USDA Wildlife Services - Staff Publications

U.S. Department of Agriculture: Animal and Plant Health Inspection Service

2023

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Michael E. Egan
Southern Illinois University Carbondale, michael.egan@siu.edu

Kim M. Pepin
USDA APHIS NWRC, Fort Collins, kim.m.pepin@aphis.usda.gov

Justin Fischer
USDA-APHIS-Wildlife Services, Justin.w.fischer@aphis.usda.gov

Scott R. Hygnstrom
University of Wisconsin-Stevens Point

Kurt C. VerCauteren
USDA-APHIS-Wildlife Services, kurt.c.vercauteren@usda.gov

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Authors

Michael E. Egan, Kim M. Pepin, Justin Fischer, Scott R. Hygnstrom, Kurt C. VerCauteren, and Guillaume Bastille-Rousseau

A R T I C L E

D i s e a s e   E c o l o g y

Social network analysis of white-tailed deer scraping behavior: Implications for disease transmission

Michael E. Egan[1,2] ![ORCID] | **Kim M. Pepin**[3] ![ORCID] | **Justin W. Fischer**[3] |
Scott E. Hygnstrom[4] | **Kurt C. VerCauteren**[3] | **Guillaume Bastille-Rousseau**[1,2] ![ORCID]

[1]Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, Illinois, USA

[2]School of Biological Sciences, Southern Illinois University, Carbondale, Illinois, USA

[3]National Wildlife Research Center, United States Department of Agriculture, Animal and Plant Health Inspection Services, Wildlife Service, Fort Collins, Colorado, USA

[4]Wisconsin Center for Wildlife, College of Natural Resources, University of Wisconsin-Stevens Point, Stevens Point, Wisconsin, USA

Correspondence
Michael E. Egan
Email: michael.egan@siu.edu

Handling Editor: Allison M. Gardner

Abstract

Host contact structure affects pathogen transmission in host populations, but many measures of host contact do not distinguish contacts that are relevant to pathogen transmission from those that are not. Scrapes are sites for chemical communication by white-tailed deer (*Odocoileus virginianus*) during the breeding season and potential sites of transmission of prions, the causative agent of chronic wasting disease (CWD). Scrape-related behaviors vary in their probability of transmitting prions to or from the environment, suggesting that behavior be combined with contact structure to better reflect potential heterogeneity in prion transmission at scrapes. We recorded visits and behaviors by deer at scrapes throughout DeSoto National Wildlife Refuge, Nebraska in 2005 and 2006. We recorded 2013 interactions by 169 unique identifiable males and 75 females. Adult males performed the most scrape-related behaviors and spent the most time at scrapes, especially smelling the overhanging branch (70%), smelling the scrape (59%), licking/grasping the overhanging branch (44%), and scraping (36%). We used social network analysis to test the effect of behavior on indirect contact networks among deer at scrapes. By weighting edges based on the frequency and duration of behaviors, we produced networks representing sources of variation in scrape use and compared these networks to evaluate the effects of behavior on network contact structure. Social networks based on scrape-related behavior were highly connected and dependent upon the frequency, duration, and type of behavior exhibited at scrapes (e.g., scraping, interacting with a scrape or overhanging branch, rub-urinating, grazing) as well as the age of the deer. Accounting for contact frequency produced networks with lower variation in contact, but higher ability to facilitate contact among disparate groups. Including behavior when defining edges did not preserve the network properties of simpler measures (i.e., unweighted networks) suggesting that heterogeneity in behaviors that affect transmission probability is important for inferring transmission networks from contact networks. High connectivity through indirect contacts suggests that scrapes

may be effective targets for management. Adult male deer had the highest connectivity, suggesting that management strategies focused on reducing their interaction with scrapes through density reduction or behavioral modification could reduce the connectivity of indirect contact networks.

KEYWORDS
behavior, chronic wasting disease, CWD, disease, network, *Odocoileus virginianus*, scrape, transmission, white-tailed deer

INTRODUCTION

Social networks are useful tools for understanding the potential for transmission of diseases through populations (Silk, Croft, Delahay, Hodgson, Boots, et al., 2017; White et al., 2017). Social networks can represent the number, strength, and spatial attributes of connections between individuals. When applying social network analysis, individuals are represented as "nodes" connected by "edges" that indicate contact between nodes. Pathogen transmission can be represented by summarizing the characteristics of network structure that describe the connectivity of the overall population (Sosa et al., 2021) (Table 1), but contact networks only represent "potential" pathogen transmission networks (Craft, 2015). How pathogens actually move through host contact networks can depend on several different components of contact. For example, the frequency and duration of host contact can affect the likelihood of pathogen shedding and uptake, as can the types of behaviors that occur during contact (e.g., talking vs. singing or

sneezing in humans) (Lotfli et al., 2020). When using contact networks to predict the spread of pathogens, it is important to understand how heterogeneity in different components of contact (frequency, duration, behavior of contact) may affect the probability of transmission during contact to better predict pathogen transmission potential (i.e., pathogen transmission networks).

Chronic wasting disease (CWD) is a fatal disease infecting deer (Cervid spp.) in North America and Europe (Haley & Hoover, 2015; Williams, 2005). It is spread by the transmission of prions shed through bodily fluids that may remain infectious in the environment for years (Hoover et al., 2017). Therefore, transmission may occur during direct social interaction such as mating or aggressive encounters, or indirectly when a deer takes up prions from the environment during feeding or other activities that occur in areas of shared space. Managers and researchers have developed control strategies that rely on understanding risk factors for CWD transmission (Mysterud et al., 2019; Uehlinger et al., 2016). For example, in many areas,

TABLE 1 Network- and individual-level social network metrics used for measuring the centrality of individuals.

Metric	Definition	Biological meaning
Mean path length	The average no. connections needed to connect each pair of individuals	Shorter mean path length indicates disease is more likely to spread among individuals
Transitivity	The no. completed triangles (groups of three individuals connected to each other) out of all possible triangles	High transitivity indicates that interactions occur more among some groups than others and that disease may not transfer among other groups as easily
Edge density	The proportion of completed edges out of all possible edges	High edge density indicates that disease may spread to all individuals within a population
Closeness	Inversely proportional to the path length from that individual to all other individuals	Individuals with greater closeness could spread disease to others with fewer intermediates
Betweenness	No. times an individual occurs on the shortest path between two other individuals	Individuals with greater betweenness connect a greater no. disparate individuals
Strength	The combined weight of all connections of an individual in a network	Individuals with greater strength interact with others more often or with interactions that have a greater risk of transmission of disease
Eigenvector centrality	A measure of influence in the network that takes into account connections and connections to connections	Individuals with greater eigenvector centrality generally have greater potential to spread disease

regulations associated with providing bait to deer have been established in attempts to lessen the congregation of deer at anthropogenic point sources of highly desirable foods because the high stability of prions can lead to build up of prion concentrations that can be spread through indirect contact (hosts in the same place at different times; Sorensen et al., 2014). Sharing saliva at a bait pile is one example of a behavior that is high risk for transmission and can occur through indirect contact. The potential transmission of CWD is dependent on both the contact rate and this heterogeneity in the propensity of a behavior to transmit prions, meaning that it is important to understand how these behaviors may impact transmission risk in contact networks (Joseph et al., 2013).

A potential route of indirect transmission of CWD prions in white-tailed deer (WTD; *Odocoileus virginianus*) is through scraping behavior. Male deer make and maintain scrapes by scraping the ground beneath an overhanging branch of one of many odor-producing trees and use them for communication among males and females during the breeding season (Alexy et al., 2001; Marchinton et al., 1990; Marchinton & Hirth, 1984; Miller & Marchinton, 1999). Typical scraping behavior is varied but most often involves scraping and smelling the ground, licking the branch, rubbing secretions from head glands on the branch, or otherwise leaving bodily fluids (Hewitt, 2011). Chemical marking by WTD likely influences the risk of disease transmission, depending on the behavior (Alexy et al., 2001; Miller et al., 1987). For example, rubbing and licking overhead branches involve contact with glands of the eyes and mouth, resulting in potential shedding or uptake of prions that cause CWD. Rub-urination may result in deer shedding prions or sniffing or licking contaminated soil (Table 2). Transmission of CWD at scrapes likely will occur due to indirect contact because prions are shed by infected deer and may be taken up by subsequent deer visiting or using scrapes (Haley & Hoover, 2015; Jennelle et al., 2014). While social networks have been studied for WTD (Schauber et al., 2015), no studies have examined social networks based on indirect contact at deer scrapes or how different behaviors could affect the likelihood of prion transmission and therein modify the structure of the social network in terms of disease transmission potential. As such, scrapes represent an understudied part of deer social behavior and network modeling could be used to evaluate the potential for disease transmission at scrapes (Kinsell, 2010).

The disease transmission potential of indirect contact networks, such as at scrapes, is a stepwise process where one individual first sheds infectious particles and then a second individual uptakes those particles. "Directed" social networks distinguish which individual is the shedder versus the individual that could uptake the pathogen using

TABLE 2 Relative risk values (0–1) of individual behaviors of white-tailed deer at scrapes, based on expert opinion.

Behavior	Uptake	Shedding
Grazing	0.8	0.4
Smelling scrape	0.6	0.2
Licking scrape or branch	1.0	1.0
Smelling branch	0.4	0.1
Scraping ground	0.1	0.1
Chewing overhanging branch	1.0	1.0
Rubbing overhanging branch with eye	0.9	0.4
Rub-urinating	0.0	0.6
Urinating	0.0	0.5
Defecating	0.0	0.7
Flehmen posture	0.9	0.3

Note: Values were derived from research- and experience-based deliberations by Scott Hygnstrom, Travis Kinsell, Nancy Matthews, and Kurt VerCauteren, 2010. The authors have >100 years of combined experience conducting research on white-tailed deer, deer behavior, wildlife diseases, and chronic wasting disease.

directional edges (arrows) that link the two individuals (Silk, Croft, Delahay, Hodgson, Weber, et al., 2017). "Weighted" networks scale the edge weight to the amount of interaction between nodes, reflecting variation in the likelihood of transmission based on how often pairs of nodes interact. In addition, edges in weighted networks may be scaled to account for behavior and duration of contact, both of which could affect transmission risk. While studies have compared social networks representing different species, subgroups, or behaviors (Perkins et al., 2009; Vander Wal et al., 2015), few have evaluated the effect of behavioral context on the network position of individuals (but see Plaza et al., 2020; Wilson et al., 2013).

