females, 12 males), and 32 juveniles (14 females, 14 males, 4 unknowns).

Behavioral observations

Group membership was recorded for all giraffe groups sighted while driving daily survey routes. Routes were predetermined so that different regions of OPC were surveyed in rotation, allowing most of the study area to be surveyed every 3 days. Each route was ~100 km in length, covered ~115 km², and traversed all habitat types. Giraffe groups observed from survey routes were followed off-road until a complete census of the individuals present was accomplished (see VanderWaal et al. 2014a for more information).

A group was defined as a solitary individual or set of individuals engaged in the same behavior, or moving in the same direction or toward a common destination, as long as each giraffe was no more than 500 m from at least one other group member by chain rule (VanderWaal et al. 2014c). The height of vegetation in OPC is largely below the height of giraffe across all habitat types; hence, giraffe that are 500 m apart are in potential visual contact with one another. This definition is very similar to group definitions used

elsewhere in the literature for giraffe (Foster and Dagg 1972; Dagg and Foster 1976; Leuthold 1979; Pratt and Anderson 1985; Le Pendu et al. 2000; Carter et al. 2012). In our study region, giraffe in a group are typically within 100 m of one another, although some individuals may be farther (Shorrocks and Croft 2009). In practice, the distance between outlying individuals and the center of the group was typically <500 m. The mean group size at OPC was 5.4 individuals (range: 1–44 giraffe). Following a gambit-of-the-group definition of association (Croft et al. 2008), all individuals observed within a group were recorded as "in association" with every other member of the group. We collected a total of 1089 sightings of giraffe groups. Each individual was observed on average 31.1 ± 7.6 SD times (approximately once per week).

Each individual's home range was mapped using the GPS locations recorded for each group sighting. Home range boundaries were determined using a fixed-kernel utilization-distribution of sightings. A 75% contour (kernel density isopleth) was used to produce a core home range for each animal (Harris et al. 1999). Average home range size was 96 km² for adult males, 64 km² for adult females, 110 km² for subadult males, 70 km² for subadult females, and 51 km² for juveniles (VanderWaal et al. 2014c).

Social network construction

We constructed a social network using 7 months of giraffe behavioral observations. Individuals were represented as nodes in a network, and nodes were linked according to observed patterns of association. Links were weighted according to the frequency with which a pair of individuals was seen together in a social group (association strength). A simple ratio index for association strength was defined as the total number of observations in which they were seen together divided by the total number in which either was observed.

Giraffe social organization

The giraffe population in OPC can be subdivided into social cliques in which associations between individuals are more frequent among members of the same clique than between cliques (VanderWaal et al. 2014c). Using data-cloud geometry (DCG) to identify network community structure (Fushing et al. 2013), past work used the social network data outlined above to identify 10 single-sex social cliques. Modularity is a network metric, ranging between 0 and 1, that can be used to quantify the insularity of communities or cliques within a population and measures the relative frequency of within- versus between-clique interactions (Newman and Girvan 2004). Higher modularity indicates stronger community structure. In practice, networks with moderate to strong community structure will have modularity values ranging from 0.3 to 0.7 (Newman and Girvan 2004). Five cliques of adult and subadult males were identified (membership 6–19 giraffes, modularity for male network = 0.32). Forty-two males could not be reliably assigned to a clique and were thus considered nonaffiliated. Five cliques of adult and subadult females were also identified (membership 3–37 giraffe, modularity for female network = 0.44). There were no females that could not be reliably assigned to a clique (VanderWaal et al. 2014c). Previous work demonstrated that individuals of the same clique had significantly higher within-clique association strength than random expectations, indicating that the social divisions defined by the DCG algorithms captured relevant underlying structure within the network (VanderWaal et al. 2014c). Modularity values further indicate that links in the network tend to be within rather than between cliques. Membership in male cliques was largely unrelated to space

use, whereas female cliques tended to occupy more distinct home ranges (VanderWaal et al. 2014c). Juveniles were not included in the DCG analysis because their behavior was not independent of their mothers (Langman 1977; Pratt and Anderson 1979; Fennessy 2004). Juveniles were assigned to their mother's clique.

