Tools and Technology Article

Spatial and Temporal Analysis of Contact Rates in Female White-Tailed Deer

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ABSTRACT White-tailed deer (*Odocoileus virginianus*) are important game mammals and potential reservoirs of diseases of domestic livestock; thus, diseases of deer are of great concern to wildlife managers. Contact, either direct or indirect, is necessary for disease transmission, but we know little about the ecological contexts that promote intrasexual contact among deer. Using pair-wise direct contacts estimated from Global Positioning System collar locations and joint utilization distributions (JUDs), we assessed habitats in which contacts occur to test whether direct contact rates among female white-tailed deer in different social groups differs among land-cover types. We also tested whether contact rates differed among seasons, lunar phases, and times of day. We obtained locations from 27 female deer for periods of 0.5–17 months during 2002–2006. We designated any simultaneous pair of locations for 2 deer <25 m apart as a direct contact. For each season, we used compositional analysis to compare land-cover types where 2 deer had contact to available land-cover weighted by their JUD. We used mixed-model logistic regression to test for effects of season, lunar phase, and time of day on contact rates. Contact rates during the gestation season were greater than expected from random use in forest and grassland cover, whereas contact rates during the fawning period were greater in agricultural fields than in other land-cover types. Contact rates were greatest during the rut and lowest in summer. Diel patterns of contact rates varied with season, and contact rates were elevated during full moon compared to other lunar periods. Both spatial and temporal analyses suggest that contact between female deer in different social groups occurs mainly during feeding, which highlights the potential impact of food distribution and habitat on contact rates among deer. By using methods to associate contacts and land-cover, we have created beneficial tools for more elaborate and detailed studies of disease transmission. Our methods can offer information necessary to develop spatially realistic models of disease transmission in deer. (JOURNAL OF WILDLIFE MANAGEMENT 72(8):1819–1825; 2008)

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Wildlife diseases are gathering increasing attention due to their impact on livestock, humans, and endangered or threatened species (McCallum and Dobson 1995, Daszek et al. 2000, Chomel et al. 2007). Reduction of habitat, contact with domestic livestock, toxicant exposure, and transport of animals by humans over great distances has altered the susceptibility and exposure of wildlife populations to diseases (Galloway and Handy 2003, Fisk et al. 2005, Chomel et al. 2007). Because wildlife diseases can threaten domestic animals and humans, stakeholders exert political and economical pressure to actively manage wildlife disease via both lethal and nonlethal approaches (Peterson et al. 2006).

Ecological factors can affect disease dynamics in wild populations by influencing rates and patterns of transmission. Therefore, information about ecological factors affecting transmission will enable managers to more effectively reduce threats posed by wildlife diseases. Pathogens can transmit by either direct contact, which requires animals to be close in time and space, or indirect contact, where only spatial proximity is required. For example, rabies transmits directly through saliva (Sterner and Smith 2006), whereas chronic wasting disease (CWD) transmits through both direct and indirect contacts because the etiologic agent can persist in the environment (Williams et al. 2002; Miller et al. 2004, 2006).

Contact rates among free-ranging animals can be affected by social grouping, concentrated resources (Miller et al. 2003, Gompper and Wright 2005, Wright and Gompper 2005), landscape structure (Fa et al. 2001, Gudelj and White 2004), and population density (de Jong et al. 1995, Ramsey et al. 2002). In social species where group composition is stable, the likelihood of an infected host contacting, and therefore infecting, members of the same group is higher than for nonmembers (Altizer et al. 2003, Schauber et al. 2007). By definition, animals interact with members of the same group both more often and more intimately than with individuals from other groups. However, a pathogen must ultimately be transmitted to other groups to persist. The fluid group structure in white-tailed deer (*Odocoileus virginianus*) may increase inter-group contact rates and, potentially, disease transmission (Hawkins and Klimstra 1970, Nixon et al. 1994, Comer et al. 2005). Hawkins and Klimstra (1970) reported that separate social groups of white-tailed deer often fed together in later winter and spring but rarely bedded together. Congregation of multiple groups at feeding sites, therefore, could accelerate contact rates. Aggregation of Rocky Mountain elk (*Cervus elaphus*) at artificial feedings sites in Wyoming facilitates transmission of brucellosis (*Brucella abortus*; Dobson and Meagher 1996, Cross et al. 2007). Transmission of bovine tuberculosis (*Mycobacterium bovis*) in white-tailed deer is also facilitated by congregation at feeding sites (Miller et al. 2003, Palmer et al. 2004).

