

FAMILIARITY BREEDS CONTEMPT: COMBINING PROXIMITY LOGGERS AND GPS REVEALS FEMALE WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) AVOIDING CLOSE CONTACT WITH NEIGHBORS

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FAMILIARITY BREEDS CONTEMPT: COMBINING PROXIMITY LOGGERS AND GPS REVEALS FEMALE WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) AVOIDING CLOSE CONTACT WITH NEIGHBORS

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ABSTRACT: Social interactions can influence infectious disease dynamics, particularly for directly transmitted pathogens. Therefore, reliable information on contact frequency within and among groups can better inform disease modeling and management. We compared three methods of assessing contact patterns: (1) space-use overlap (volume of interaction [VI]), (2) direct contact rates measured by simultaneous global positioning system (GPS) locations (<10 m apart), and (3) direct contact rates measured by proximity loggers (PLs; 1-m detection) among female white-tailed deer (*Odocoileus virginianus*). We calculated the PL:GPS contact ratios to see whether both devices reveal similar contact patterns and thus predict similar pathogen transmission patterns. Contact rates measured by GPS and PLs were similarly high for two within-group dyads (pairs of deer in the same social groups). Dyads representing separate but neighboring groups (high VI) had PL:GPS contact ratios near zero, whereas dyads further apart (intermediate VI) had higher PL:GPS contact ratios. Social networks based on PL contacts showed the fewest connected individuals and lowest mean centrality measures; network metrics were intermediate when based on GPS contacts and greatest when based on VI. Thus, the VI network portrayed animals to be more uniformly and strongly connected than did the PL network. We conclude that simultaneous GPS locations, compared with PLs, substantially underestimate the impact of group membership on direct contact rates of female deer and make networks appear more connected. We also present evidence that deer coming within the general vicinity of each other are less likely to come in close contact if they are in neighboring social groups than deer whose home ranges overlap little if at all. Combined, these results provide evidence that direct transmission of disease agents among female and juvenile white-tailed deer is likely to be constrained both spatially and by social structure, more so than GPS data alone would suggest.

Key words: Contact rate, disease transmission, GPS, *Odocoileus virginianus*, proximity logger, social behavior, white-tailed deer.

INTRODUCTION

Host social structure can significantly affect pathogen transmission and prevalence (Cross et al. 2012; Griffin and Nunn 2012). In particular, intragroup and intergroup characteristics, such as sex, age, and patterns of space-use, can influence contact rates (Altizer et al. 2003; Magle et al. 2013). Such social structuring of contacts can reduce how many individuals each host contacts, thereby impeding pathogen transmission and establishment relative to the same mean contact rate in a well-mixed population (Keeling 1999). However, pathogen transmission rates are often high within social groups, which can decrease the likelihood of

stochastic pathogen extinction early in an epizootic (Newman 2003; Krause et al. 2007). Socially structured contact rates have been proposed as a mechanism for frequency-dependent disease transmission (McCallum et al. 2001; Begon et al. 2002), which can confound attempts to control disease (Potapov et al. 2012). In extreme cases, frequency-dependent transmission could drive hosts extinct (e.g., devil facial tumor disease; McCallum et al. 2009). Reliable estimates of contact rates within and between social groups should enhance our ability to predict disease dynamics and impacts on wildlife populations.

Quantifying contacts relevant to pathogen transmission is difficult for free-living

wildlife. Past researchers have quantified contact rates by visual observations (Totton et al. 2002), simultaneous telemetry locations (very high frequency [VHF] or global positioning system [GPS]) within a specified distance (e.g., <10 m, Ramsey et al. 2002; Schaubert et al. 2007), or proximity loggers ([PLs]; Ji et al. 2005; Prange et al. 2011) but, few studies compare these methods (Walrath et al. 2011). Visual observations are challenging for nocturnal and cryptic animals, except at feeding or watering areas. Simultaneous VHF or GPS locations are collected at discrete times and are subject to location error of several to hundreds of meters, but they locate contacts in space. In contrast, PLs operate continuously and detect each other only at very close range (e.g., <1 m) but fail to record some proximity events (Walrath et al. 2011) and do not provide location of contacts. Researchers have also used space-use overlap to quantify potential for contact (Millsbaugh et al. 2004; Schaubert et al. 2015). No metric based on proximity or space use can perfectly quantify the probability of pathogen transmission, and each method is likely to best reflect a different type of transmission. For instance, approaching within several meters is necessary for direct physical contact, but the probability of actual contact (and disease transmission) given proximity may depend substantially on the age, sex, familiarity, and status of the interacting individuals. Very close physical proximity could occur during fighting, mating, allogrooming, or dominance display, each of which represents a very different scenario for pathogen transmission.