Helminth collection and analysis

Fecal samples were collected from 96 giraffe in the month following the conclusion of the behavioral study period. Sampling included 39 adult males, 31 adult females, 9 subadult males, 6 subadult females, 5 juvenile males, and 6 juvenile females. In order to avoid biasing our estimates of helminth prevalence by over- or under-sampling parts of the study area, sample collection was conducted across 10 spatial blocks within OPC, with 8–10 fecal samples collected per block (Figure 1). Although animals may move across block boundaries, this approach allowed us to coarsely place an individual's home range within the study area for descriptive analyses of spatial variation in infection. Nine cliques were sampled with >33% of members sampled. One clique was not sampled, but it was extremely small with only 3 females. Fecal samples were preserved in 10% formalin.

The force of infection experienced by individual giraffe may vary across the landscape due to environmental conditions that promote or deter parasite survival. If underlying environmental conditions create hotspots for parasite survival, then these hotspots in parasite infection should occur for all susceptible ungulate species. To account for such underlying spatial distributions in these multi-host parasites, 116 fecal samples were collected from 7 other ungulate species in OPC (15 buffalo, *Syncerus caffer*; 14 domestic cattle, *Bos indicus*; 18 eland, *Taurotragus oryx*; 14 hartebeest, *Alcelaphus buselaphus*; 18 impala, *Aepyceros malampus*; 19 Thomson's gazelle, *Gazella thomsonii*; and 18 plains zebra, *Equus burchelli*) (VanderWaal et al. 2014b). Samples were stored in 10% formalin until further analysis. Parasitological analyses were also performed on these samples, and prevalence was calculated for each species and for each spatial block.

A modified sedimentation technique was used to assess helminth egg presence/absence (VanderWaal et al. 2014b). A pestle was first used to gently mash fecal samples. Three grams of fecal material were mixed with 45 mL distilled water, stirred, and strained. Sediment was left to stand for 30 min before the supernatant was decanted. The sediment was resuspended with 45 mL of water. Decanting and resuspension was repeated 2–3 times until the suspension was clear.
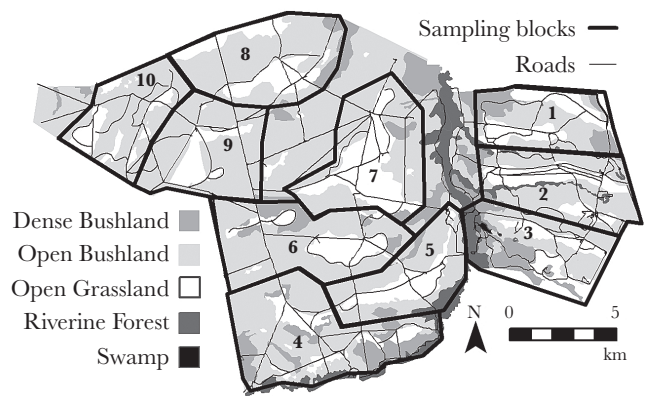

Figure 1
Map of Ol Pejeta Conservancy depicting habitat types, road network, and sampling blocks. Reproduced from VanderWaal et al. (2014b).

At this point, 3 glass slide preparations were made and examined at ×100 magnification under a digital light microscope (Leica, DM500, Sciencescope, Nairobi, Kenya). Morphological features such as shape, size, and color were used to identify most eggs to the genus level, with the exception of strongyle-type eggs (Foreyt 2001). Eggs of nematodes in the order Strongylida are morphologically indistinguishable at the genus level and thus referred to by the general term "strongyle." Common genera within this order include *Haemonchus*, *Oesophagostomum*, *Cooperia*, and *Bunostomum*. An individual was considered infected if at least 1 egg was detected.

Helminth prevalence for each age-class and for each spatial block was calculated as the proportion of individuals in which helminth eggs were detected. Parasite species richness per individual was calculated as the number of different helminth taxa detected within an individual.

Statistics

We calculated 4 standard measures of social network connectivity for each individual. Because links in the social network were weighted by association strength, weighted versions of each measure were used (Opsahl et al. 2010). "Overall tie strength" quantified the summed strength of associations in which a node was engaged. For each individual, we also calculated the summed strength of associations that were with members of the same social clique ("within-clique tie strength") or a different clique ("between-clique tie strength" or "weak ties"). For males that could not be reliably assigned to a clique (*n* = 42), all of their associations were considered between clique. "Betweenness" was also calculated, which essentially measures the extent to which an individual lies on paths through the network that connect other pairs of individuals (Wasserman and Faust 1994; Opsahl et al. 2010). Tie strength and betweenness have been shown in other studies to correlate with infection risk (Corner et al. 2003; Fenner et al. 2011).