Land use and land-cover affect deer behavior and movement across the landscape, and therefore affect

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contact rates. Farnsworth et al. (2005) found that CWD prevalence in mule deer (*O. hemionus*) was higher in developed areas than in undeveloped areas, suggesting higher contact rates on developed land. Deer activity patterns and social cohesion also vary temporally, which could produce predictable changes in contact rates. The effects of moon phase on deer activity and movement are ambiguous. Some studies have not found any influence of moon phase on deer activity (Zagata and Haugen 1974, Kufeld et al. 1988, Beier and McCullough 1990), whereas others have reported that deer movements increased during a full moon (Kammermeyer 1975 cited in Beier and McCullough 1990) and use of open habitats decreased during a full moon (Newhouse 1973 cited in Beier and McCullough 1990). Finally, deer are crepuscular, so elevated contact rates at dawn and dusk would indicate that contacts occur mainly when deer are moving, whereas elevated contacts during midday would indicate that contacts occur mainly while bedding.

Understanding factors that mediate contact rates could aid in managing or predicting the spread and persistence of diseases in deer, and we found no studies in the literature that analyze temporal and spatial influences on contact rates in deer. New technologies, such as remote cameras (Beringer et al. 2004), contact loggers (Ji et al. 2005), and Global Positioning System (GPS) collars (Schauber et al. 2007) facilitate the study of contacts between individual animals. Our objectives were to test whether certain land-cover types serve as foci for inter-group contacts between deer using GPS collar locations and to determine if seasonal and daily variations in behavior affect contact probabilities.

STUDY AREA

We conducted our study in an exurban setting approximately 4 km southeast of Carbondale, Illinois, USA (37°42′14″N, 89°9′2″E). The climate was characterized by moderate winters and hot, humid summers, with a mean January low temperature of −6.2° C and mean July high temperature of 31° C (Midwest Regional Climate Center 2007). The study area comprised a mix of contiguous patches of oak–hickory forest (57%) with some hay fields and other grasslands (26%). Row-crop agriculture (12%) consisted primarily of soybeans, and the area had minor components of urban land use including lawns and old fields. Average home-range sizes for female deer in the study area were 53.0 ± 5.2 ha during the fawning season and 90.6 ± 9.7 ha during the winter season (Storm et al. 2007). The study area and exurban Carbondale deer population are further described elsewhere (Schauber et al. 2007, Storm et al. 2007).

METHODS

Deer Capture and Handling

We captured deer at sites baited with corn or apples, primarily by darting with 3-cm^3 barbed darts (Pneu-Dart, Inc., Williamsport, PA) containing 2:1 mix of Telazol hydrochloride (HCL; 4 mg/kg; Fort Dodge Animal Health, Fort Dodge, IA) and xylazine HCL (2 mg/kg; Bayer Corp., Shawnee Mission, KS; Kilpatrick and Spohr 1999). We fired darts from elevated stands approximately 20 m away from the bait site, and each dart contained a radiotransmitter for locating darted animals. We also used rocket-propelled nets (Hawkins et al. 1968) or drop-nets (Ramsey 1968) to capture deer, which we then immobilized with an intramuscular injection of 10 mg/kg ketamine HCL (Fort Dodge Animal Health). We blindfolded all deer during handling and visually observed them after handling until they were able to stand on their own. We specifically focused on capturing females >1 year old. Although we captured and collared some fawns and males, we programmed their collars to drop off after only a few months to avoid constriction due to growth in fawns and neck swelling of male deer during the rut. We did not include males in analyses due to small sample size. Deer capture and handling methods were approved by the Southern Illinois University Carbondale Institutional Animal Care and Use Committee (protocol no. 03-003).