Here, we analyze the characteristics of indirect contact networks among male WTD due to scrape use and how behavioral variation among male deer at scrapes might affect the structure of the network. While we are focusing on a behavioral dataset without explicit data on disease transmission and prevalence, our analysis is aimed primarily at understanding how potential sources of heterogeneity may impact disease transmission and management implications. We built social networks representing components of contact and compared individual-level metrics among networks and individuals. We hypothesized that heterogeneity in contact and probability of transmission during contact would result in differences between networks based on simple definitions of contact to estimates of contact that account for individual behavior (H1). We predicted that accounting for contact frequency, duration, and scrape-related behavior would result in variation in network structure because

individuals differ in how often they visit scrapes, how much time they spend, and what they do behaviorally at those scrapes. Additionally, we predicted that the age of deer and proportion of agricultural cover around scrapes would be positively related to their network centrality (the relative importance of an individual defined by their effect on other individuals in the network) because adult deer are more active and more dominant at scrapes (DeYoung et al., 2006) and food resources associated with agricultural production maintain higher densities of deer (Magle et al., 2015). Understanding how behavior of WTD affects indirect contact network characteristics will provide improved knowledge for managing and reducing transmission of CWD.

MATERIALS AND METHODS

Study area

The study was conducted in DeSoto National Wildlife Refuge (DNWR) located 32 km north of Omaha, Nebraska between Blair, Nebraska, and Missouri Valley, Iowa, USA. The DNWR was a 3166-ha mosaic of forest, grassland, wetland, and agricultural fields administered by the US Fish and Wildlife Service. Wooded areas at DNWR consisted largely of mature eastern cottonwood (*Populus deltoides*) with understory vegetation that included hackberry (*Celtis occidentalis*), red mulberry (*Morus rubra*), and green ash (*Fraxinus pennsylvanica*). In 2005–2006, about 400 ha of the refuge were farmed by neighboring producers. Crops included corn, soybean, sorghum, clover, alfalfa, oats, and wheat. Approximately 10% of crops were left standing as food plots for wildlife. Preharvest densities of WTD at DNWR were estimated at 41–51 deer/km^2 from 2004 to 2007 (Hefley et al., 2013). Female:male ratios were 2.15:1 and 1.86:1 and fawn:doe ratios were 1.28:1 and 1.43:1 in 2005 and 2006, respectively (Clements et al., 2011). During this time, 20–25 females and 20–30 males were radio-collared and ear-tagged at DNWR and an additional estimated 42 males and 17 females were marked with ear tags alone. We estimate up to 24% of the males and 6% of the females were marked on DNWR during the study. At the time of the study, no cases of CWD had been detected in the area. The study site was selected to represent a typical Midwestern landscape where deer behavior is representative of what is seen in most of the region with a focus on deer social behavior and not CWD per se.

Field methods

Data on deer behavior at scrapes in this study originated from previous research conducted to monitor deer in DNWR (Kinsell, 2010). During the fall breeding season (October–November 2005 and 2006), 478 scrapes were located in the study area by walking forest-field edges, trails, and roads through the forest. Eighty-five of these scrapes were monitored in 2005 and 44 were monitored in 2006. Scrapes were selected for monitoring if they appeared to be recently active and associated with an overhanging "lick" branch. Sixty-two of the 85 scrapes were located on forest-field edges and 23 were in forest interiors. Scrapes were monitored with remote infrared motion-activated video cameras (StumpCam, Tyler, TX, USA) and motion-activated digital cameras (Reconyx Silent Image, LaCrosse, WI, USA). StumpCams were checked every 3–4 days and Reconyx cameras once per week. StumpCams monitored scrapes for a combined 976 functional camera days. Reconyx cameras monitored scrapes for a combined 519 functional camera days. We programmed StumpCams to record for 3 min when triggered with a 10-s (hardware minimum) recycle period between triggers. We programmed Reconyx cameras to take 1 frame/s for 30 s, with a 1-s recycle time between triggers. We noted an encounter with a scrape when a WTD came within 2 m of a scrape and could identify and interact with the scrape (e.g., deer walks near the scrape vs. running past the scrape). An "interaction" with a scrape occurred when a deer approached a scrape and performed any scrape-related behaviors as defined below. We examined videos and images frame by frame to identify behaviors associated with scrapes and overhanging branches. Individual WTD were identified by collars, ear tags, antler characteristics, and other unique markings. We recorded occurrence and duration (in seconds) of each scrape-related behavior for each interaction and generated sex- and age-specific descriptive statistics for occurrence and duration of each scrape-related behavior.

Behavioral categories included: grazing, smelling scrape, licking scrape or branch, smelling branch, scraping ground, chewing overhanging branch, rubbing overhanging branch with eye, rub-urinating, urinating, defecating, and flehmen posture (Alexy et al., 2001; Hirth, 1977; Kile & Marchinton, 1977; Kinsell, 2010; Miller et al., 1987; Pruitt, 1953; Table 2). We assigned a value to each behavior that represented the likelihood of shedding or uptake of prions and, ultimately, risk of transmitting infectious prions. No studies have assessed the probability of the transmission of prions based on sampling deer for the prevalence of the disease before and after each behavior, so risk values were assessed based on expert opinions and the biology of prion transfer. These values were determined by thorough familiarity of the body of knowledge in the peer-reviewed and popular literature on scrapes (Hewitt, 2011; Marchinton et al., 1990; Miller et al., 1987, 2004); empirical observation and qualitative assessment were done by Scott Hygnstrom, Nancy Matthews, and Kurt

VerCauteren, who have >100 years combined extensive research experience with WTD and wildlife diseases.

Social network analysis

We generated social networks with individual deer as nodes and edges based on two deer using the same scrape (Farine & Whitehead, 2015). Social networks were generated for 2005 and 2006 separately. We assumed that identifiable deer within the population were consistent within a season, meaning that each network represented deer using scrapes during the breeding season for that year only. We estimated social networks by generating adjacency matrices using five methods representing increasingly complex edge definitions (Figure 1). All networks were directed networks where, for any two deer (deer 01 and deer 02), a contact was counted only if deer 01 visited the scrape before deer 02. It is possible that a scrape visit resulted in a direct contact between deer, resulting in two deer making both direct and indirect contact through sequential scrape use; however, we include all contacts that meet the criteria to at least be defined as indirect contact and refer to networks as "indirect contact networks" (Wilber et al., 2022). At the least complex level, any two deer that made an indirect contact were given an edge
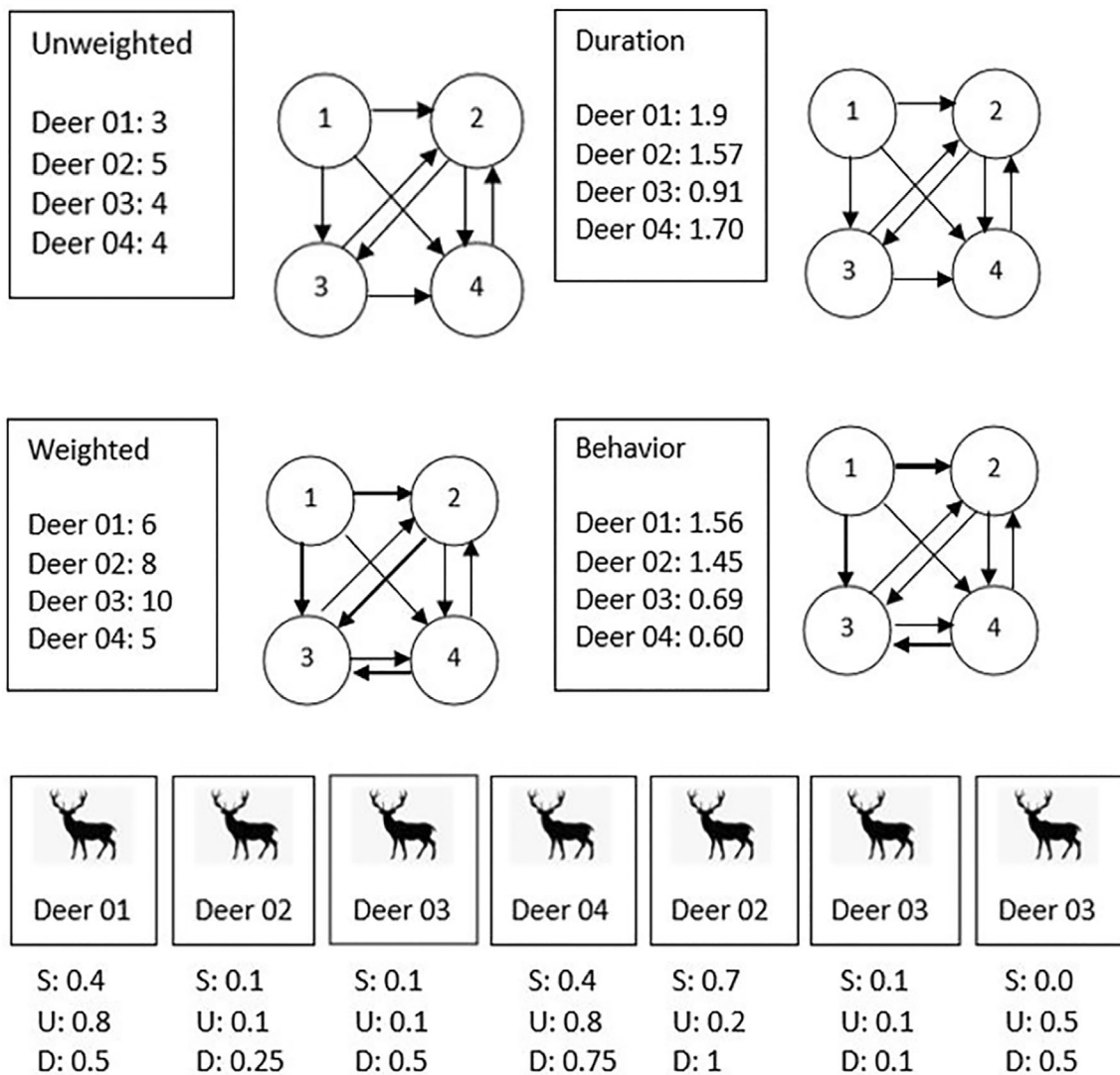

FIGURE 1 Example social networks based on a sequence of visits to a scrape (bottom row). Differences in networks and metrics are listed using edge weight as an example. Each deer visits and receives a shedding (S) and uptake (U) value based on the scrape-related behavior performed and duration (D) in minutes. For unweighted networks, each deer that visits a scrape has a connection to every other deer that visits the scrape and strength is the total number of connections. For weighted, arrows are weighted based on the number of visits made by each deer. For duration, edge weights are based on duration of the scrape visit. For behavior, these values are modified based on shedding and uptake values. Networks may also include both behavior and duration by weighting based on all three values.

with a weight of one. In these networks, node strength and degree were equivalent since each connection to another node was unweighted. These networks were referred to as "unweighted" networks. At the second level, an interaction was recorded each time two deer visited the same scrape and edge weight was equal to the number of interactions to produce "weighted" networks. At the third level, each unique contact was weighted by the amount of time each deer spent at the scrape during an interaction to produce "duration" networks. At the fourth level, every time a deer visited a scrape, they were assigned a shed and uptake score based on the behaviors they exhibited, and edge weight was modified based on the product of the shed score of the first deer and the uptake score of the second. These networks are referred to as "behavior" networks. At the fifth level, edges were weighted based on the interaction between behavior and duration and referred to as "duration × behavior" networks. As a result, we recorded "social network method" as a factor with five levels that represented increasing complexity of edge definitions, referred to for the rest of the text as "edge complexity" from the previous level, and compared the effect of each level to the reference level unweighted.