To investigate which factors influenced the risk of infection by helminths, we performed generalized linear models (GLMs) with a binomial distribution and logit link function. The outcome variable (0/1) was whether an individual was infected by helminths. Because of nonindependence concerns with network data, regression coefficients were determined using GLMs and *P* values were calculated via permutation methods for both univariate and multivariate models (3000 permutations) (Hanneman and Riddle 2005; Croft et al. 2011; Rushmore et al. 2013; VanderWaal et al. 2014a). Covariates examined included sex, age, home range size, tie strength (overall, within clique, and weak ties), and betweenness. Covariates in which *P* < 0.1 in univariate regressions were included in multivariate

models. An interaction between age and sex was also considered in multivariate models. Multivariate models of infection risk were backward selected from the full model. Before performing multivariate models, correlations among covariates were examined (Pearson's correlation coefficient). Variance inflation factors were also calculated for each multivariate model to assess any potential collinearity issues, where factors of >2.0 were considered problematic (Graham 2003). The performance of univariate and multivariate models were compared using Akaike's information criterion (AICc), corrected for small sample size (Burnham and Anderson 2002). All analyses were performed using R v3.1.1.

RESULTS

The prevalence of helminths in the sampled giraffe population in OPC was 9.4% (95% confidence interval: 3.5–15.3%). The 3 helminth taxa observed in giraffe were *Trichostrongylus* spp., *Trichuris* spp., and strongyle-type nematodes. Males were significantly more likely to be infected than females, and subadults were more likely to be infected than adults or juveniles (Tables 1 and 2). Prevalence in subadult males (>40%) was substantially higher than in all other age-classes (Table 1). A higher proportion of giraffe sampled from blocks 6–9 were infected (Supplementary Figure S1a). However, there was no clear spatial pattern in helminth prevalence for other host species (Supplementary Figure S1b), even when prevalence calculations were based only on helminth genera that were also found in giraffe (Supplementary Figure S1c). All infected individuals were members of social cliques.

We examined all multivariate models for collinearity issues. Variance inflation factors of >2.0 appeared only in the full model, which received <2% model weight. There were no collinearity issues for models in the remaining multivariate models. To further contrast the relative roles of home range, weak ties, and age, we ran 3 additional multivariate models to directly contrast models containing each possible 2-way combination of these variables. Again, there were no collinearity concerns identified for these additional models. Subadults were more likely to be infected than adults and juveniles in a univariate model containing age, although no multivariate model containing age received >12% of AICc weight. Males were slightly more likely to be infected than females (Tables 2 and 3). An interaction between age and sex was not statistically significant.

Weak ties were among the most important factors predicting infection in giraffe. The 3 best-fit models, which accounted for >70% of AICc weight, all included weak ties (Table 3, Figures 2a and 3). Infection risk was also related to larger home range sizes

Table 1

Summary of helminth infection in giraffe by age and sex. Prevalence for each helminth taxa are reported as proportions ± standard error

	Adult		Subadult		Juvenile	
	F	M	F	M	F	M
Strongyles	0	0.03 ± 0.04	0	0.11 ± 0.10	0	0
Trichotrongylus	0.03 ± 0.03	0.07 ± 0.05	0	0.11 ± 0.10	0	0
Trichuris	0.03 ± 0.03	0	0	0.33 ± 0.16	0	0.2 ± 0.18
Overall prevalence	0.05 ± 0.03	0.07 ± 0.05	0	0.44 ± 0.17	0	0.2 ± 0.18
Sample size	39	31	6	9	6	5
Richness (individual)	1	1.5	0	1.25	0	1
Prevalence by age	0.06 ± 0.03		0.27 ± 0.11		0.09 ± 0.09	

and age (Table 3, Figure 2c), but univariate models of these 2 variables received far less weight than the weak ties model (Table 2). Individuals with high betweenness and overall tie strength were also more likely to be infected (Figures 2b and 3), though neither factor was significant in the best multivariate models. Both factors received far less weight in comparisons of univariate models.

