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RH: Contact Rates among White-Tailed Deer • *Kjær* et al.

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

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ABSTRACT: White-tailed deer are important game mammals and potential reservoirs of diseases of domestic livestock, so diseases in 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. Our objective was to test whether pairwise direct contact rates among female white-tailed deer in different social groups differed among landcover types, seasons, lunar phases, and times of day. Using global positioning system collars, we obtained locations from 27 female deer for periods of 0.5-17 months during 2002-06. We designated any simultaneous pair of locations for 2 deer <25 m apart as a contact. For each season, we used compositional analysis to compare landcover types where

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2 deer had contact to available landcover weighted by their joint utilization distribution. 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 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 during the rut were generally greater in forest than expected. 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 does in different social groups occurs mainly during feeding. These results highlight the potential impact of food distribution and habitat on contact rates among deer, and provide information necessary to develop spatially realistic models of disease transmission in deer.

KEY WORDS: compositional analysis, contact rate, disease transmission, Global Positioning System, habitat, lunar phase, *Odocoileus virginianus*, southern Illinois, space use.

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 movement of animals by humans over great distances have 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 the 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 within close proximity in time and space, or indirect contact, where only spatial and not temporal 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, Miller et al. 2006).

Contact rates among free-ranging animals can be affected by social grouping, concentrated resources (Palmer et al. 2004), 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 non-members (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 (Hawkins and Klimstra 1970, Nixon et al. 1994, Comer et al. 2005) may increase intergroup contact rates and, potentially, disease transmission. Hawkins and Klimstra (1970) reported that separate social groups of white-tailed deer in southern Illinois 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 Yellowstone National Park 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 might affect deer behavior and movement across the landscape, and therefore affect 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. Abundant food in developed areas could have caused deer to be more sedentary and therefore have smaller home ranges. Another explanation was that urban areas were refugia from hunting and natural predators so deer there survived longer to shed the infectious agent. Finally, fragmentation of suitable habitat in urban areas may have concentrated the deer population and thereby accelerated transmission.

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 not concretely clear. 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 while 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 have found no other 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. In this study, we used GPS collars to estimate direct contacts between pairs of deer. Our objectives were to test whether certain landcover types serve as foci for intergroup contacts between deer, and determine if seasonal and daily variations in behavior affected contact probabilities.

STUDY AREA

We conducted our study in an exurban setting ca. 4 km southeast of Carbondale, Illinois, USA (37° 42´14´´N, 89° 9´2´´E). The climate is 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 relatively 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 only minor components of urban land use and old fields. The study area is 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-cc barbed darts (Pneu-Dart, Inc., Williamsport, PA) containing 2:1 mix of Telazol 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 ca. 20 m away from the bait site, and each dart contained a radio transmitter 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, Overland Park, KS). We blindfolded all deer during handling and visually observed them after handling until they were able to stand on their own. Deer capture and handling methods were approved by the Southern Illinois University Carbondale Institutional Animal Care and Use Committee (protocol #03-003). We specifically focused on females >1 year old. Although we captured and collared some fawns and males, we programmed their collars to drop off (see below) after only a few months to avoid constriction due to growth in fawns and neck swelling of bucks during the rut. Males were not included in the analyses we report here.

GPS Collar Data

We fitted 27 female deer with GPS collars (Model TGW-3500, weight 700g; Telonics, Mesa, AZ), that 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 their locations every hour in November and December to account for greater deer activity during the rut. We programmed all collars to determine their locations within 3 minutes of one another, and 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: gestation (1 Jan - 14 May), fawning (15 May - 31 Aug), prerut (1 Sep - 31 Oct), and rut (1 Nov - 31 Dec).

Contact Locations and Joint Space Use

Our sampling unit for all 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). To better identify the landcover "available" for a pair of deer, we calculated the joint utilization distribution (JUD) of each deer pair and season. 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). 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 (ESRI, Redlands, CA). We then calculated the JUD of a deer pair as the product of the 2 utilization distributions at each point in a grid with 40-m spacing overlaying the study area.