We fitted 27 female deer with GPS collars (Model TGW-3500, wt 700 g; Telonics, Mesa, AZ), which stored location data internally with a manufacturer-reported error range of 13–36 m. Schauber et al. (2007) found median and 95th-percentile position errors were 8.8 m and 30 m, respectively, for stationary collars under closed canopy. Collars deployed in 2002 and 2003 recorded locations hourly and we programmed their release mechanisms to drop off after 4–5.5 months. We programmed collars deployed in 2004–2005 to record deer locations every 2 hours and to drop off after 12–17 months. However, collars recorded locations every hour in November and December to account for greater deer activity during the rut. We programmed all collars to determine locations within 3 minutes of one another, and we excluded estimated locations with elevation >100 m different from the known elevation of the study area. We also excluded locations from the first 3 days after capture to account for altered behavior due to capture and handling. We identified 3 pairs of deer as being in the same social groups because their movements were highly correlated (Schauber et al. 2007), and our analysis only included pairs of deer in different groups. To account for seasonal variations in behavior, we separated location data into 4 seasons pertinent to deer biology: gestation (1 Jan–14 May), fawning (15 May–31 Aug), prerut (1 Sep–31 Oct), and rut (1 Nov–31 Dec).

Our sampling unit for all contact analyses was a pair of deer. We defined 2 deer to be in direct contact if their concurrent GPS locations were <25 m apart. We chose this proximity criterion as the median of the GPS-collar accuracy. We calculated the location of each direct contact between 2 deer as the midpoint between their concurrent GPS locations (Schauber et al. 2007).

Spatial and Temporal Analysis of Contact Rates

We used ArcView 3.2 to create a digital map of the land-cover types (Table 1) in a 10 × 10-km area encompassing all

Table 1. Land-cover types in the 10 × 10-km study area used in analyzing contact habitat for white-tailed deer in southern Illinois, USA, 2002–2006. Percentages can be obtained by dividing total areas by 100.

Land-cover code	Total area (ha)	Description of cover type
Agriculture	1,405.6	Agricultural fields, mainly corn and soybeans
Aqua[a]	7.5	Aquaculture center
Fish[a]	16.0	Fish hatchery
Forest	5,565.2	Forest consisting mainly of oak–hickory
Grassland	609.9	Native grasses, not mowed
Lawn	427.9	Mowed and tended lawns close to buildings
Marsh[a]	13.9	Marsh
Oldfield	136.7	Field in late-successional state, with brush and trees
Pasture	442.6	Grassy fields, grazed by livestock
Road	80.0	Highways, roads, and gravel roads
Urban	117.7	Buildings and houses
Water	1,181.2	Lakes, ponds, and rivers

[a] No home ranges overlapped these cover types, and we omitted them from all analyses.

known locations of the GPS-collared deer. We used 1998 digital orthophoto quarter quadrangles (Illinois Geospatial Data Clearing House 1997) and ground-truthing to identify and delineate land-cover types (Storm et al. 2007).

We used compositional analysis (Aebischer and Robertson 1992, Aebischer et al. 1993) to compare land-cover types where 2 deer came in contact with land-cover types jointly used by the 2 deer. Using the digital map of the study area, we characterized the land-cover associated with each contact by calculating the proportion of each cover type (Table 1) within a 12.5-m-radius buffer (to account for GPS errors) centered on the contact location. We averaged these proportions over all contact locations for a given deer pair and season to represent used land-cover. To reduce problems associated with zero use-values (Bingham and Brennan 2004), we excluded from analysis for each season any land-cover type that was unused (seasonal use-value = 0) by $\geq$80% of deer pairs in that season.

We used the joint utilization distribution (JUD) of a deer pair in a given season to define available land-cover for contacts. The JUD describes the joint probability that both members of a pair will be found in the same area, assuming independent movements. The JUD thus indicates both the amount of space jointly used and how similarly the 2 animals use space within that overlap zone (Millspaugh et al. 2004). We used JUD to define available land-cover, first because 2 deer are unlikely to contact each other outside both animals' home ranges or in areas of exclusive use. Second, and perhaps more importantly, deer clearly select particular habitats (e.g., ecotones) within their home ranges; such selection is well-documented and, thus, not especially interesting for our analyses. Simply put, little would be learned if we determined that deer are most likely to contact other deer in preferred deer habitat. Therefore, we specifically sought to test whether deer contacts occur in certain habitats more frequently than would be expected on the basis of their joint use. Because the JUD indicates the probability the 2 deer will be located concurrently in the same area assuming independent movements, a difference in land-cover proportions between contact locations and JUD essentially indicates that the direct contact rate (i.e., proportion of concurrent locations in a given land-cover type that are <25 m apart) differs among land-cover types. In other words, does the tendency of 2 deer to approach one another in a particular area, given that they both use that area, differ depending on the area's land-cover type?