All infected individuals were from blocks 6–9. To remove any interdependence between an individual's engagement in weak ties and being in a geographically central location (potentially overlapping spatially with a greater diversity of cliques), we restricted the analysis to only the giraffe from these central spatial blocks. Weak ties remained correlated within infection risk ($P = 0.02$), whereas age and home range dropped out of significance.

DISCUSSION

The risk of infection by helminths was highly correlated with an individual giraffe's position within the social network. Giraffe that more frequently engaged in weak ties by associating with individuals from other social cliques were more likely to be infected. Subadults and individuals with large home ranges also had higher infection risk (Table 2, Figure 2). However, models including home range size or age had less predictive value than models that included weak ties. Given that giraffe home range size was correlated with weak ties and with the total number of giraffe with which an individual interacted (VanderWaal et al. 2014a), the effect of home range may be potentially mediated through its impact on interaction patterns (VanderWaal et al. 2014a). Alternatively, widely ranging individuals potentially acquire parasites from a greater diversity of environments and host species. Although age and sex were less important predictors of infection (Table 2), subadult males exhibited the highest parasitism, weak ties, and home range size. Thus, it is difficult

to tease apart the interrelated effects of age-correlated social and ranging behavior and other age-correlated factors that may affect the likelihood of acquiring infection, such as immunosuppression by testosterone (Folstad and Karter 1992; Poulin 1996; Zuk and McKean 1996; Grear et al. 2009; Krasnov et al. 2012; Godfrey 2013). In addition, acquired immunity, which may lead to suppression of egg production by parasites, could also generate a decline in prevalence in adults (Wilson et al. 2002). Nevertheless, the importance of weak ties overshadowed the effects of ranging behavior and age in determining helminth infection patterns as demonstrated by the inclusion of weak ties in 4 out of 5 of the best-fit models. When these 3 factors were included together in multivariate models, weak ties remained significant even after controlling for age and home range size. The relative importance of weak ties is even more apparent when comparing only univariate models, in which weak ties received >75% of AICc weight (Table 2).

The observed relationship between the social network and helminth infection risk seems counterintuitive because helminths are environmentally transmitted; relationships in the social network should not necessarily be predictive of transmission opportunities, though it is possible that males may engage in fecal–oral contact with females when inspecting their rumps for estrus cues. An examination of spatial patterns in parasite prevalence across sampling blocks revealed that all positive fecal samples were collected in the central sampling blocks of OPC (Figure 1 and Supplementary Figure S1). Giraffe in these areas may be central in the social network in part because they live in areas that are geographically central. Thus, they may engage in more weak ties because their geographic location enhances their social connectivity to giraffe located across the eastern, western, and southern regions. However, even when statistical analyses were restricted to only the 40 giraffe from the central spatial blocks, weak ties remained an important predictor of risk, whereas age and home range dropped out of significance.

Because of the geographic clustering of infections, it may at first seem possible that the importance of weak ties does not arise from social patterns, but rather from some aspect of the environment in these central areas that made environmental transmission more likely (e.g., moisture, sunlight exposure, contaminated water holes, higher levels of fecal contamination). If such transmission hotspots existed, then helminth prevalence should be higher in these spatial blocks for all host species, but this was not the case. Prevalence across spatial blocks was fairly uniform for other host species (Supplementary Figure S1b). Even considering only those helminth taxa that also occurred in giraffe (strongyles, *Trichostrongylus*, and *Trichuris*), prevalence showed no clear spatial pattern in other host species (Supplementary Figure S1c). Thus, spatial hotspots for transmission cannot explain why geographically central giraffe
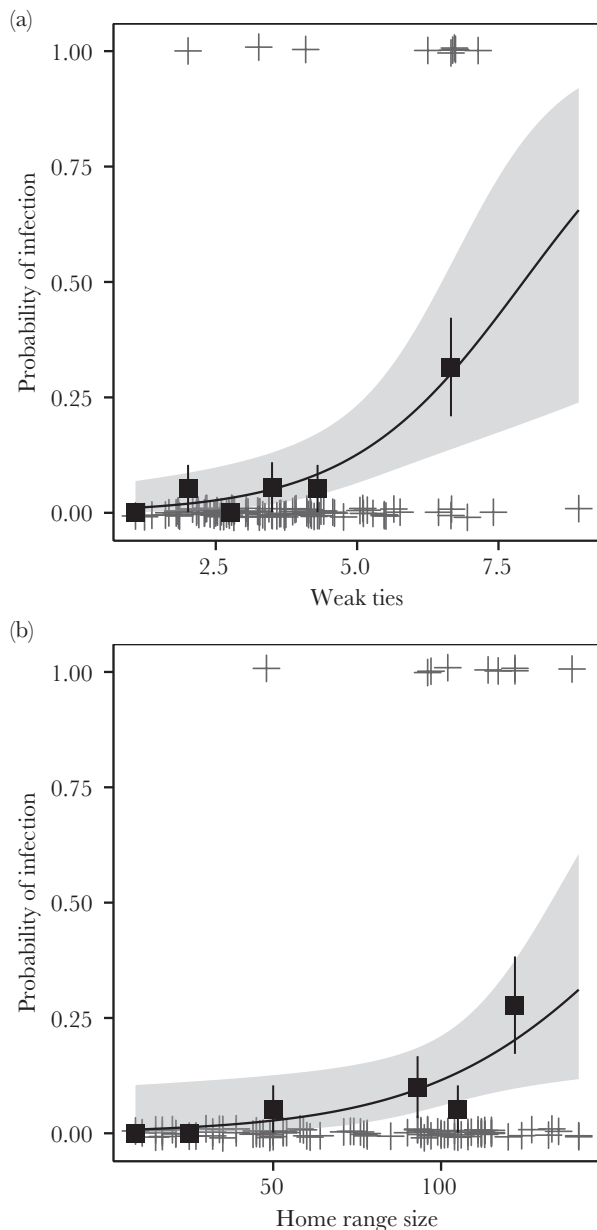
Table 2