We calculated social network metrics including closeness, betweenness, strength, and eigenvector centrality (Sosa et al., 2021; Table 1). These metrics characterize the centrality of individuals and therefore their importance in spreading disease. Strength is always greater in weighted

networks, so we focused on the variation in strength by standardizing each score to 0–1. We also calculated network-level metrics and mean values of individual-level metrics (Table 3). Network metrics were estimated and displayed using the igraph package in R (Csardi & Nepusz, 2006).

Covariates

For each individually identifiable male WTD, we collected covariates characterizing age and resource use. Deer were classified in one of two age classes: subadult buck or adult buck based on body size and antler growth. Female WTD were included in the scrape monitoring and behavioral observations at scrapes but were not included in the network analysis because of challenges with individual identification and most scraping behavior is performed by males. We collected landscape-level resource data from the scrapes used by deer based on data from the 2006 National Land Cover Database (NLCD) reclassified to the categories agriculture, forest, open water, wetland, and urban. We generated a 500-m-radius buffer around each scrape to summarize scrape-level landscape features. Buffers were meant to characterize as much of the landscape available to deer as possible; therefore, we selected a buffer size of approximately the average home range of deer in this region without resulting in significant overlap among

TABLE 3 Summary statistics for social networks of white-tailed deer at DeSoto National Wildlife Refuge, 2005 and 2006, based on each method for weighting social networks.

Metric	Unweighted	Weighted	Duration	Behavior	Duration × behavior
2005					
Mean path length	2.84	2.84	2.86	2.86	2.87
Transitivity	0.48	0.48	0.48	0.52	0.52
Edge density	0.054	0.054	0.053	0.036	0.036
Relative strength	0.25	0.12	0.090	0.077	0.068
Closeness	3.8×10^{-4}	3.5×10^{-4}	1.1×10^{-4}	7.0×10^{-5}	6.0×10^{-5}
Betweenness	307.58	382.08	501.45	357.96	387.19
Eigenvector centrality	0.25	0.089	0.057	0.043	0.040
2006					
Mean path length	2.98	2.98	3.00	3.46	3.46
Transitivity	0.59	0.59	0.59	0.61	0.61
Edge density	0.070	0.070	0.069	0.049	0.049
Relative strength	0.29	0.15	0.15	0.11	0.11
Closeness	8.3×10^{-4}	7.3×10^{-4}	1.7×10^{-4}	3.2×10^{-4}	1.5×10^{-4}
Betweenness	210.60	269.77	358.57	315.15	327.97
Eigenvector centrality	0.21	0.063	0.060	0.054	0.051

Note: Values of three network-level metrics (mean path length, transitivity, and edge density) and mean values for individual-level metrics are listed.

buffers. For each buffer, we calculated the proportion of each land cover type. For each deer, we calculated the average proportion of agricultural cover at all the scrapes visited by that deer, because agriculture was the predominant land use category in the study area. We calculated the correlation between proportion of agriculture estimated based on buffer sizes from 50 to 500 m to assess the robustness of these estimates (Appendix S1: Table S1). Landscape covariates were estimated with the raster package in R (Hijmans & van Etten, 2012).

Hypothesis testing

We tested the effects of the social network method and individual covariates on centrality metrics using a randomization test comparing observed relationships to randomized social networks (Silk, Croft, Delahay, Hodgson, Weber, et al., 2017). For observed networks, we determined the relative effects of the social network method and individual covariates using mixed-effects linear regression. We ran four models with closeness, betweenness, relative strength, and eigenvector centrality as the respective dependent variables and proportion of agricultural field, deer age, and social network method as fixed effects. We included individual deer and year as random effects. In addition, we compared the performance of models including interaction effects among each individual covariate and social network method. For each centrality measure, we ran seven additional models including all combinations of interaction terms. We ranked models with corrected Akaike information criterion (AIC_c) (Burnham & Anderson, 2002) and retained the best performing model.

We tested the impact of covariates using a randomization approach comparing observed coefficients to 1000 randomized social networks. Random social networks were computed using a datastream randomization approach (Farine & Whitehead, 2015). In this approach, deer retained the same individual-level characteristics as in observed networks. We simulated 1000 sampling periods by randomly assigning individuals to a sequence of scrape visits equal in length to the original data. Social networks were generated based on these randomly permuted sequences of scrape visits and coefficients calculated based on the same regression models used for observed data. We tested the effect of each covariate by comparing the observed coefficient values from empirical models with the distribution of values from randomized networks. For deer age and proportion of agricultural field, we compared the value of coefficients to values from randomized networks. For social network method and interaction terms,

we compared the effect of each level of edge complexity relative to unweighted as the reference level. We compared the differences in coefficient values to differences in coefficients from 1000 randomizations. We determined that a covariate had an effect on network metrics if <5% of the randomized values were further from 0 than observed values.

Sensitivity analysis

We performed sensitivity analysis to evaluate sources of uncertainty in our network analysis. First, we evaluated the effect that unidentified individuals may have on our social network metrics. Recent studies have raised concerns over the effect that missing individuals may have on social network metrics (Davis et al., 2018; Silk et al., 2015). Some individual WTD in our study area using scrapes likely were not observed during the study. To estimate how these missing individuals might affect network metrics, we randomly removed a proportion of the individuals in our sample from 1% to 50%. We then generated social networks from these subsets of data and recalculated all social network metrics (Appendix S1: Figures S1–S4). Second, there is potential uncertainty in the shedding and uptake values assigned by expert assessment used to weight edges in behavioral networks. By varying these values, we evaluate how mischaracterizing the risk associated with a behavior may impact social networks. To test this, we reduced an individual shedding or uptake value by 10% and recalculated networks with these new values. We repeated this for every behavior for both shedding and uptake values and recalculated networks to assess the consequences of misspecifying the relative risk of prion transmission for each behavior (Appendix S1: Figures S5–S12).

Finally, we identified individuals with the potential to have disproportionate effects on networks and tested the sensitivity of networks to their removal. We identified the most and least important individuals in networks based on the ranks of each individual in each centrality metric. We compared these individuals with how they ranked in the number of times they performed each scrape-related behavior. For each behavior, we ranked individuals based on how many times they performed that behavior during a visit to a scrape. We tested the effect of these individuals and behaviors on networks by removing highly impactful individuals that performed each behavior the greatest number of times and recalculated networks. We sequentially removed without replacement the 10 highest ranking individuals for each behavior and assessed the effect of these removals on the network metrics.

RESULTS

We recorded 5607 encounters of WTD at 85 scrapes in 2005 and 44 scrapes in 2006, including 2013 interactions by 169 unique identifiable males and 75 unique identifiable females (Figure 2). The most frequently exhibited behaviors included smell overhanging branch (67%), smell scrape (61%), lick/grasp overhanging branch (39%), scrape ground (27%), and preorbital marking of the overhanging branch (22%), rub-urinating (14%), and grazing (11%) (Appendix S1: Tables S2–S5). The frequency of scrape-related behaviors differed among sex–age classes, with adult males exhibiting the preponderance of all behaviors, especially smelling the overhanging branch (70%), smelling the scrape (59%), licking or grasping the overhanging branch (44%), and scraping (36%). Subadult males exhibited nearly the full range of behaviors at scrapes (except flehmen posture), albeit far less frequent than adult males (Appendix S1: Table S2). Adult females and fawns interacted with scrapes much less frequently than males, yet >75% smelled scrapes, 40.9% and 22.4%, respectively, smelled the overhanging branch, and about 16% grazed within 2 m of a scrape (Appendix S1: Table S2). The mean duration of scrape-related behaviors also differed among sex–age classes, with adult males exhibiting the preponderance of all behaviors. Adult males spent most of their time at scrapes grazing ($x = 32$ s), smelling the overhanging branch ($x = 13$ s), and scraping ($x = 11$ s). The majority of time spent at scrapes by subadult males included grazing, scraping, and defecating. Adult females and fawns spent most of their time at scrapes grazing ($x = 37$ and 30 s, respectively), but they also spent a considerable amount of time smelling the overhanging branch, smelling the scrape, defecating, and urinating (Appendix S1: Table S3).

Visual inspection of graphs of social networks indicates a pattern of change with increasing edge complexity of the method used to generate the network. Most importantly, in social networks including behavior, not all individuals were connected, and this is reflected in the network and mean individual-level metrics (Table 3). We found differences in centrality measures related to the level of edge complexity of the social network method (Figure 3). Compared with the unweighted network, deer in weighted networks had lower closeness, relative strength, and eigenvector centrality and higher betweenness. Deer in behavior networks had lower closeness, relative strength, and eigenvector centrality and higher betweenness. Deer in duration networks had lower relative strength and eigenvector centrality and higher betweenness. Deer in duration × behavior networks had lower relative strength and eigenvector centrality and higher betweenness. These results are based on total strength of each individual, for a full summary of in

and out strength for each network, see Appendix S1: Tables S8 and S9.

Individual-level covariates indicated that intrinsic and extrinsic factors contributed to the centrality of individual deer (Figure 4). Younger deer had lower betweenness than older deer. Younger deer had lower values of other metrics as well; however, these effects did not differ from random chance. Deer using areas with more agricultural fields had higher relative strength but lower betweenness. Model selection indicated that the best model contained either zero or one interaction terms for all dependent variables other than betweenness. Proportion of agriculture was negatively related to betweenness for all network methods except those including behavior, where the relationship was positive (Appendix S1: Figure S13). Younger deer had greater betweenness in all network types (Appendix S1: Figure S13).

Based on the magnitude of social network metrics, we identified individuals that performed the greatest number of each behavior at scrapes and had the greatest impact on social networks (Figure 5). Removing the individuals that performed the greatest number of each behavior disproportionately altered individual-level network metrics, however a few important patterns stand out (Figure 6). For closeness, removal of some individuals increased the connectivity in networks, but most behavioral removals produced sharp decreases in connectivity. Most notably, removing individuals that licked/grasped branches the most resulted in the strongest decreases in closeness. For strength, removal of individuals based on all behaviors produced decreased numbers and weights of connections, and for most behaviors, removal of just a few individuals sharply reduced strength. Betweenness was not affected much relative to randomly removing individuals; however, removing individuals that scraped and licked/grasped branches the most decreased the ability of individuals to facilitate connections in the network. For eigenvector centrality, removing only a few individuals sharply increased centrality, particularly when removing individuals that licked/grasped branches, made eye contact with branches, or smelled branches.