Contact within and between groups of white-tailed deer (*Odocoileus virginianus*) has received attention because of bovine tuberculosis and chronic wasting disease (CWD), maladies of concern because of potential impacts on livestock and free-living deer populations (Williams et al. 2002; Conner et al. 2008). Female white-tailed deer form relatively stable matrilineal groups, which typically comprise a

dominant adult doe, her most recent offspring, and her older female offspring (Hawkins and Klimstra 1970; Nixon et al. 1991). Multiple groups often feed together in larger aggregations in late winter and spring (Hawkins and Klimstra 1970). Group structure typically dissolves by June in preparation for parturition, when females become territorial around their fawns, and re-forms in autumn (Nixon et al. 1991; Bertrand et al. 1996).

These social and familial bonds influence both space-use and contact patterns among white-tailed deer. Magle et al. (2013) observed that female dyads with high space-use overlap tended to be closely related. Schaubert et al. (2015) found that direct contact (simultaneous locations in close proximity) rates of females and juveniles were much higher within than between groups, even after accounting for shared space-use, and Walrath et al. (2011), using PLs, showed that penned deer contacted close relatives with greater frequency and duration than unrelated deer. These studies all consider proxies rather than actual disease transmission, but their findings accord with Gear et al. (2010), who demonstrated that the probability of a female deer contracting CWD was greatly amplified if a closely related female in the vicinity was also infected. Thus, both spatial and social structure appear to be important in pathogen transmission among deer, so quantifying intragroup and intergroup contact rates is crucial in understanding and effectively managing disease in free-ranging deer (Drewe 2010).

These studies are not directly comparable, however, because each method illuminates a different aspect of behavior relevant to pathogen transmission. Directly comparing results between metrics can help illuminate behavioral interactions and implications for disease. Consider two dyads (pairings) of hosts that spend similar amounts of time in the general vicinity of each other, but the members of one dyad rarely approach each other more

closely. This behavioral pattern could manifest as both dyads having similar frequency of contacts identified by GPS (e.g., within 10 m) but one dyad generating much fewer PL contacts (e.g., within 1 m) than the other, and thus having a lower PL:GPS contact ratio. This disparity between methods would provide evidence that 1) the social relationships differ between the dyads, 2) direct pathogen transmission rates differ between the dyads, and 3) GPS contact rates provide insufficient information to assess either behavioral interactions or potential direct transmission. We evaluated whether space-use overlap, simultaneous GPS locations, and PLs yield similar or disparate pictures of how space-use and social structure influence differences in contacts among free-living female white-tailed deer.

MATERIALS AND METHODS

We captured and collared female white-tailed deer at two study areas (“Johnson” and “Touch of Nature”) in southern Illinois, US, from October 2011 to January 2012. We used drop nets, rocket nets, and darts, focusing on capturing groups of mature females and fawns. Captured deer were immobilized by intramuscular injection of 4 mg/kg Telazol® (Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and 2 mg/kg xylazine HCl, ear-tagged, and aged as a fawn (ca. 0.5 yr old), yearling (ca. 1.5 yr old), or adult (>2 yr old) by tooth replacement and wear (Severinghaus 1949). We aimed to equip one deer from each group with a GPS collar (TGW-4500; Telonics, Inc., Mesa, Arizona, USA) with a PL (SirTrack, Inc., Havelock North, New Zealand) secured to the GPS casing using epoxy. The GPS units were programmed to record locations hourly, within a 3-min window. In contrast, each PL functioned continuously and was calibrated to detect other PLs ≤ 1 m away. Collars were programmed to detach on 1 June 2012 because social structure breaks down at the onset of parturition. As part of a larger experiment, we removed noncollared deer from five groups containing collared deer during 27 March to 13 April 2012. One of these removal groups contained two collared deer, one of which was removed. Capture and sampling procedures were approved by the

Institutional Animal Care and Use Committee at Southern Illinois University Carbondale (protocol 11-027).