Univariate model results for potential social and ecological predictors of helminth infection risk in giraffe

Covariate	Coefficient	*P* value	dAICc	AICc weight
Weak ties	0.68	<0.01	0	0.75
Home range	0.03	0.01	3.8	0.11
Overall tie strength	0.5	0.01	5.7	0.04
Betweenness	0.002	0.03	6.3	0.03
Sex: male	1.53	0.04	6.6	0.03
Age				
Juvenile	0.50	0.29		
Subadult	1.89	0.01	7.4	0.02
Intercept only	−2.26	0.60	8.6	0.01
Within-clique tie strength	−0.16	0.22	10.1	<0.01

AICc weights were calculated relative to other univariate models.

Table 3

Coefficients of best-fit models for helminth infection risk in giraffe

Model	Weak ties	Home range	Age: juvenile	Age: subadult	Betweenness	dAICc	AICc weight
A	0.68**					0	0.52
B	0.61*	0.19^	1.85*	0.39		3.0	0.11
C	0.67**		1.25^	0.54		3.2	0.11
D		0.03*				3.8	0.08
E	0.49*	0.02	1.78^	0.74	0.001	4.2	0.06

Only models receiving >5% AICc weight are shown. AICc weights were calculated relative to all univariate and multivariate models.
*P < 0.05, **P < 0.01, ^P < 0.1.

Figure 2

Relationship between infection risk and (a) weak ties, and (b) home range size. Crosses indicate observed data. Black squares indicate proportion (±standard error) of giraffe infected, summarized by quintile. Regression lines are shown in black, with shaded areas indicating 95% confidence intervals.

were more likely to be infected. One caveat to this spatial analysis is the possibility of animal movement between blocks. We cannot assume that individuals were infected in the same location as they were sampled, though many of the smaller species (gazelles, impala, hartebeest) have very localized home ranges (Jones et al. 2009). Although animals may move across block boundaries, our blocking approach allowed us to coarsely place an individual's home range within the study area for the purposes of descriptive analyses of spatial variation in infection.

The relative importance of weak ties over overall tie strength for predicting infection risk was somewhat unexpected given that tie strength has been shown in numerous studies to be predictive of infection risk (Godfrey et al. 2010; Fenner et al. 2011; Bull

et al. 2012). Although correlated ($\rho = 0.52$), weak ties performed remarkably better than overall tie strength in univariate models (AICc weight of 0.75 vs. 0.04, respectively). For giraffe, weak ties were indicative of the diversity of social cliques with which an individual interacted (Figure 3), and this information is lost when considering only overall tie strength. The relative embeddedness of infected versus uninfected nodes within their cliques can be visually assessed by zooming in on the immediate neighbors of a node (Figure 3a,b). The contacts of individuals with fewer weak ties were nested within a single social clique (Figure 3a). Such an individual may have high overall tie strength, but moderate or low between-clique associations. Contrast this to individuals with more weak ties, whose connections are dispersed across multiple cliques (Figure 3b). With these insights, it becomes clear how "socially adventurous" individuals engaging in more weak ties can potentially experience more diverse sources of exposure to parasites.