DISCUSSION

Host contact is a fundamental component of pathogen transmission in host populations. Contacts vary in their propensity for disease transmission, meaning it is important to consider heterogeneity in the probability of transmission to produce potential transmission networks (Craft, 2015). We found that when including additional factors that affect the probability of prion transmission
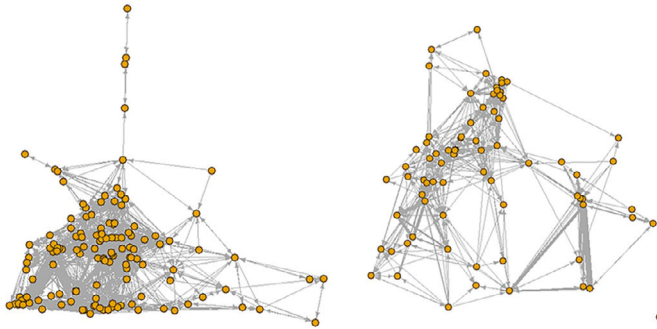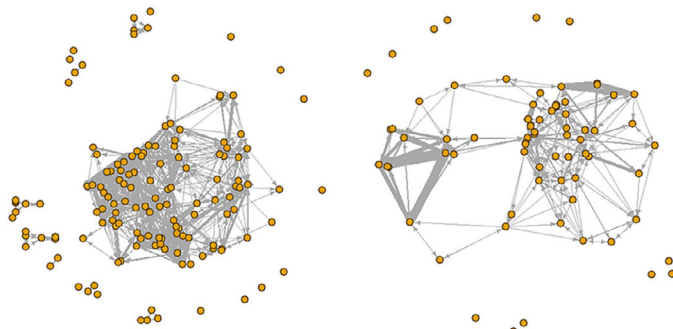
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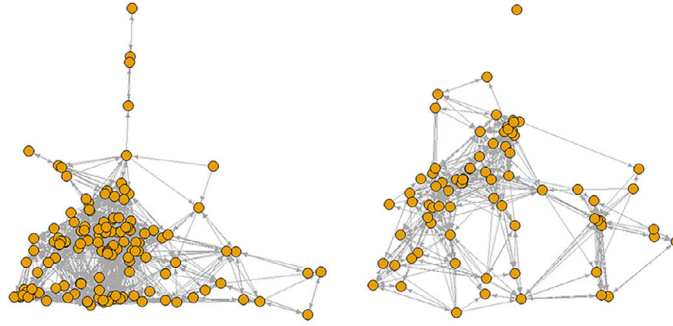
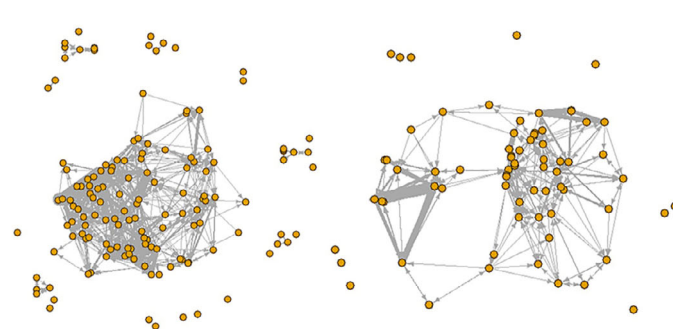**Weighted**
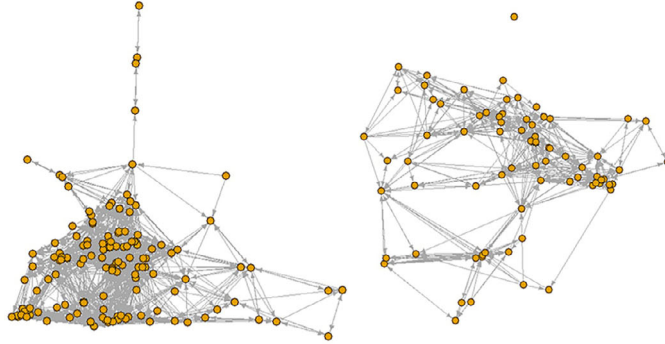
Duration

Behavior

Duration and Behavior

2005   **2006**
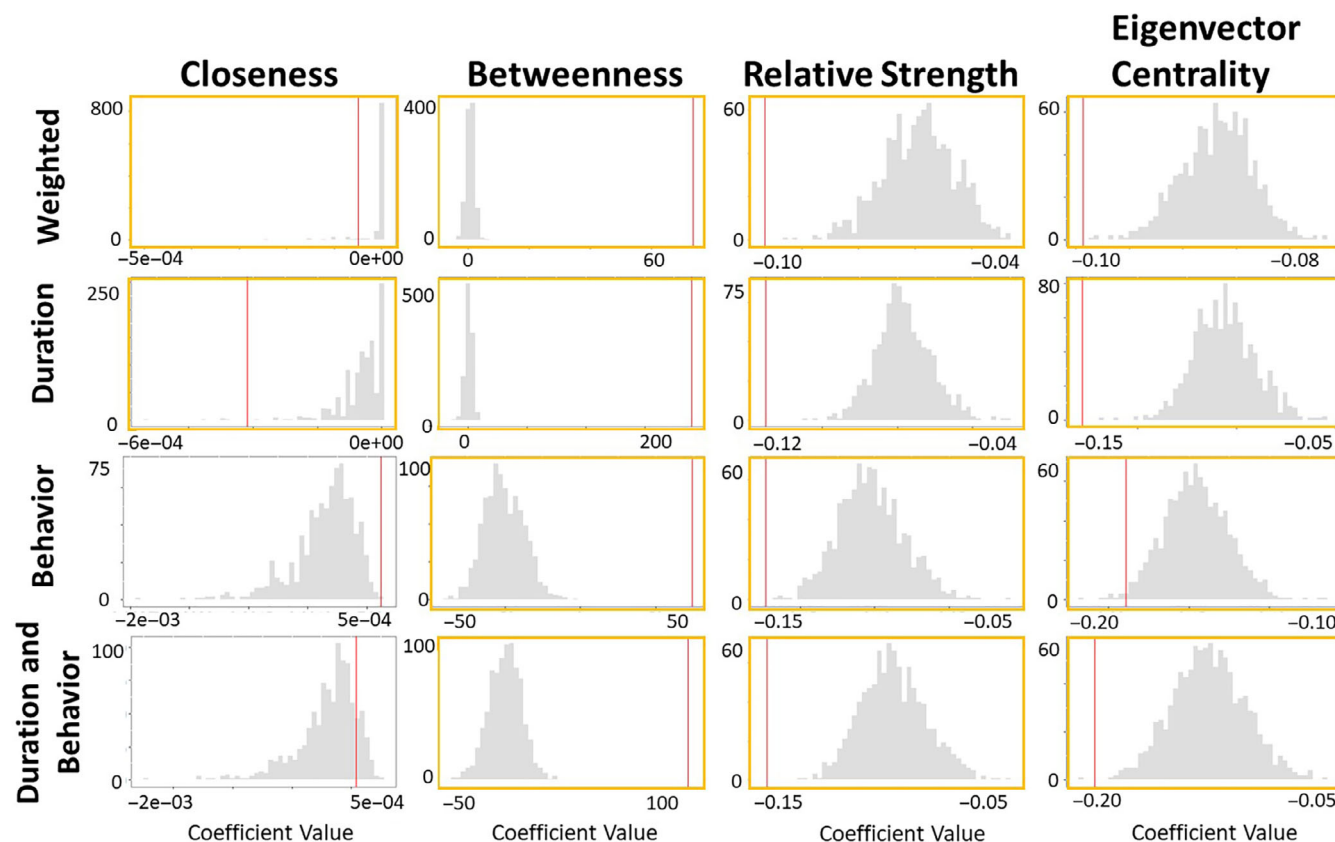
F I G U R E 2   Legend on next page.

FIGURE 3 Differences in coefficient values from observed networks and randomized social networks of white-tailed deer at DeSoto National Wildlife Refuge, 2005 and 2006. Plots are outlined in yellow if observed values (vertical red lines) were further from 0 than 95% of randomized values. This indicates that centrality differed among levels for this metric. Results are shown for closeness, betweenness, relative strength, and eigenvector centrality. Each plot shows the difference relative to the reference level of unweighted. From top to bottom, plots show values for weighted, behavior, duration, and behavior × duration networks.

during contact such as frequency, duration, or type of behavior, there was greater heterogeneity in the potential to transmit disease. Removing individuals based on how individuals ranked in the number of behaviors they performed revealed that not all behaviors and not all contacts are equally important in connecting the population and that individuals differ in their behavioral profiles at scrapes. Specifically, rare but high-risk behaviors may have as much impact on transmission potential as common but low-risk behaviors. Therefore, weighting contact networks based on the behavior during contact may be important for capturing transmission dynamics. Based on this result, removing the individuals that perform

high-risk behaviors, for example, reproductive-age bucks that shed saliva through branch interactions, may have the greatest impact on overall connectivity.