To calculate the JUD, we first estimated the fixed-kernel utilization distribution (Seaman and Powell 1996, Seaman et al. 1998) from 200 randomly selected GPS locations for each deer and season, with smoothing parameter estimated by least-squares cross-validation in the Home Range extension (Rodgers et al. 2005) in ArcView 3.2:

$$\mathrm{UD}(i,s)_{xy} = \frac{\sum_{k=1}^{200} \exp\left[-\frac{(x-x_k)^2+(y-y_k)^2}{2h^2}\right]}{200 \times 2\pi h^2}$$

where x and y are coordinates on the landscape, x_k and y_k are coordinates of location k within the set of 200 locations for deer i and season s, and h is the smoothing parameter. The denominator adjusts for sample size and ensures that the UD has volume = 1. We used 200 locations per home range to balance sample size requirements for fixed-kernel home ranges while minimizing computing time (Seaman et al. 1999).

We then calculated the seasonal JUD of each deer pair (i and j) as the product of the 2 utilization distributions at each point in a grid with 40-m spacing overlaying the study area: $\mathrm{JUD}(ij,\ s)_{xy} = \mathrm{UD}(i,\ s)_{xy} \times \mathrm{UD}(j,\ s)_{xy}$. We chose 40-m spacing to ensure thorough coverage ($\geq$500 points within a typical home range; Storm et al. 2007) while reducing computation time. Note that neither UD nor JUD is a discrete area; both take nonzero (albeit often extremely small) values for any coordinates within or beyond the study area. Unlike the UD, the JUD has volume <1. The JUD also differs from the volume of intersection (Millspaugh et al. 2004) in accounting for home-range size; 2 deer with perfectly overlapping home ranges will have volume of intersection = 1 no matter their home-range size. However, large home ranges dilute the opportunity for simultaneous occupancy at a given location, which is reflected in low JUD.

We calculated available land-cover proportions for each deer pair as the weighted average (wt = JUD) proportions of

Table 2. Seasonal tests for random distribution of pair-wise contact locations among land-cover types for between-group pairs of female white-tailed deer in southern Illinois, USA, 2002–2006.

Season	Wilk's lambda	F	df	P
Gestation	0.37	4.91	6,17	0.004
Fawning	0.23	7.59	4,9	0.002
Prerut	0.60	2.64	3,12	0.100
Rut	0.57	3.64	4,19	0.023

the land-cover types within the JUD:

$$\hat{p}_a = \frac{\sum_{cell=1}^{N} p_{a,cell}\overline{\mathrm{JUD}}_{cell}}{\sum_{cell=1}^{N} \overline{\mathrm{JUD}}_{cell}}$$

where $\hat{p}_a$ is the weighted average proportion of land-cover type a, $p_{a,cell}$ is the proportion of land-cover type a in a given cell, $\overline{\mathrm{JUD}}_{cell}$ is the average JUD value of the cell's 4 corners, and N is the number of cells in the study area. Recall that the JUD is not a discrete area, but land-cover types in areas with infrequent joint use by a deer pair were given low weight. Weighting by JUD gave small available proportions for some land-cover types and deer pairs. The smallest available proportion associated with a nonzero use proportion was 10^{-9}, so we treated every land-cover type with available proportion below 10^{-10} (one order of magnitude smaller; Aebischer et al. 1993) as unavailable (zero availability) to remove small values. If a particular land-cover type was unavailable to a deer pair, we treated it as a missing value. As indicated previously, we excluded land-cover types in each season with zero use by $\geq$80% of deer pairs. Because compositional analysis is based on log ratios and log(0) is undefined, we replaced zero use-proportions with values of 10^{-10} for available land-cover types included in the analysis.

In the compositional analysis, the resulting log-ratios were not normally distributed, so we used randomization to test the global null hypothesis of random distribution of contacts with respect to joint use ($\alpha = 0.05$ throughout) and to test for pair-wise differences in contact frequencies among cover types. We used the BYCOMP macro (Ott and Hovey 2002) in SAS (SAS Institute, Cary, NC) to perform compositional analysis. Because all tests were based on 999 randomizations of the data, the smallest obtainable P-value was 0.001.