We compared contact and space-use patterns among all possible dyads within the same study area, beginning when the last collar was deployed in each study area (18 December 2011 at Johnson and 15 January 2012 at Touch of Nature) and ending 1 June 2012 when the collars dropped off. Exceptions were one collared deer that was removed on 29 March 2012 and one collared deer killed by a vehicle 1 April 2012. We measured space-use overlap for each dyad with the volume of intersection (VI) of their fixed-kernel use distributions, which we calculated with the kernel overlap function in the *AdehabitatHR* package (Calenge 2006) in program R (R Version 2.14.1; R Development Core Team 2011) using 500 randomly selected GPS locations and a smoothing parameter determined by reference bandwidths for each animal (Seaman and Powell 1996; Seaman et al. 1999). We defined a GPS contact for a dyad as simultaneous (same 3-min window) locations < 10 m apart. We chose a 10-m criterion to balance depicting close physical contact with sample size and GPS location error. We defined a PL contact for a dyad as any communication between their PLs (nondirectional) > 30 s apart from any other such communication (as described in Walrath et al. 2011). We noted a reciprocal contact if both PLs in the dyad detected each other < 30 s apart, and we noted a duplicate record for a dyad if both a PL contact and a GPS contact occurred within 1 h. For each dyad and type of contact (GPS or PL), we calculated contact rate as contacts per week.

To measure how strongly correlated were the movements of the two deer comprising each dyad, we used the dynamic interaction metric of Long et al. (2014). This metric generalizes the vector correlation coefficient of Shirabe (2006) to allow examination of short time periods and does not involve physical proximity. Each pair of successive GPS locations (hours t and $t+1$) for 1 deer (i) defined a vector with length $d_{i,t}$ and direction $\theta_{i,t}$. For dyad (ij) at hour t , the dynamic interaction index (DI) was calculated as follows:

$$DI_t = \left(1 - \frac{|d_{i,t} - d_{j,t}|}{d_{i,t} + d_{j,t}} \right) \cos(\theta_{i,t} - \theta_{j,t}) \quad (1)$$

We averaged hourly DI_t values over the entire data set to measure the overall movement correlation for the dyad DI.

Based on high DI and VI values and inconsistent proximity, we concluded that we inadvertently collared two animals in the same group in each study area; one adult-juvenile dyad and one adult-yearling dyad (Fig. 1). To examine how three metrics of potential contact (VI, GPS contact rate, and PL contact rate) are influenced by social structure, we calculated the within:between group contact ratio using contact rates averaged across dyads of each category (within-group $n=2$ or between-group $n=43$) with ≥ 1 contact (GPS or PL). We assessed uncertainty in the within:between ratios for PL and GPS contact rates by bootstrapping (Supplementary Material, Appendix I).

We assessed statistical support for the post hoc hypothesis that neighboring between-group dyads (high VI) had anomalously low PL contact rates given their GPS contact rates. In other words, did these neighboring dyads avoid coming into close contact (1 m) despite often being in the same vicinity (10 m)? For between-group dyads with ≥ 1 contact, we compared the ratio of PL to GPS contact rates (i.e., the PL:GPS ratio) among dyads in three categories of space-use: low ($VI < 0.2$), intermediate ($0.2 \leq VI < 0.4$), and high ($0.4 \leq VI < 0.8$). We quantified uncertainty in each PL:GPS ratio by bootstrapping (Supplementary Material, Appendix I). To compare PL:GPS ratios more formally, we used zero-inflated Poisson regression to fit the following model, with dyad as the unit of analysis:

$$\ln(PL) = \ln(Weeks) + \ln(GPSrate) + \beta_0 + \beta_{low} VI_{low} + \beta_{high} VI_{high} \quad (2)$$

where PL is the expected number of observed PL contacts, $Weeks$ is the number of weeks both deer in the dyad were available to contact, $GPSrate$ is the observed number of GPS contacts divided by $Weeks$ (zero values replaced by 0.01), VI_{low} and VI_{high} are indicator variables (0,1) for low and high VI, respectively (intermediate VI provides the reference level), and the β s are the fitted parameters. $Week$ and $GPSrate$ have no associated β parameters because they were treated as offset variables. The model can be rewritten as follows:

$$\frac{PL}{GPS} = \exp(\beta_0) \exp(\beta_{low} VI_{low}) \exp(\beta_{high} VI_{high}) \quad (3)$$

showing how $\exp(\beta_{low})$ and $\exp(\beta_{high})$ represent multiplicative differences in the PL:GPS