Landcover Delineation and Analysis

We used ArcView 3.2 to create a digital map of the landcover types (Table 1) in a 10 ×10-km area encompassing all known locations of the GPS-collared deer. We used 1998 digital orthophoto quarter quadrangles (Illinois Geospatial Data Clearing House (IGDCH) 1997) and ground-truthing to identify and delineate landcover types (Storm et al. 2007).

We used compositional analysis (Aebischer and Robertson 1992, 1993) to test for nonrandom distribution of direct contacts between a deer pair among landcover types. We conducted compositional analysis separately by season. We would expect the most contacts in areas frequently used by both deer in a pair, so such areas should be considered as having high "availability" for contacts to occur. Therefore, in the compositional analysis, we defined "used" landcover for a deer pair as the landcover near contact locations and "available" landcover as composition of the study area weighted by the JUD of the deer pair. With this approach, differing used and available landcover proportions indicates differences in the probability of 2 deer coming in contact (i.e., contact rate) given that both deer use the landcover type. We characterized the landcover associated with each contact by calculating the proportion of each cover type within a circular buffer of 12.5 m radius centered on the contact location; this buffer was chosen to account for errors in GPS accuracy. We averaged these proportions over all contact locations for a given deer pair and season. We calculated available landcover proportions as the weighted average proportions of the landcover types on the study area. The landcover proportions in each 40×40-m grid cell were weighted by the average joint utilization value of the cell. Weighting by joint utilization values gave extremely small available proportions for some landcover types and deer pairs. The smallest available proportion associated with a nonzero use proportion was 10^{-9}, so we treated every landcover type with available proportion below 10^{-10} (1 order of magnitude smaller; Aebischer and Robertson 1993) as unavailable (zero availability). If a particular landcover type was unavailable to a deer pair, it was treated as a missing value. We also gave unused but available landcover types a used proportion value of 10^{-10}, because the number 0 cannot be log transformed. To avoid problems associated with replacing 0% use-values with small non-zero values (Bingham and Brennan 2004), our analysis for each season only included landcover types included in ≥20% of contact location buffers.

The resulting log-ratios were not normally distributed, so we used randomization to test the global null hypothesis of random distribution of contacts ($\alpha = 0.05$ throughout) and to test for pairwise differences in contact frequencies between 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.

Temporal Analysis of Contact Rates

We used mixed-model logistic regression (SAS PROC GLIMMIX) to test how contact rates varied among seasons (as described for Landcover Delineation and Analysis), lunar phases (quarters of the lunar cycle centered on the new, full, and quarter moons), and diel periods (morning: 0300-0900, midday: 0900-1500, evening: 1500-2100, night: 2100-0300 Central Standard Time). The binary response variable was whether a pair of concurrent locations constituted a contact, deer pair was treated as a random effect, and the 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. Tukey's multiple range test was used to separate means.

RESULTS

Landcover Analysis

Compared with joint space use, contacts did not occur randomly among landcover types during gestation, fawning, and rut seasons (all $P \leq 0.023$, Table 2), whereas we did not find that contacts in prerut differed from random use ($P = 0.1$, Table 2). During gestation ($n = 23$ pairs), contact rates were higher in forest than in any other cover type. Road cover had lower contact rates than lawn and grassland (Fig. 1a). During the fawning season ($n = 13$ pairs), contact rates were higher in agricultural fields and grassland than in lawn and road, and also higher in agricultural fields than in forest (Fig 1b). Contact rates during the rut ($n = 23$ pairs) were higher in forest than grassland, water, agricultural fields, and lawn (Fig. 1c).

Temporal Analysis

The effect of diel period on contact rates varied with season ($F_{9,838} = 4.90$, $P < 0.0001$), with contact rates relatively high at night and low around dawn during fawning and prerut and the opposite pattern during rut and gestation (Fig. 2a). In general, contact rates were consistently highest during the rut and lowest during fawning (Fig. 2a). Contact rates also differed among lunar phases ($F_{3,838} = 9.14$, $P < 0.0001$), being ca. 30% higher during full moon than in other seasons (Fig 2b).