We calculated average number of contacts per deer pair per season. We used mixed-model logistic regression (SAS PROC GLIMMIX) to test how contact rates varied among seasons (as described in GPS Collar Data), lunar phases (quarters of the lunar cycle centered on the new, full, waning, and quarter moons), and diel periods (dawn: 0300–0900 hr, midday: 0900–1500 hr, dusk: 1500–2100 hr, and night: 2100–0300 hr). The binary response variable was whether each pair of concurrent locations for a deer pair were $\leq$25 m apart. We treated deer pair as a random effect and temporal variables as fixed effects. We initially fitted a model with all possible interactions among fixed effects but then dropped the nonsignificant 3-way interaction and any nonsignificant 2-way interactions. We used Tukey's multiple range test to separate means.

RESULTS

Spatial and Temporal Analysis

Compared with joint space use (JUD), contacts did not occur randomly among land-cover types during gestation, fawning, and rut seasons (all $P \leq 0.023$; Table 2), whereas we did not find that contacts in prerut ($n = 15$ pairs) differed from random use ($P = 0.1$; Table 2). The following results are all based on differences in log ratios of used habitat versus available habitat. During gestation ($n = 23$ pairs), contact rates were higher in forest than in any other cover. Road cover had lower contact rates than lawn and grassland (Fig. 1). During the fawning season ($n = 13$ pairs), contact rates were higher in agricultural fields and grassland than in road and lawn cover and also higher in agricultural fields than in forest (Fig. 1). Contact rates during the rut ($n = 23$ pairs) were higher in forest than grassland, water, agricultural fields, and lawn (Fig. 1).

Average number of contacts per deer pair were 19.67 (SE = 5.30), 8.86 (SE = 3.32), 6.17 (SE = 2.15), and 16.07 (SE = 6.98) for the gestation, fawning, prerut, and rut seasons, respectively. The effect of diel period on contact rates varied with season ($F_{9,838} = 4.90$, $P < 0.001$), with contact rates high at night and low around dawn during fawning and high at dusk and low at dawn during prerut, rut, and gestation (Fig. 2A). In general, there was a >2-fold difference in contact rates between rut and fawning season with rut having the highest contact rates (Fig. 2A). Contact rates also differed among lunar phases ($F_{3,838} = 9.14$, $P < 0.001$), being approximately 30% higher during full moon than in other seasons (Fig. 2B).

DISCUSSION

Because we used JUDs to assess available land-cover types, differences we found in contact rate among land-cover types are not simply due to differences in the amount of time deer spend in such land-cover. Instead, our findings reflect differences in behavior of deer while they occupy different land-cover types. Our results indicate that contact is more likely in habitats where deer feed or take cover, corresponding to what is known about seasonal activity patterns and habitat selection of deer. Deer tend to aggregate in areas with high food availability (Miller et al. 2003, Gompper and Wright 2005, Wright and Gompper 2005) such as growing agricultural crops (Nixon et al. 1991, Vercauteren and Hygnstrom 1998). High contact probabilities in agricultural fields during the fawning season could be explained by the crops planted in our study area (corn and soybeans) mainly growing during late spring and summer. The high contact probabilities in forest during the rut and gestation seasons (autumn–winter) could also reflect use of forest habitat as concealment and thermal cover.

Contact rates between females were elevated during the rut, a time of high activity by deer of both sexes, particularly