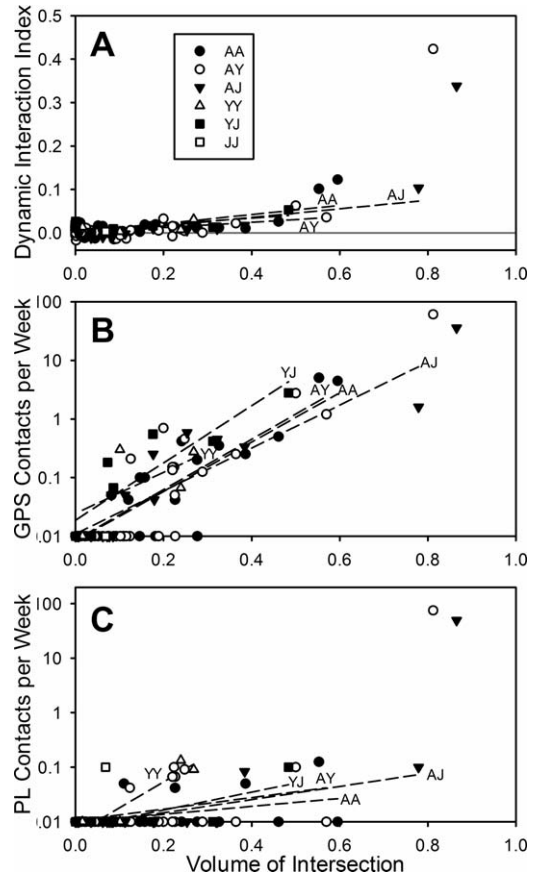


FIGURE 1. Metrics of social affiliation and contact, as a function of space use overlap (volume of intersection) for dyads of female white-tailed deer (*Odocoileus virginianus*) in southern Illinois, USA, from 18 December 2011 to 1 June 2012. (A) Correlation of movements based on an hourly dynamic interaction index averaged over the entire data set, according to Long et al. (2014). (B) Weekly contact rates based on simultaneous geographic positioning system (GPS) locations < 10 m apart. (C) Weekly contact rates based on proximity logger (PL) detections (< 1 m). Contact rate values of zero were replaced with 0.01. Dashed lines represent linear regressions for data from each dyadic age combination (A=adult; Y=yearling; J=juvenile), excluding two apparent within-group dyads with the highest volume of intersection and contact rates.

contact relative to the intermediate VI reference category.

Finally, we tested whether contact method affected the apparent topology of between-group social networks. We used the program NetDraw (Borgatti et al. 2002) to visualize networks and used the *sna* package (Butts 2010) in program R to calculate network

centrality metrics (node degree and flow-betweenness) to identify important nodes. Node degree measures the number of immediate neighbors (i.e., direct connections), and flow-betweenness accounts for both direct and indirect connections where an individual is an intermediary in the shortest path (Freeman et al. 1991; Krause et al. 2007). Both measures are highly applicable to pathogen transmission networks and are relatively stable even for networks that are sparsely sampled (Bell et al. 1999; Costenbader and Valente 2003). We used Kruskal-Wallis tests to compare network centrality metrics among networks based on different methods.

RESULTS

We collared 26 female deer (five juveniles, six yearlings, 15 adults), but we excluded four individuals from analysis because of capture-related deaths, unrecovered PL units, and incomplete GPS data. Of the 126 possible dyads, 45 had ≥ 1 GPS or PL contact. The GPS fix success rate averaged 98.3%, ranging among individuals from 95.5% to 99.6%, and mean \pm SE horizontal GPS location error was 5.7 ± 0.01 m. During the 20-wk (Touch of Nature) and 24-wk (Johnson) data-analysis periods, we detected 1,629 within-group contacts (719 and 910 per dyad) and 540 between-group contacts using GPS locations. The PLs recorded 2,113 within-group contacts (989 and 1,124 per dyad); 380 (17.2%) of which were reciprocal detections, compared with only 23 between-group contacts (≤ 3 PL contacts per dyad) with no reciprocal detections. The PLs recorded duplicate contacts (within 1 h) for 454 of 1,629 (27.9%) within-group GPS contacts, but only four of 540 (0.7%) between-group GPS contacts. As the space-use overlap (VI) of dyads increased, so did their dynamic interaction index (DI), GPS contact rate (per week), and PL contact rate (per week), with similar slopes regardless of the age composition of the dyad (Fig. 1). The relationships with DI and PL contact rate, however, were clearly discontinuous at very high VI values (Fig. 1A, C).