Our results provide an empirical demonstration of the effect of contact and transmission probability in representing transmission networks (Craft, 2015; McCallum et al., 2017). Numerous theoretical and empirical examples have demonstrated the need to consider heterogeneity in all aspects of the disease transmission process (VanderWaal & Ezenwa, 2016; White et al., 2017). However, previous empirical results have provided counterexamples in which contact networks alone were good predictors of transmission. VanderWaal et al. (2013) found that social and

FIGURE 2 Social networks of white-tailed deer at DeSoto National Wildlife Refuge, 2005 and 2006, constructed with five methods. In unweighted networks, two individual deer that used the same scrape were connected with an edge of weight 1. In weighted networks, networks were built with the same method as for unweighted networks, but edges were weighted based on the number of times deer visited the scrape. In duration networks, edge weights were based on the number of visits to a scrape and the length of time spent there. In behavior networks, edge weights were based on the number of times a deer visited a scrape and the behaviors performed during visits. In duration × behavior networks, edge weights are based on the number of visits, length of time for the visit, and behavior exhibited during the visit.
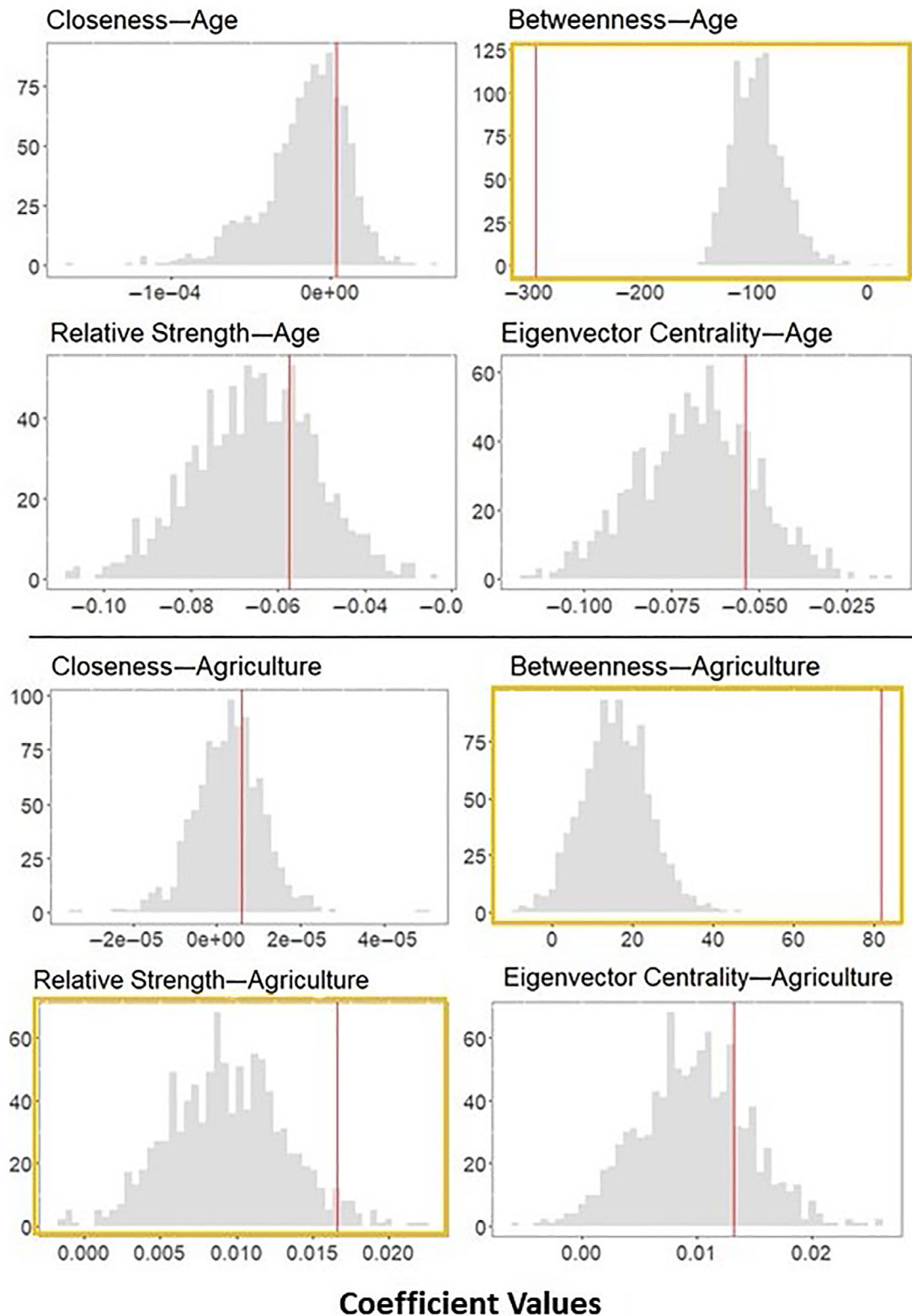
FIGURE 4 Coefficient values from observed networks and randomized social networks for individual-level covariates of white-tailed deer at DeSoto National Wildlife Refuge, 2005 and 2006. Plots are outlined in yellow if observed values (vertical red lines) were further from 0 than 95% of randomized values.

transmission networks of *Escherichia coli* in giraffes (*Giraffa camelopardalis*) were strongly correlated and Sandel et al. (2020) found that contact networks predicted disease incidence in chimpanzees (*Pan troglodytes*). Alternatively, our results align with numerous examples in which the probability of transmission depends on
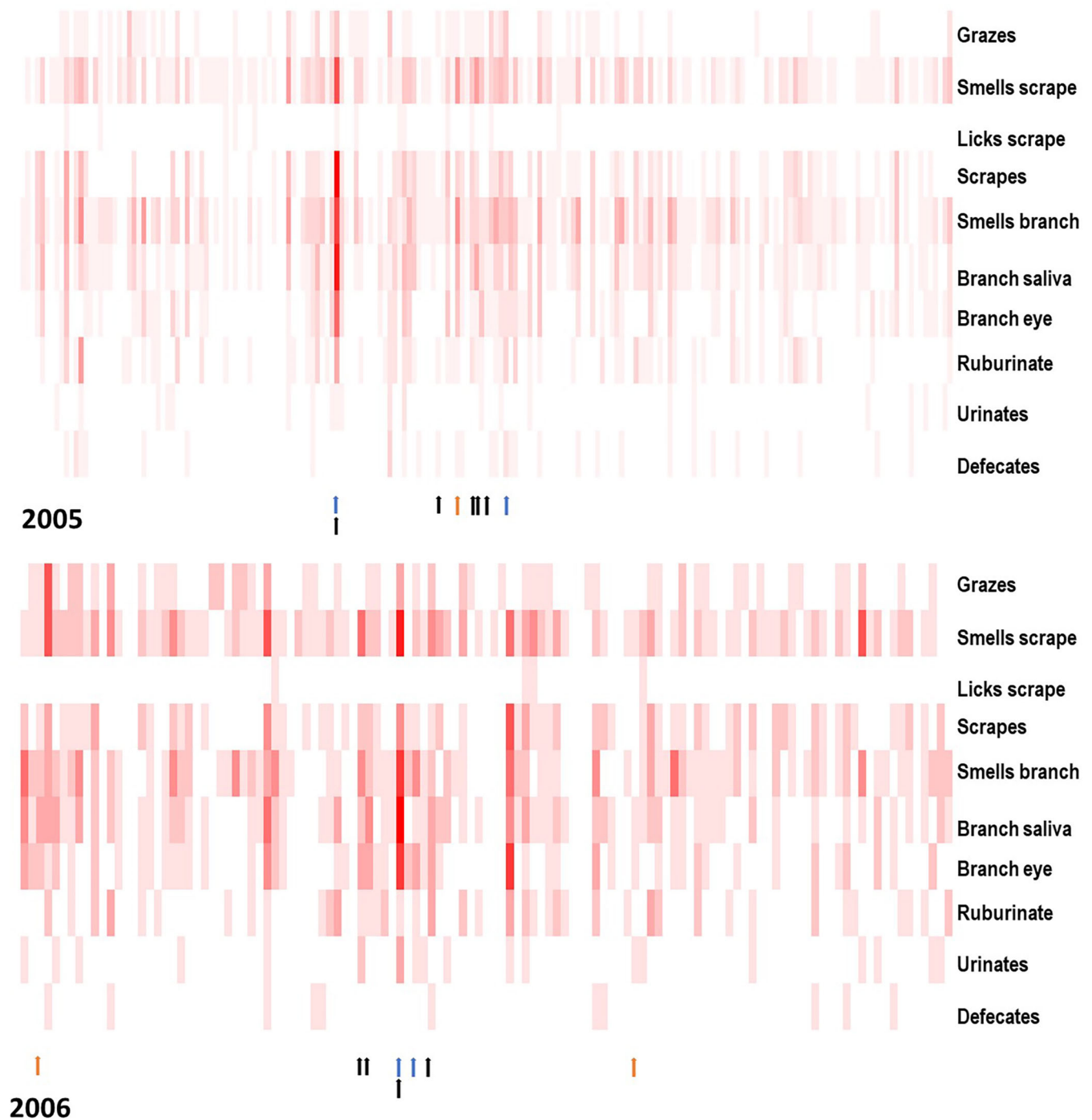
FIGURE 5 Heat maps representing the number of times each individual performed each behavior on camera in 2005 (top) and 2006 (bottom). Each column of bars represents an individual deer. Arrows indicate individuals identified as being outliers based on high strength (blue), betweenness (orange), or eigenvector centrality (black).

heterogeneity in factors such as the frequency duration and type of contact (Aiello et al., 2016; Natoli et al., 2005) or properties of the individual such as body condition (MacIntosh et al., 2012; Perkins et al., 2008). Our results emphasize the importance of considering these sources of heterogeneity in addition to host contact structure because of their potential impacts on transmission networks.

To our knowledge, only one previous study has produced social networks from scrape visitation data (Hearst et al., 2021); however, other studies have generated social networks in deer without considering scrapes (Schauber et al., 2015; Tosa et al., 2015). Indirect contact networks at scrapes differ in several important ways from direct contacts that may influence deer social networks. Generally,
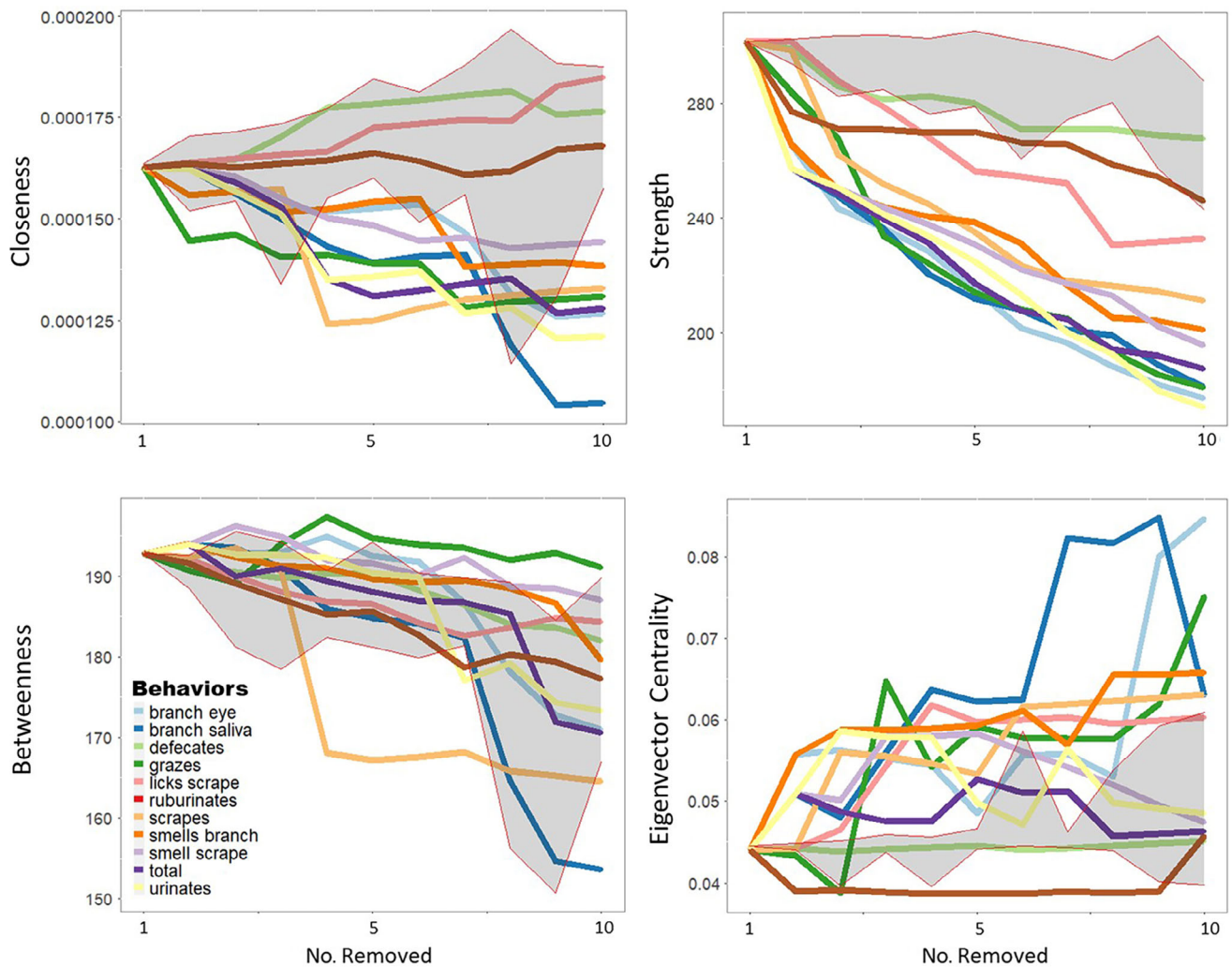
FIGURE 6 Plots showing the effect of removing highly influential individuals from the duration × behavior network. Lines representing the mean value from individual-level covariates in the network. For each behavior, individuals were ranked based on the number of times they performed each behavior. The top ranked individual was removed, the network was reproduced, and the metrics were recalculated. This was repeated until the top 10 individuals were removed. Gray ribbons represent the distribution of values from networks in which individuals were removed randomly from the population.