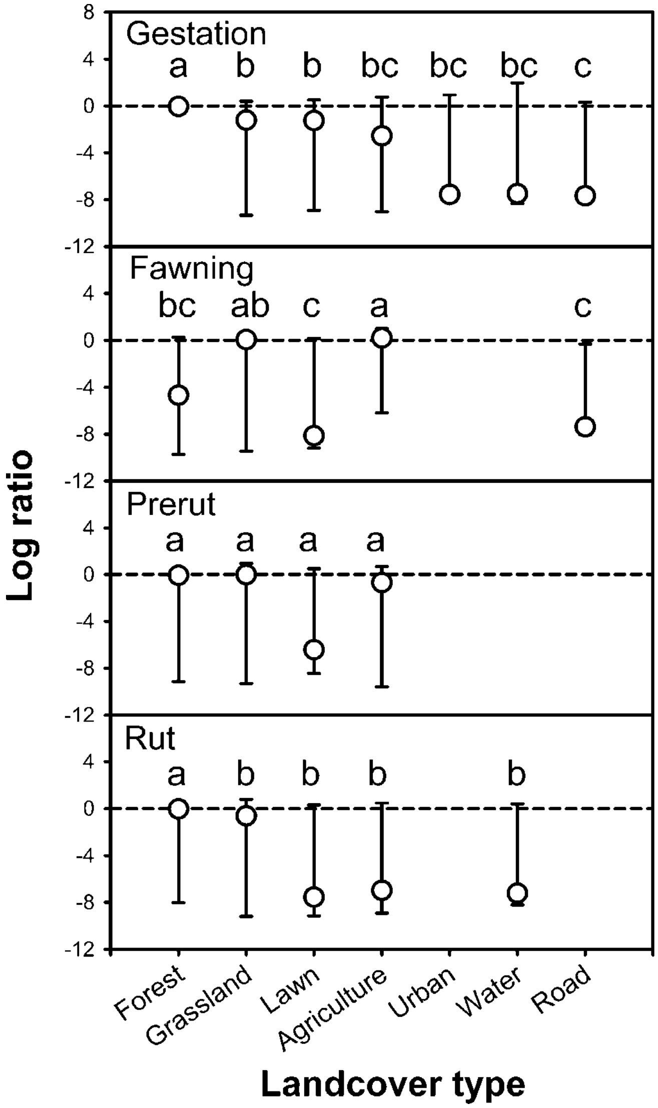

Figure 1. Log ratios, log(contact landcover/available landcover), for gestation, fawning, prerut, and rut seasons for white-tailed deer in southern Illinois, USA, 2002–2006. Values are medians and their respective 10th and 90th percentiles. A positive log ratio for a given land-cover type indicates greater contact rates than expected on the basis of availability. For each season, land-cover types sharing a letter did not have statistically different ($\alpha = 0.05$) log ratios based on Tukey's multiple range test.

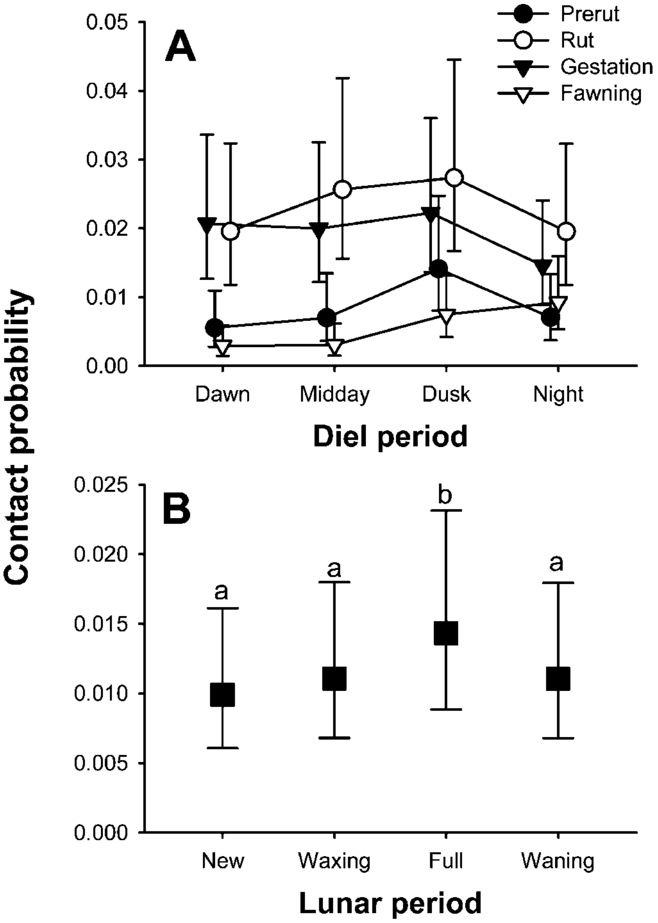

Figure 2. Contact probabilities for (A) seasons and diel periods and (B) lunar periods for white-tailed deer in southern Illinois, USA, 2002–2006. In (B), periods sharing a letter did not have statistically different ($\alpha = 0.05$) contact rates based on Tukey's multiple range test.

during midday, perhaps because females are more active during the day in autumn (Beier and McCullough 1990). As expected, contact probabilities were high during gestation, when deer tend to form larger groups (Hawkins and Klimstra 1970, Nixon et al. 1991) and low during fawning season when female deer isolate themselves (Nixon 1992, Bertrand et al. 1996). Decreased contact probabilities during midday in the fawning season may reflect deer being able to meet their nutritional needs in a shorter time on summer forage, and therefore avoiding activity in midday heat (Beier and McCullough 1990). Elevated contact rates during full moon could reflect increased nocturnal activity, but the observed lunar effect was generally slight.