DISCUSSION

Our findings reveal daily and seasonal variations in contact rates and contact habitat for female white-tailed deer. Because we used JUDs to assess available landcover types, differences we found in contact rate among habitats are not simply due to differences in the amount of time deer spend in such habitats. Instead, our findings reflect differences in behavior of deer while they occupy different landcover types. We interpret our results from the compositional analysis as evidence that contact is more likely in habitats where deer feed or take cover. Deer tend to aggregate in areas with high food availability (Palmer et al. 2004) and the landcover types providing food vary with season. Growing agricultural crops are important food for deer (Nixon et al. 1991, Vercauteren and Hygnstrom 1998) and the crops planted in our study area (corn and soybeans) mainly grow during fawning season (late spring-summer). Winter wheat, which would provide food during the gestation season, was not grown on the study area during this study. During gestation, deer feed mostly in forest, grassland and agricultural fields (Nixon et al. 1991), but we also found elevated contact rates in lawns on this exurban study area. People start tending their lawns in spring, and increased contacts could reflect the nutritious new growth provided by lawns or ornamental plants.

The high contact frequencies in forest during the rut and gestation seasons could also reflect the use of habitat as cover. Winter includes both rut and gestation periods in southern Illinois, and forest provides thermal cover for deer in cold weather. Aggregation of deer in areas of dense forest cover could thus elevate contact rates. Rohm et al. (2007: 852) found that fawns were typically hidden along grassland-forest edges in southern Illinois, which could explain high contact frequencies among does in grassland during the fawning season.

Contact rates between females were elevated during the rut, a time of high activity by deer of both sexes (Beier and McCullough 1990), which could be explained by bucks harassing females and forcing them to increase their movements into neighboring female home ranges or by females moving to seek mating opportunities (Relyea and Demarais 1994). Increased activity of female white-tailed deer during the rut was found in both penned deer (Ozoga and Verme 1975) and free-ranging deer (Ivey and Causey 1981). As expected, contact probabilities were high during the gestation season, when deer tend to form larger groups (Hawkins and Klimstra 1970, Nixon et al. 1991), and low during fawning season when does isolate themselves (Nixon 1992, Bertrand et al. 1996).

Deer are generally crepuscular (Beier and McCullough 1990), so we expected higher contact rates around dawn and dusk. However, the timing of contacts differed according to season, which could relate to deer activity levels. Crepuscular peaks in contact rates were evident during gestation and somewhat during prerut. During the rut, contact rates were high during midday and evening and were low during the night and early morning. This pattern is in partial agreement with the findings of Beier and McCullough (1990) that during fall, male white-tailed deer were more active during the night whereas females were more active during the day. During the fawning season, we found decreased contact probabilities during midday. Beier and McCullough (1990) found a similar pattern in activity, which they explained by deer being able to meet their nutritional needs in a shorter time on summer forage, therefore avoiding the midday heat.

Effects of moon phase on deer behavior are a topic of much debate, which is why we included this analysis in our study. Many hunters believe that deer hunting is more difficult during a full moon because deer feed at night (Kufeld et al. 1988). Our results could support this, assuming that higher contact rates reflect increased activity and feeding at night. However, our data did not show an evident lunar × diel interaction, which would have indicated that activity was higher at night during a full moon.

Caveats

In this study, we only collared does due to neck swelling in bucks during the rut. Monitoring bucks 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 bucks (Farnsworth et al. 2005). The use of expandable collars to monitor intra- and intersexual contacts involving bucks should be considered for further studies of disease transmission in deer.

Our identification of contacts is limited by the accuracy of the GPS collars used in this study. 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 (which could lead to 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 1 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, which could have caused elevated contact frequencies in this landcover 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. Therefore, we did not find clear evidence that bait sites substantially affected landcover-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 the effects of landscape composition, season, and diel period on contact rates in deer. Knowledge of how such factors affect contact rates could be useful for building and refining models of disease establishment and transmission for deer. Such models 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 the relative frequency of contact during feeding, bedding, and traveling.

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Table 1. Landcover types used in analyzing contact habitat for white-tailed deer in southern Illinois, 2002-06. Percentages can be obtained by dividing total areas by 100.