The role of weak social ties between groups and strong ties within groups is implicit in pathogen transmission models that use social group or herd as the epidemiological unit. Such models essentially focus solely on weak ties and do not model transmission within an infected group, which is assumed to be rapid (Green et al. 2006; Kao et al. 2006; Craft et al. 2011; Bajardi et al. 2012). Weak ties are also central to the social bottleneck hypothesis, which proposes that clique-like structuring within social groups slows the spread of pathogens (Nunn et al. 2015). In both these scenarios, it is also implicit that any introductions of a pathogen into a new social group or subgroup must be mediated through those individuals that engage in extra-group contact. Hence, such individuals would experience higher infection risk. This pattern has only rarely been demonstrated in wildlife. In a territorial species of lizard (*Tiliqua adelaidensis*), Fenner et al. (2011) showed that individuals infected with nematodes had a greater number of neighbors that were new to the area than noninfected individuals. Although this does not directly show the importance of weak ties, it does suggest that individuals originating elsewhere were a potential source of infection. Drewe (2010) demonstrated that between-group roving behavior by male meerkats (*Suricata suricatta*) put them at higher risk of tuberculosis infection (*Mycobacterium tuberculosis* complex), though individuals interacting with rovers did not experience higher risk. Here, we demonstrate that even for species like giraffe, which exhibit highly overlapping space use and fluid fission–fusion dynamics, interactions with numerous different social cliques may elevate an individual's risk of acquiring infections, whereas repeated interactions with a core group of associates has relatively little impact on risk.

Our results demonstrate that social networks quantify data relevant for predicting infection patterns for multi-host pathogens with environmental transmission. It may be important to note that giraffe exhibit much lower helminth prevalence than sympatric ungulate species, perhaps because they rarely forage on the ground and thus their exposure to fecal-contaminated forage is limited (Apio et al. 2006; VanderWaal et al. 2014b). The effect of social patterns may be more obscured for host species that experience higher levels of exposure to fecal-contaminated forage. We found strong interrelationships between age-class, network position, and parasitism, making it difficult to conclude that parasitism imposed a cost on sociality for giraffe. Rather, it is more accurate to suggest that increased parasitism was a consequence of age-specific behaviors exhibited by subadult males, which were captured by the social network. Patterns in social behavior and infection would have been difficult to show using other approaches that rely on group-level metrics of sociality (e.g., group size) because giraffe group
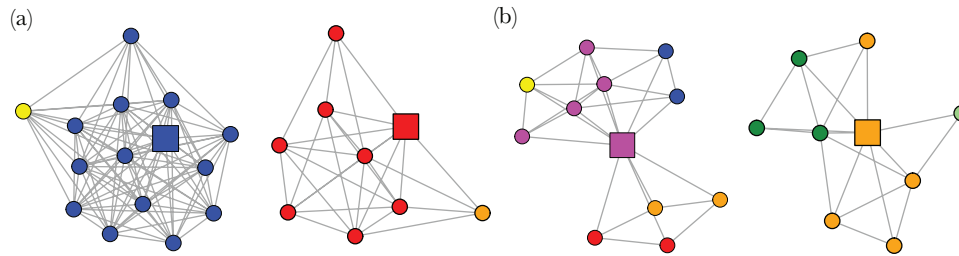
Figure 3

Immediate neighbors of 2 randomly selected uninfected giraffe (square nodes in a) and 2 infected giraffe (square nodes in b), illustrating the extent to which uninfected nodes were embedded within their social clique, whereas infected nodes engaged in more between-clique associations. Square nodes indicate the focal node. Coloration of nodes represents clique membership. For visualization purposes, only links with association strength >13.1% are shown (mean + 1 SD).

membership is fluid and constantly shifting on a daily or even hourly timeframe. These sorts of fission–fusion dynamics make group size a poor metric of the social environment experienced by an individual, whereas network analysis offers a much more elegant and discriminating approach for capturing individual variation in social behavior.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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