social networks derived from direct contacts indicate frequent contacts between members of the same social groups and less frequent contacts between deer from social groups with spatially overlapping ranges (Koen et al., 2017). Indirect contact networks at scrapes include contacts between deer with little spatial overlap and potentially over large distances. Variation in scraping behavior may also be greater than variation in behavior during direct contact, resulting in greater heterogeneity in social network position. Therefore, including scrape-related indirect contacts likely will increase the number of individuals and geographic extent of networks and alter the relative influence of some individuals.

Our results have implications for different aspects of deer social behavior depending on the centrality metric of interest (Sosa et al., 2021). For weighted networks, deer varied less in their propensity to transmit disease,

but deer more frequently had the potential to facilitate transmission from one deer to another. These results have three important implications for understanding the role scrapes may play in the transmission of CWD. First, to identify individuals with disproportionate impacts on networks, network models must consider second-order interactions and the effect of specific behaviors (Araujo et al., 2016; Modlmeier et al., 2014). Second, scrapes may be important for spreading CWD among groups of deer or over geographic areas. Third, including more sources of heterogeneity in the probability of transmission resulted in changes to networks such as reduced relative strength and disconnected networks. These patterns may help differentiate which individuals have the highest relative transmission potential, because disconnected individuals are less likely to spread disease (Marchinton et al., 1990; Miller et al., 1987, 2004).

Some individuals in host populations may act as superspreaders when they consistently engage in behaviors that make them more contagious (Lloyd-Smith et al., 2005). For WTD, individuals may be more likely to transmit CWD prions depending on the frequency, duration, and type of contact. Consistent with our expectations, we found that adult WTD occupied more central positions in social networks and therefore had greater potential to spread CWD at scrapes (Bonnot et al., 2018), likely because reproductive-age males are more active at scrapes (DeYoung et al., 2006). This result is consistent with commonly observed patterns of prevalence of CWD in deer populations (Grear et al., 2006). While highly influential individuals have generally been identified based on age or sex, our results indicate that highly influential individuals may be identified based on behavior. Additionally, the relationship between agriculture, relative strength, and betweenness suggests that individuals may differentially impact networks depending on resource associations. When accounting for behavior, some individuals and behaviors have a greater impact on networks than others. Removal of these individuals may help lower network connectivity, which could be helpful in disease management. Accounting for behavior in the edges of networks helps to better characterize the heterogeneity of the contact structure, identify superspreaders, and provide criteria for determining which individuals and contacts are most relevant to disease transmission.

Frequency-dependent processes in disease transmission typically diminish the effectiveness of management strategies such as population reduction. Frequency-dependent transmission occurs when some transmission processes are unrelated to host density (Potapov et al., 2016; Schauber & Woolf, 2016). Evidence suggests that transmission of CWD prions may occur through a mix of density and frequency dependence partly due to indirect transmission and social structuring of contacts (Almberg et al., 2011; Uehlinger et al., 2016). To combat frequency-dependent transmission, managers have considered factors beyond density reduction such as culling based on patterns of prevalence of the disease in the population (Manjerovic et al., 2014; Mysterud et al., 2019). For example, Rogers et al. (2022) suggested that increased harvest of males could be effective at reducing epidemics when high CWD prevalence in males was caused by high male-to-male transmission of prions. Similarly, Ketz et al. (2021) found higher susceptibility and prevalence of CWD in males and that increased harvest of male WTD could reduce the prevalence of CWD. Here, we highlight the potential for elevated male-to-male transmission through indirect contact at scrapes; therefore, scrapes deserve more attention for research and management strategies. While our results only begin to

uncover the implications of scrapes as a source of indirect contact, they do support the notion that managers should encourage hunters to harvest greater numbers of reproductive-age males to reduce contamination at scrapes and the degree of indirect contact occurring at them. As new methodologies to detect prions in environmental samples emerge (Bravo-Risi et al., 2021; Tennant et al., 2020), it will be possible to develop strategies for detecting contaminated scrape sites and reducing the spread of CWD via scrapes.

Social network analysis has been applied to study behavior (Plaza et al., 2020; Wilson et al., 2013) and disease (Hirsch et al., 2016; Perkins et al., 2009; Silk, Croft, Delahay, Hodgson, Boots, et al., 2017), but fewer studies have used social networks to link behavior and disease transmission (Wilber et al., 2019). Future work could improve the application of social networks in these two disciplines in several ways. First, researchers should be careful to choose between undirected or directed networks and unweighted or weighted networks depending on the biology of the system (Farine & Whitehead, 2015; Silk, Croft, Delahay, Hodgson, Boots, et al., 2017). Second, behavioral ecologists have assessed individual variation in behavior and identified consistent personalities by comparing separate social networks based on different behaviors or at different times (Plaza et al., 2020; Wilson et al., 2013). We were unable to use the same methods as these studies because they relied on comparing independent networks based on separate behaviors. Our data could be compared with independent networks across years to assess temporal changes or locations to determine the effects of local conditions. Finally, we were limited in the amount of individual-level data that were collected. Capturing deer would have allowed collection of additional individual-level data such as genetic information, more precise ages, and measurements of body condition. Locational data, especially based on GPS technology, also could be used to assess direct and indirect contacts at scrapes and surrounding areas. These methods could identify how additional factors such as body size, dominance status, or personality may impact an individual's propensity to spread disease (Bonnot et al., 2018; DeYoung et al., 2006; Miller et al., 1987). Alternatively, methods to estimate the behavioral state of an animal from telemetry data could be used to produce behaviorally explicit social networks in other systems (Morales et al., 2004).

Our results provide insight into the social structure of male WTD at scrapes by comparing social networks to randomly permuted networks. Recently, several authors have advised caution when using these approaches to derive inference about the effect of extrinsic factors on social networks (Farine & Carter, 2022; Weiss et al., 2020). Data

permutation approaches, in which the sequence of interactions shaping the network is randomized, are appropriate for testing against the null hypothesis of random social structure, but node-level permutations may be more appropriate for avoiding high type-1 error rates when testing the effect of extrinsic factors. Here, we use a network-level permutation because we sought to compare differences in networks to what would be expected given random social structure. Another issue that commonly affects social network analysis is unobserved individuals on social network metrics. Based on sensitivity analysis, we did observe changes to networks with increasing numbers of missing individuals; however, these changes were relatively small when only a small percentage of individuals were removed (Appendix S1: Figures S1–S4). Specifically, we believe that potential under-sampling is unlikely to affect our results because changes to networks were generally consistent at each level of edge complexity, meaning that our comparisons between networks are less likely to be affected. Despite this, we caution that any form of social network analysis will be affected by missing individuals, particularly for betweenness values, which we found were most impacted by missing individuals.

Our results provide an important first step in evaluating the potential role of scrapes in the transmission and spread of CWD. Other studies have demonstrated the importance of other attractants, such as baits and mineral licks in the transmission of CWD among cervids (Miller et al., 2004; Plummer et al., 2018; Sorensen et al., 2014). We found a high level of indirect contact at scrapes supporting the idea that points of attraction may facilitate disease transmission. Scrapes may be particularly important for environmental transmission because scrape-related behaviors likely facilitate the transfer of prions among individual deer and the environment. We observed numerous behaviors that are likely to shed prions, making scrapes a potential model system for studying the effects of prion accumulation and the factors that promote prion persistence (Almberg et al., 2011; Miller et al., 2004). Some studies suggest that treating an area with an enzyme solution may reduce the infectivity of prions in soils (Saunders et al., 2010, 2011). Enzyme treatments, therefore, may have potential to reduce environmental transmission at scrapes and other points of attraction for deer.

CONCLUSION

Our analysis reveals an important role for scrapes in increasing the connectivity of deer populations. Studies that estimate the role of scrape-related contact relative to other types of indirect contact or direct contact will be important for understanding the potential impacts on CWD transmission dynamics. Specifically, our results highlight the importance of considering many sources of heterogeneity in the probability of prion transmission during scrape-related behavior and that individuals that perform certain behaviors frequently have a disproportionate impact on social networks. Our results are focused on social behavior in the absence of explicit disease data, but another important avenue will be to measure prion concentrations at scrapes and within individual deer to test which behaviors correlate most strongly with CWD transmission. Spatially targeted management aimed at reducing connectivity is difficult due to challenges in predicting where deer will move and make among-group contacts (Osnas et al., 2009). If scrapes are hotspots for indirect contact, microscale harvest management could consider the spatial arrangement of scrapes. Intensive management, such as high hunting pressure along barriers to movement between disparate scrape lines, may help slow the spread of CWD beyond its current range. Based on our results, these strategies may be most effective if combined with management efforts such as harvest of reproductive-age males and environmental management to reduce prion buildup.