The two within-group dyads (adult-juvenile and adult-yearling) had the greatest space-use overlap (VI=0.87 and VI=0.81, respectively) and movement correlations (DI=0.34 and DI=0.42, respectively; Fig. 1A). Although some between-group dyads had nearly as much space-use overlap (maximum VI=0.78), their movements were substantially less correlated (maximum DI=0.11) (Fig. S1). The within-group dyads also had contact rates greater than sevenfold (GPS) and >300 -fold (PL), higher than any other dyad (Fig. 1). Mean \pm SE contact rates of the two within-group dyads were broadly similar for PL (62.2 ± 12.7 /wk) and GPS (48.3 ± 12.4 /wk), but between-group dyads in aggregate had much lower contact rates based on PL (0.029 ± 0.007 /wk) than those based on GPS (0.61 ± 0.17 /wk). Consequently, the overall mean \pm bootstrap SE within:between contact ratios were $2,156.4 \pm 546.5$ for PL, 79.8 ± 3.0 for GPS, and 3.1 for VI. Thus, the within:between contact ratio was >25 -fold greater for PL than it was for GPS and >690 -fold greater for PL than it was for VI. In short, PL contact rate was the most sensitive indicator of social structuring.

Among between-group dyads, PL and GPS contact rates were most disparate (i.e., lowest PL:GPS ratio) for those dyads with high VI (GLM, $\beta_0 = -1.1 \pm 0.4$, $P < 0.01$; $\beta_{low} = -1.2 \pm 1.1$, $P = 0.24$; $\beta_{high} = -2.4 \pm 0.5$, $P < 0.001$). The seven between-group dyads with high VI (0.4–0.8), collectively, had GPS locations <10 m apart on 387 occasions, but were detected <1 m apart by PLs only nine times (PL:GPS ratio = 0.023 ± 0.008 bootstrap SE). In comparison, the 20 between-group dyads with intermediate VI (0.2–0.4) collectively generated more ($n=12$) PL contacts, despite only 102 GPS contacts (PL:GPS ratio = 0.118 ± 0.036 bootstrap SE). The 16 between-group dyads with low VI (<0.2), excluding dyads with no observed contacts, collectively had two PL contacts and only 51 GPS contacts (PL:GPS ratio = 0.039 ± 0.029 bootstrap SE). This shift in PL:GPS contact pattern

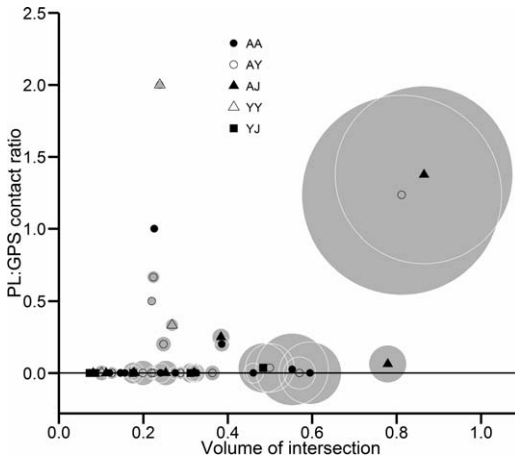


FIGURE 2. Ratio of proximity logger (PL) contacts to simultaneous geographic positioning system (GPS) locations <10 m (PL:GPS10) versus volume of intersection of female white-tailed deer dyads in southern Illinois from December 2011 to June 2012. Area of the gray circle surrounding each symbol indicates the relative number of total GPS contacts. Symbol shape-fill combinations indicate age composition of each dyad (A=adult; Y=yearling; J=juvenile).

across categories of overlap does not appear to correlate with any obvious pattern in age-composition of dyads (Fig. 2).