Our novel application of compositional analysis to test for habitat-specific contact rates presents both advantages and challenges. Despite some complex mathematics for calculating UDs and JUDs, our approach can easily be used whenever concurrent animal locations and land-cover data are available. Designating as used the land-cover types around contact locations for a pair of deer is straightforward, but the designation of available land-cover is challenging. The JUD provides a pre-existing metric of habitat-specific joint use, and using JUD to define available land-cover types allows researchers to disentangle behaviors specifically related to contact (i.e., approach vs. avoidance upon detection) from individual habitat utilization and space use in the absence of animals from other social groups. Some drawbacks of applying compositional analysis to study contact patterns are 0% use-values and small availability values for some land-cover types, both of which present problems associated with log transformation. We minimized these problems by excluding rarely used land-cover types and determining the replacement value for zeroes by the smallest value for used land-cover.

Instead of JUDs, we could have defined available habitat on the basis of the combined utilization distribution of each pair (summing the UDs to indicate probability of either animal using the area but not necessarily both), but doing so would prevent us from interpreting the results in the context of contact rates. An even simpler approach would be to delineate a discrete area of joint use for each pair of animals, which would avoid excessively small availability values. However, discrete home-range overlap provides no measure of space use within the overlap zone and, thus, cannot delineate if contact occurs in a specific habitat because of specific deer behavior or because of higher levels of space use by both animals.

In analyzing temporal patterns of contact rates, we used mixed-model analysis to account for nonindependence of the set of concurrent locations from each pair of animals. A simpler approach would have been to calculate the contact rate in each season as a proportion (one data point per pair per season, perhaps arcsine-transformed) and analyze with a standard repeated-measures approach. However, arcsine transformation does not account for variance in proportions associated with the number of trials (i.e., concurrent locations), which are likely to differ among pairs and seasons. Besides accounting for differing numbers of trials, the mixed-model approach can also account for missing data because all pairs may not be monitored in all temporal periods.

We only analyzed collared female deer due to neck swelling in males during the rut. Monitoring males would offer insights into intersexual contacts and potential for sexual transmission of pathogens. Sexual contact may be a transmission route of CWD, because CWD prevalence is elevated in mature males (Farnsworth et al. 2005). The use of expandable collars to monitor intra- and intersexual contacts involving male deer should be considered for further studies of disease transmission in deer.

Our identification of contacts is limited by the accuracy of the GPS collars we used. Collar accuracy could affect our contact estimates and our proximity criterion of 25 m could cause an overestimation of direct contact rate. However, Schauber et al. (2007) found that location errors caused observed distances between GPS collars to generally exceed the true distance, indicating that our criterion of 25 m may actually underestimate the true contact rate. Also, the likelihood of effective contact (i.e., contact sufficient for disease transmission) given that 2 deer in different groups come within 25 m of each other is unknown. However, we assume that probability of effective contact is a positive function of the probability of one deer coming within 25 m of another deer.

The use of bait sites for deer capture could impact local contact rates, providing concentrated food resources during the capture season. Kilpatrick and Stober (2002) noticed that deer shifted their core areas to encompass a bait site within their home ranges. Most of our bait sites were located in grassland cover, which could have caused elevated contact frequencies in this land-cover type. We used bait from October to March, which covers prerut to gestation. In the compositional analysis we did find grassland to have a high ranking for prerut, rut, and gestation, but we also observed the same pattern for the fawning season when no bait sites were present. We know of one private landowner in our study site who baited deer on his property year-round, but none of our contacts were situated near that bait site. Therefore, we did not find clear evidence that bait sites substantially affected land-cover–specific contact rates, but nevertheless the potential effect of bait sites on contact rates should not be discounted.

MANAGEMENT IMPLICATIONS

Our research provides wildlife managers with information about effects of landscape composition, season, and diel period on contact rates in deer. Knowledge of how such factors affect contact rates could help wildlife managers in projecting the effects of habitat alteration on disease transmission, as well as identifying variables that need to be investigated in future field research, such as relative frequency of contact during feeding, bedding, and traveling. Furthermore, our methods can aid in targeting areas for population management to potentially reduce contacts and disease spread. Our finding of elevated female–female contact rates during rut indicates that management practices affecting breeding behavior (e.g., immunocontraception) can affect both intra- and intersexual contact.

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