ORCID
Michael E. Egan https://orcid.org/0000-0002-9952-5602
Kim M. Pepin https://orcid.org/0000-0002-9931-8312
Guillaume Bastille-Rousseau https://orcid.org/0000-0001-6799-639X

REFERENCES
Aiello, C. M., K. E. Nussear, T. C. Esque, P. G. Emblidge, P. Sah, S. Bansal, and P. J. Hudson. 2016. "Host Contact and Shedding Patterns Clarify Variation in Pathogen Exposure and Transmission in Threatened Tortoise *Gopherus agassizii*:

Implications for Disease Modelling and Management." *Journal of Animal Ecology* 85: 829–42.

Alexy, K. J., J. W. Gassett, D. A. Osborn, and K. V. Miller. 2001. "Remote Monitoring of Scraping Behaviors of a Wild Population of White-Tailed Deer." *Wildlife Society Bulletin* 29(3): 873–8.

Almberg, E. S., P. C. Cross, C. J. Johnson, D. M. Heisey, and B. J. Richards. 2011. "Modeling Routes of Chronic Wasting Disease Transmission: Environmental Prion Persistence Promotes Deer Population Decline and Extinction." *PLoS One* 6(5): e19896. https://doi.org/10.1371/journal.pone.0019896.

Araujo, A., L. Kirschman, and R. W. Warne. 2016. "Behavioural Phenotypes Predict Disease Susceptibility and Infectiousness." *Biology Letters* 12(8): 20160480. https://doi.org/10.1098/rsbl.2016.0480.

Bonnot, N. C., M. Goulard, A. J. M. Hewison, B. Cargnelutti, B. Lourtet, Y. Chaval, and N. Morellet. 2018. "Boldness-Mediated Habitat Use Tactics and Reproductive Success in a Wild Large Herbivore." *Animal Behaviour* 145: 7–115. https://doi.org/10.1016/j.anbehav.2018.09.013.

Bravo-Risi, F., P. Soto, T. Eckland, R. Dittmar, S. Ramírez, C. S. G. Catumbela, C. Soto, M. Lockwood, T. Nichols, and R. Morales. 2021. "Detection of CWD Prions in Naturally Infected White-Tailed Deer Fetuses and Gestational Tissues by PMCA." *Scientific Reports* 11: 18385.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach*, 2nd ed. New York: Springer-Verlag.

Clements, G. M., S. E. Hygnstrom, J. M. Gilsdorf, D. M. Baasch, M. J. Clements, and K. C. Vercauteren. 2011. "Movements of White-Tailed Deer in Riparian Habitat: Implications for Infectious Diseases." *The Journal of Wildlife Management* 75(6): 1436–42.

Craft, M. E. 2015. "Infectious Disease Transmission and Contact Networks in Wildlife and Livestock." *Philosophical Transactions of the Royal Society B: Biological Sciences* 370(1669): 20140107. https://doi.org/10.1098/rstb.2014.0107.

Csardi, G., and T. Nepusz. 2006. "The Igraph Software Package for Complex Network Research." *InterJournal, Complex Systems* 1695: 1–9.

Davis, G. H., M. C. CroFoot, and D. R. Farine. 2018. "Estimating the Robustness and Uncertainty of Animal Social Networks Using Different Observational Methods." *Animal Behaviour* 141: 29–44.

DeYoung, R. W., S. Demarais, R. L. Honeycutt, K. L. Gee, and R. A. Gonzales. 2006. "Social Dominance and Male Breeding Success in Captive White-Tailed Deer." *Wildlife Society Bulletin* 34(1): 131–6. https://doi.org/10.2193/0091-7648(2006)34[131:SDAMBS]2.0.CO;2.

Egan, M., K. M. Pepin, J. W. Fischer, S. Hygnstrom, K. C. Vercauteren, and G. Bastille-Rousseau. 2022. "Social Network Analysis of White-Tailed Deer Scraping Behavior: Implications for Disease Transmission." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.c.6306876.v1.

Farine, D. R., and G. R. Carter. 2022. "Permutation Tests for Hypothesis Testing with Animal Social Network Data: Problems and Potential Solutions." *Methods in Ecology and Evolution* 13(1): 144–56. https://doi.org/10.1101/2020.08.02.232710.

Farine, D. R., and H. Whitehead. 2015. "Constructing, Conducting and Interpreting Animal Social Network Analysis." *Journal of Animal Ecology* 84(5): 1144–63. https://doi.org/10.1111/1365-2656.12418.

Grear, D. A., M. D. Samuel, J. A. Langenberg, and D. Keane. 2006. "Demographic Patterns and Harvest Vulnerability of Chronic Wasting Disease Infected White-Tailed Deer in Wisconsin." *Journal of Wildlife Management* 70(2): 546–53. https://doi.org/10.2193/0022-541X(2006)70[546:DPAHVO]2.0.CO;2.

Haley, N. J., and E. A. Hoover. 2015. "Chronic Wasting Disease of Cervids: Current Knowledge and Future Perspectives." *Annual Review of Animal Biosciences* 3(1): 305–25. https://doi.org/10.1146/annurev-animal-022114-111001.

Hearst, S., S. Streeter, J. Hannah, and G. Taylor. 2021. "Scraping Network Analysis: A Method to Explore Complex White-Tailed Deer Mating Systems." *The Southeastern Naturalist* 20(1): 192–211.

Hefley, T. J., S. E. Hygnstrom, J. M. Gilsdorf, G. M. Clements, M. J. Clements, A. J. Tyre, D. M. Baasch, and K. C. VerCauteren. 2013. "Effects of Deer Density and Land Use on Mass of White-Tailed Deer." *Journal of Fish and Wildlife Management* 4(1): 20–32.

Hewitt, D. G. 2011. "Nutrition." In *Biology and Management of White-Tailed Deer*, edited by D. G. Hewitt, 75–105. Boca Raton, FL: Taylor and Francis.

Hijmans, R. J., and J. van Etten. 2012. "Raster: Geographic Analysis and Modeling with Raster Data." R Package Version 2.0-12. http://raster.r-forge.r-project.org/.

Hirsch, B. T., J. J. H. Reynolds, S. D. Gehrt, and M. E. Craft. 2016. "Which Mechanisms Drive Seasonal Rabies Outbreaks in Raccoons? A Test Using Dynamic Social Network Models." *Journal of Applied Ecology* 53(3): 804–13. https://doi.org/10.1111/1365-2664.12628.

Hirth, D. H. 1977. "Social Behavior of White-Tailed Deer in Relation to Habitat." *Wildlife Monographs* 53: 30–9.

Hoover, C. E., K. A. Davenport, D. M. Henderson, N. D. Denkers, C. K. Mathiason, C. Soto, M. D. Zabel, and E. A. Hoover. 2017. "Pathways of Prion Spread during Early Chronic Wasting Disease in Deer." *Journal of Virology* 91(10): 1–15. https://doi.org/10.1128/JVI.00077-17.

Jennelle, C. S., V. Henaux, G. Wasserberg, B. Thiagarajan, R. E. Rolley, and M. D. Samuel. 2014. "Transmission of Chronic Wasting Disease in Wisconsin White-Tailed Deer: Implications for Disease Spread and Management." *PLoS One* 9(3): e91043. https://doi.org/10.1371/journal.pone.0091043.

Joseph, M. B., J. R. Mihaljevic, A. L. Arellano, J. G. Kueneman, D. L. Preston, P. C. Cross, and P. T. J. Johnson. 2013. "Taming Wildlife Disease: Bridging the Gap between Science and Management." *Journal of Applied Ecology* 50(3): 702–12. https://doi.org/10.1111/1365-2664.12084.

Ketz, A. C., S. J. Robinson, C. J. Johnson, and M. D. Samuel. 2021. "Pathogen-Mediated Selection and Management Implications for White-Tailed Deer Exposed to Chronic Wasting Disease." *Journal of Applied Ecology* 59: 982–96.

Kile, T. L., and R. L. Marchinton. 1977. "White-Tailed Deer Rubs and Scrapes: Spatial, Temporal and Physical Characteristics and Social Role." *American Midland Naturalist* 97: 257–66.

Kinsell, T. C. 2010. "Scraping Behavior in Male White-Tailed Deer as a Potential Means of Transmitting Chronic Wasting Disease." Master's thesis, University of Nebraska.

Koen, E. L., M. I. Toas, C. K. Nielsen, and E. M. Schauber. 2017. "Does Landscape Connectivity Shape Local and Global Social Network Structure in White-Tailed Deer?" *PLoS One* 12(3): e0173570.

Lloyd-Smith, J. O., S. J. Schreiber, P. E. Kopp, and W. M. Getz. 2005. "Superspreading and the Effect of Individual Variation on Disease Emergence." *Nature* 438(7066): 355–9. https://doi.org/10.1038/nature04153.

Lotfli, M., M. R. Hamblin, and N. Rezaei. 2020. "COVID-19: Transmission, Prevention, and Potential Therapeutic Opportunities." *Clinica Chimica Acta* 508: 254–66.

MacIntosh, A. J. J., A. Jacobs, C. Garcia, K. Shimizu, K. Mouri, M. A. Huffman, and A. D. Hernandez. 2012. "Monkeys in the Middle: Parasite Transmission through the Social Network of a Wild Primate." *PLoS One* 7: e51144.

Magle, S. B., L. H. Kardash, A. O. Rothrock, J. C. Chamberlin, and N. E. Mathews. 2015. "Movements and Habitat Interactions of White-Tailed Deer: Implications for Chronic Wasting Disease Management." *The American Midland Naturalist* 173(2): 267–82. https://doi.org/10.1674/amid-173-02-267-282.1.

Manjerovic, M. B., M. L. Green, N. Mateus-Pinilla, and J. Novakofski. 2014. "The Importance of Localized Culling in Stabilizing Chronic Wasting Disease Prevalence in White-Tailed Deer Populations." *Preventive Veterinary Medicine* 113(1): 139–45. https://doi.org/10.1016/j.prevetmed.2013.09.011.

Marchinton, R. L., and D. H. Hirth. 1984. "Behavior." In *White-Tailed Deer: Ecology and Management*, edited by L. K. Halls, 129–68. Harrisburg, PA: Stackpole Books.

Marchinton, R. L., K. L. Johansen, and K. V. Miller. 1990. "Behavioral Components of White-Tailed Deer Scent Marking—Social and Seasonal Effects." In *Chemical Signals in Invertebrates*, edited by D. W. MacDonald, D. Müller-Schwarze, and S. E. Natynczuk, 295–301. Oxford: Oxford University.

McCallum, H., A. Fenton, P. J. Hudson, B. Lee, B. Levick, R. Norman, S. E. Perkins, M. Viney, A. J. Wilson, and J. Lello. 2017. "Breaking Beta: Deconstructing the Parasite Transmission Function." *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 372(1719): 1–11.