Social network analysis revealed that most deer were connected to each other at each site, regardless of the method used to quantify contact (Fig. 3). Networks based on PL contacts yielded approximately one-third the connections that GPS did (ratio=11:31) and about one-eighth the connections VI did (ratio=11:85), suggesting that direct contacts between deer are much sparser than indicated by GPS and VI. Comparing network centrality, mean \pm SE node degree was greater for networks based on VI (8.5 ± 0.7) and GPS (3.1 ± 0.4) than on PL (1.1 ± 0.2) (Kruskal-Wallis test, $H=43.57$, $df=2$, $P<0.001$) and mean \pm SE flow-betweenness was greater for networks based on VI (39.5 ± 5.5) and GPS (10.1 ± 2.2) than on PL (1.9 ± 0.7) (Kruskal-Wallis test, $H=36.25$, $df=2$, $P<0.001$). In addition, each method identified different animals as most important to

network connectivity (Fig. 3). The VI network identified all deer at the Johnson site of similar importance, but GPS and PL identified different individuals (nos. 0210 and 0112, respectively) as most central. At the Touch of Nature site, all methods identified deer no. 0115 as important, but the VI network identified deer no. 0616 and the GPS network identified deer no. 0811 as also having crucial roles, whereas the PL network did not.

DISCUSSION

By comparing the contact rates of wild deer carrying both PLs and GPS devices, our study produced three main findings: 1) PLs and simultaneous GPS locations yield diverging views of contact patterns and network structure—within-group contact rates were underestimated and between-group contact rates were overestimated using simultaneous GPS locations; 2) female deer from neighboring groups (high space-use overlap) frequently came within about 10 m but rarely culminated in close physical contact; and 3) female deer that were less familiar (intermediate space-use overlap) were rarely in the same vicinity (ca. 10 m), but when they were, they were more likely to approach each other closely (<1 m) than did neighbors. These patterns were qualitatively unaffected by changing the GPS contact criterion (3, 5, or 25 m, data not shown), so they reflect fundamental capabilities of the instruments to detect between-group contacts, not a specific distance criterion.

Observations of animals in the same area and simultaneous GPS relocations have been used to compare within- and between-group contact rates (Kjær et al. 2008; Magle et al. 2013), assuming a specified level of proximity is an indicator of potential contact regardless of group membership. Our findings strongly question that assumption by showing that the same degree of proximity led to less probability of close contact for neighboring groups than for deer in the same group

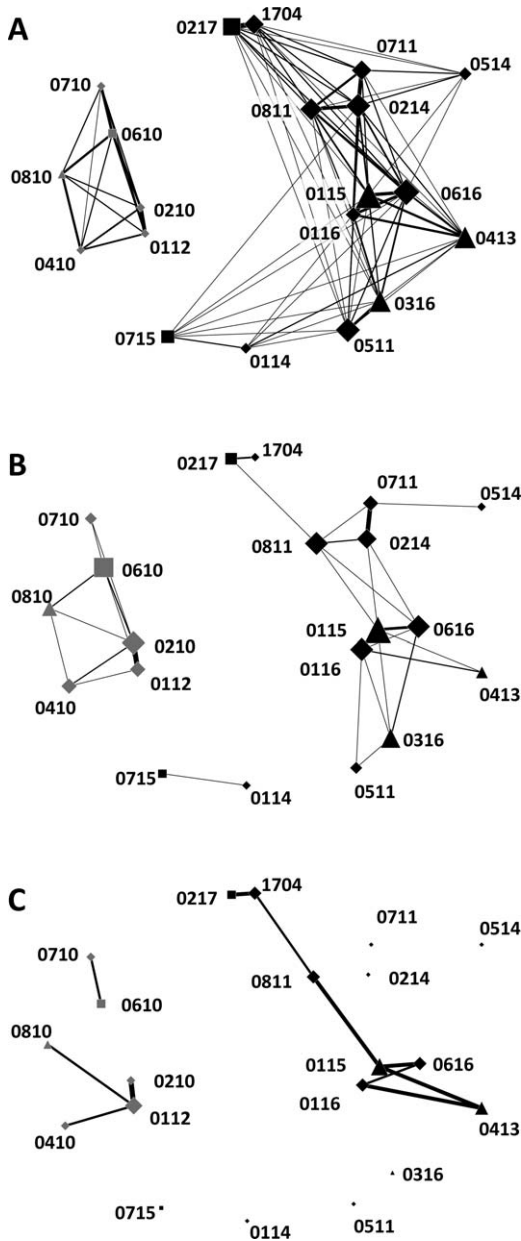


FIGURE 3. Social networks for female and juvenile white-tailed deer December 2011 to June 2012 at Johnson property (left) and Touch of Nature Environmental Center (right) in southern Illinois, USA, drawn using three metrics for potential infectious contact: (A) volume of intersection, (B) simultaneous geographic positioning system locations <10 m apart, and (C) proximity logger contacts. Three age classes are represented: adults (diamonds), yearlings (triangles), and juveniles (squares). Proximity of nodes is based on greater volume of intersection and thickness of lines

or more distant groups. Consequently, our results imply that the effect of social group membership on direct contact rates has been underestimated by GPS data. This underestimation helps explain why CWD shows a stronger group membership effect than do GPS-based contact rates. Schaubert et al. (2007) found that odds of direct contacts were about 10-fold greater for within-group than for between-group pairs of female and juvenile white-tailed deer, based on GPS locations <10 m apart, and Schaubert et al. (2015) revised that estimate downward to ≤ 6.4 -fold. In contrast, Gear et al. (2010) reported that the odds of a female white-tailed deer being infected with CWD increased >100-fold when a CWD-infected close relative was harvested <3.2 km away compared with an infected nonrelative from the same distance. Our findings also suggest that infected deer could be as likely to directly transmit disease to unfamiliar females and fawns as to a neighbor, despite less-frequent proximity, although we expect much more frequent indirect transmission between neighbors based on overlap of space-use and high frequency of moderate proximity (ca. 10 m).

Identifying contacts is limited by the instrument used: GPS locations often have errors of approximately 10 m, and PL detection range depends on the orientation of the device. Previous authors using PL observed a higher percentage of reciprocal contacts than we did (Prange et al. 2006; Walrath et al. 2011; Watson-Haigh et al. 2012), especially for animals from different groups. High percentages of reciprocal contacts may signify that deer frequently interact at distances shorter than the PL detection range and thus have more opportunities to be detected by both

←
between nodes represent greater metrics for potential infectious contact. Symbol size represents node degree.

units. Low percentages of reciprocal contacts, however, may signify that deer are interacting at the outer ranges of PL detection or for only brief periods, and thus, have only a small window of time for detection.

If a disease outbreak were to occur in this study population, the three social networks predict differing rates of disease spread. The network based on VI, which is likely most appropriate for pathogens transmitted indirectly via environmental contamination, predicts the most rapid disease spread among social groups because of the large number of connections between individuals, high node degree values, and high flow-betweenness values. In contrast, the network based on PLs, which is most appropriate for direct transmission, predicts the slowest spread of the disease because of the few connections between individuals, the low node degree values, and the low flow-betweenness values. In addition, the three social networks predict different responses to disease management; the many connections in the VI network allows it to be more robust to disturbances and allows for more certainty that the pathogen will be transmitted to all other members of the population. In other words, each female deer was connected to many more individuals in the VI network, so regardless of whether the connections were strong or weak, any individual could transmit a pathogen to many other animals in the population, even if one of the connections or even a node was removed. In the PL network, however, only a few individuals were highly connected, indicating that those few animals may have a larger role in epizootics, but removal of those individuals can be highly effective for disease control. Relatively high node degree values (compared with other nodes in the network) identify “super spreaders” within the population (Lloyd-Smith et al. 2005), and relatively high flow-betweenness values identify important “bridges” through which the pathogen may travel to

more individuals. Identifying those super spreaders and bridges can help population management efforts that may reduce contact rates and disease spread.

There are limitations to this study. Our sample size is small, with only 1 yr of data and only two within-group dyads. The discrepancy, however, in direct contact patterns between within-group and between-group dyads is striking enough to argue against assuming that intermediate proximity is equally indicative of potential contact, regardless of social affiliation. Second, not all direct contacts within the population were recorded because of imperfect detections (Walrath et al. 2011) and because only one animal was monitored in most groups. We assume, however, that the detection failures are independent of group membership or space-use overlap, which allows for comparison. Third, we only considered the number of direct contacts and did not account for contact duration. Undoubtedly, type of contact and variations in direct contact duration influence the probability of transmission. Fourth, our findings are limited to populations of female deer during winter–spring, outside of both the breeding and fawning seasons. We specifically chose this period as the time of greatest social interaction among white-tailed deer matriline (Hawkins and Klimstra 1970), when intergroup transmission was most likely. Nevertheless, we believe our findings reflect fundamental differences in the way PLs and simultaneous GPS locations estimate contacts. We conclude that GPS contacts probably underestimate the partitioning of contacts within vs. between groups in female deer, and combining GPS and PL technologies can enhance our understanding of where contacts occur.

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SUPPLEMENTARY MATERIAL

Supplementary material for this article is online at <http://doi:10.7589/2013-06-139>.

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