Miller, K. V., and R. L. Marchinton. 1999. "Temporal Distribution of Rubbing and Scraping by a High-Density White-Tailed Deer, *Odocoileus virginianus*, Population in Georgia." *Canadian Field Naturalist* 113: 519–21.

Miller, K. V., R. L. Marchinton, K. J. Forand, and K. L. Johansen. 1987. "Dominance, Testosterone Levels, and Scraping Activity in a Captive Herd of White-Tailed Deer." *Journal of Mammalogy* 68(4): 812–7. https://doi.org/10.2307/1381558.

Miller, M. W., E. S. Williams, N. T. Hobbs, and L. L. Wolfe. 2004. "Environmental Sources of Prion Transmission in Mule Deer." *Emerging Infectious Diseases* 10(6): 1003–6. https://doi.org/10.3201/eid1006.040010.

Modlmeier, A. P., C. N. Keiser, J. V. Watters, A. Sih, and J. N. Pruitt. 2014. "The Keystone Individual Concept: An Ecological and Evolutionary Overview." *Animal Behaviour* 89: 53–62. https://doi.org/10.1016/j.anbehav.2013.12.020.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. "Extracting More Out of Relocation Data: Building Movement Models as Mixtures of Random Walks." *Ecology* 85: 2436–45. https://doi.org/10.1890/03-0269.

Mysterud, A., K. Madslien, H. Viljugrein, T. Vikøren, R. Andersen, M. E. Güere, S. L. Benestad, et al. 2019. "The Demographic Pattern of Infection with Chronic Wasting Disease in Reindeer at an Early Epidemic Stage." *Ecosphere* 10(11): e02931. https://doi.org/10.1002/ecs2.2931.

Natoli, E., L. Say, S. Cafazzo, R. Bonanni, M. Schmid, and D. Pontier. 2005. "Bold Attitude Makes Male Urban Feral Domestic Cats more Vulnerable to Feline Immunodeficiency Virus." *Neuroscience and Biobehavioral Reviews* 29: 151–7.

Osnas, E. E., D. M. Heisey, R. E. Rolley, and M. D. Samuel. 2009. "Spatial and Temporal Patterns of Chronic Wasting Disease: Fine-Scale Mapping of a Wildlife Epidemic in Wisconsin." *Ecological Applications* 19(5): 1311–22. https://doi.org/10.1890/08-0578.1.

Perkins, S. E., F. Cagnacci, A. Stradiotto, D. Arnoldi, and P. J. Hudson. 2009. "Comparison of Social Networks Derived from Ecological Data: Implications for Inferring Infectious Disease Dynamics." *Journal of Animal Ecology* 78(5): 1015–22. https://doi.org/10.1111/j.1365-2656.2009.01557.x.

Perkins, S. E., M. F. Ferrari, and P. J. Hudson. 2008. "The Effects of Social Structure and Sex-Biased Transmission on Microparasite Infection." *Parasitology* 135: 1561–9.

Plaza, M., T. Burke, T. Cox, A. Flynn-Carroll, A. Girndt, G. Halford, D. A. Martin, et al. 2020. "Repeatable Social Network Node-Based Metrics across Populations and Contexts in a Passerine." *Journal of Evolutionary Biology* 33(11): 1634–42. https://doi.org/10.1111/jeb.13703.

Plummer, I. H., C. J. Johnson, A. R. Chesney, J. A. Pedersen, and M. D. Samuel. 2018. "Mineral Licks as Environmental Reservoirs of Chronic Wasting Disease Prions." *PLoS One* 13(5): e0196745.

Potapov, A., E. Merrill, M. Pybus, and M. A. Lewis. 2016. "Chronic Wasting Disease: Transmission Mechanisms and the Possibility of Harvest Management." *PLoS One* 11(3): e0151039.

Pruitt, W. O., Jr. 1953. "Rutting Behavior of the White-Tailed Deer (*Odocoileus virginianus*)." *Journal of Mammalogy* 35: 129–30.

Rogers, W., E. E. Brandell, and P. C. Cross. 2022. "Epidemiological Differences between Sexes Affect Management Efficacy in Simulated Chronic Wasting Disease Systems." *Journal of Applied Ecology* 59: 1122–33.

Sandel, A. A., J. Rushmore, J. D. Negrey, D. M. Lyons, and D. Caillaud. 2020. "Social Network Predicts Exposure to Respiratory Infection in a Wild Chimpanzee Group." *EcoHealth* 17: 437–48.

Saunders, S. E., J. C. Bartz, K. C. VerCauteren, and S. L. Bartelt-Hunt. 2010. "Enzymatic Digestion of Chronic Wasting Disease Prions Bound to Soil." *Environmental Science and Technology* 44: 4129–35.

Saunders, S. E., J. C. Bartz, K. C. VerCauteren, and S. L. Bartelt-Hunt. 2011. "An Enzymatic Treatment of Soil-Bound Prions Effectively Inhibits Replication." *Applied and Environmental Microbiology* 7(13): 4313–7.

Schauber, E. M., C. K. Nielsen, L. J. Kjær, C. W. Anderson, and D. J. Storm. 2015. "Social Affiliation and Contact Patterns among White-Tailed Deer in Disparate Landscapes: Implications for Disease Transmission." *Journal of Mammalogy* 96(1): 16–28. https://doi.org/10.1093/jmammal/gyu027.

Schauber, E. M., and A. Woolf. 2016. "Chronic Wasting Disease in Deer and Elk: A Critique of Current Models and Their Application." *Wildlife Society Bulletin* 31(3): 610–6.

Silk, M. J., D. P. Croft, R. J. Delahay, D. J. Hodgson, M. Boots, N. Weber, and R. A. McDonald. 2017. "Using Social Network Measures in Wildlife Disease Ecology, Epidemiology, and Management." *Bioscience* 67(3): 245–57. https://doi.org/10.1093/biosci/biw175.

Silk, M. J., D. P. Croft, R. J. Delahay, D. J. Hodgson, N. Weber, M. Boots, and R. A. McDonald. 2017. "The Application of Statistical Network Models in Disease Research." *Methods in Ecology and Evolution* 8(9): 1026–41. https://doi.org/10.1111/2041-210X.12770.

Silk, M. J., A. L. Jackson, D. P. Croft, K. Colhoun, and S. Bearhop. 2015. "The Consequences of Unidentifiable Individuals for the Analysis of an Animal Social Network." *Animal Behaviour* 104: 1–11.

Sorensen, A., F. M. van Beest, and R. K. Brook. 2014. "Impacts of Wildlife Baiting and Supplemental Feeding on Infectious Disease Transmission Risk: A Synthesis of Knowledge." *Preventive Veterinary Medicine* 113(4): 356–63. https://doi.org/10.1016/j.prevetmed.2013.11.010.

Sosa, S., C. Sueur, and I. Puga-Gonzalez. 2021. "Network Measures in Animal Social Network Analysis: Their Strengths, Limits, Interpretations and Uses." *Methods in Ecology and Evolution* 12(1): 10–21. https://doi.org/10.1111/2041-210X.13366.

Tennant, J. M., M. Li, D. M. Henderson, M. L. Tyer, N. D. Denkers, N. J. Haley, C. K. Mathiason, and E. A. Hoover. 2020. "Shedding and Stability of CWD Prion Seeding Activity in Cervid Feces." *PLoS One* 15(3): e0227094.

Tosa, M. I., E. M. Schauber, and C. K. Nielsen. 2015. "Familiarity Breeds Contempt: Combining Proximity Loggers and GPS Reveals Female White-Tailed Deer (*Odocoileus virginianus*) Avoiding Close Contact with Neighbors." *Journal of Wildlife Diseases* 51(1): 79–88.

Uehlinger, F. D., A. C. Johnston, T. K. Bollinger, and C. L. Waldner. 2016. "Systematic Review of Management Strategies to Control Chronic Wasting Disease in Wild Deer Populations in North America." *BMC Veterinary Research* 12(1): 173. https://doi.org/10.1186/s12917-016-0804-7.

Vander Wal, E., M. Festa-Bianchet, D. Réale, D. W. Coltman, and F. Pelletier. 2015. "Sex-Based Differences in the Adaptive Value of Social Behavior Contrasted against Morphology and Environment." *Ecology* 96(3): 631–41. https://doi.org/10.1890/14-1320.1.

VanderWaal, K. L., E. R. Atwill, L. A. Isbell, and B. McCowan. 2013. "Linking Social and Pathogen Transmission Networks Using Microbial Genetics in Giraffe (*Giraffa camelopardalis*)." *Journal of Animal Ecology* 83(2): 406–14.

VanderWaal, K. L. and V. O. Ezenwa. 2016 "Heterogeneity in Pathogen Transmission: Mechanisms and Methodology." *Functional Ecology* 30(10): 1606–22.

Weiss, M. N., D. W. Franks, L. J. N. Brent, S. Ellis, M. J. Silk, and D. P. Croft. 2020. "Common Datastream Permutations of Animal Social Network Data Are Not Appropriate for Hypothesis Testing Using Regression Models." *Methods in Ecology and Evolution* 12(2): 255–65.

White, L. N., J. D. Forester, and M. E. Craft. 2017. "Using Contact Networks to Explore Mechanisms of Parasite Transmission in Wildlife." *Biological Reviews* 92: 389–409.

Wilber, M. Q., K. M. Pepin, H. Campa, S. E. Hygnstrom, M. J. Lavelle, T. Xifara, K. C. VerCauteren, and C. T. Webb. 2019. "Modelling Multi-Species and Multi-Mode Contact Networks: Implications for Persistence of Bovine Tuberculosis at the Wildlife–Livestock Interface." *Journal of Applied Ecology* 56(6): 1471–81. https://doi.org/10.1111/1365-2664.13370.

Wilber, M. Q., A. Yang, R. Boughton, K. R. Manlove, R. S. Miller, K. M. Pepin, and G. Wittemyer. 2022. "A Model for Leveraging Animal Movement to Understand Spatio-Temporal Disease Dynamics." *Ecology Letters* 25: 1290–304.

Williams, E. S. 2005. "Chronic Wasting Disease." *Veterinary Pathology* 42: 530–49.

Wilson, A. D. M., S. Krause, N. J. Dingemanse, and J. Krause. 2013. "Network Position: A Key Component in the Characterization of Social Personality Types." *Behavioral Ecology and Sociobiology* 67(1): 163–73. https://doi.org/10.1007/s00265-012-1428-y.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Egan, Michael E., Kim M. Pepin, Justin W. Fischer, Scott E. Hygnstrom, Kurt C. VerCauteren, and Guillaume Bastille-Rousseau. 2023. "Social Network Analysis of White-Tailed Deer Scraping Behavior: Implications for Disease Transmission." *Ecosphere* 14(2): e4434. https://doi.org/10.1002/ecs2.4434