Landcover code	Total area (ha)	Description of cover type
agriculture	1405.6	Agricultural fields, mainly corn and soybeans
aqua[a]	7.5	Aquaculture center
fish[a]	16.0	Fish hatchery
forest	5565.2	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	1181.2	Lakes, ponds, and rivers

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

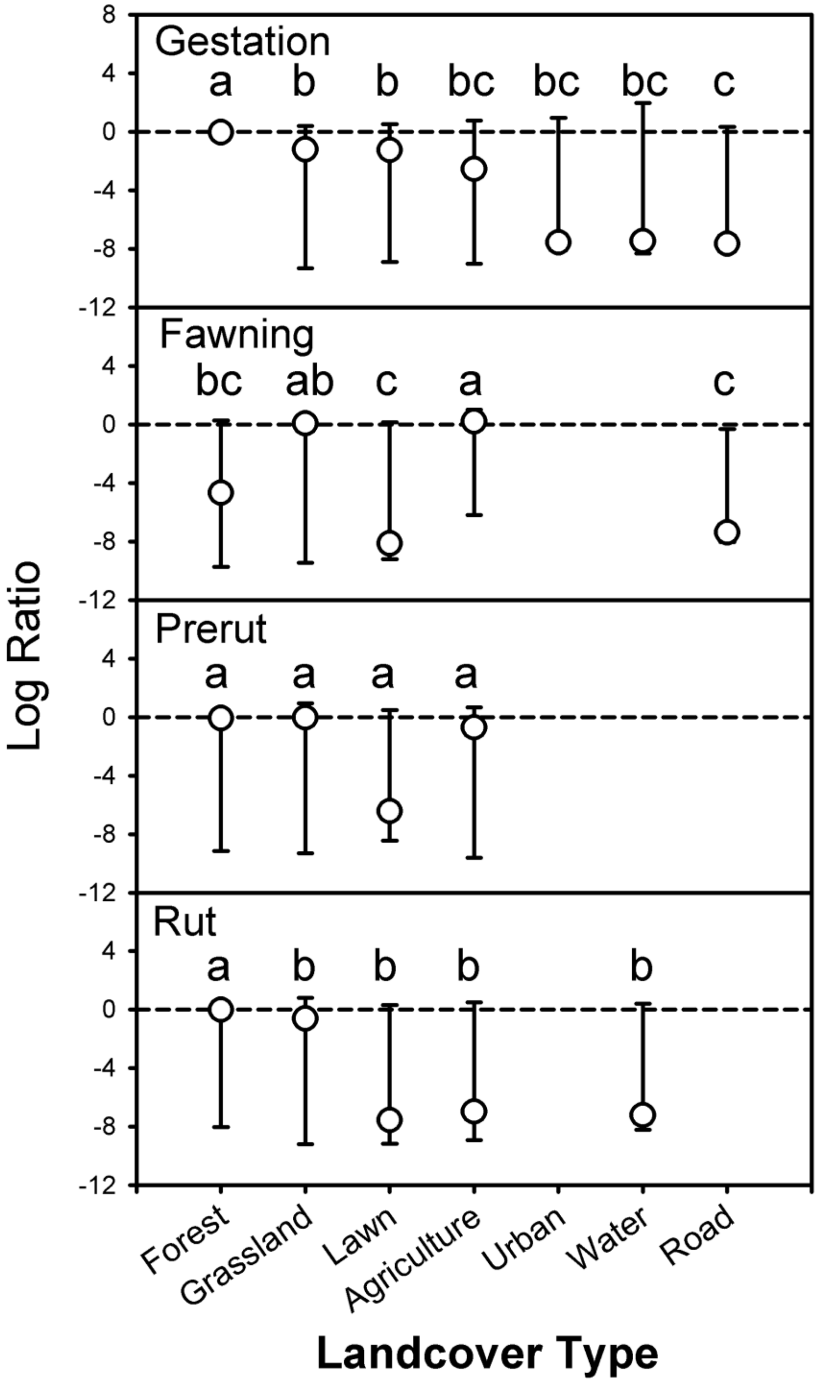
Table 2. Seasonal tests for random distribution of pairwise contact locations among landcover types for between-group pairs of female white-tailed deer in southern Illinois, 2002-06.

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

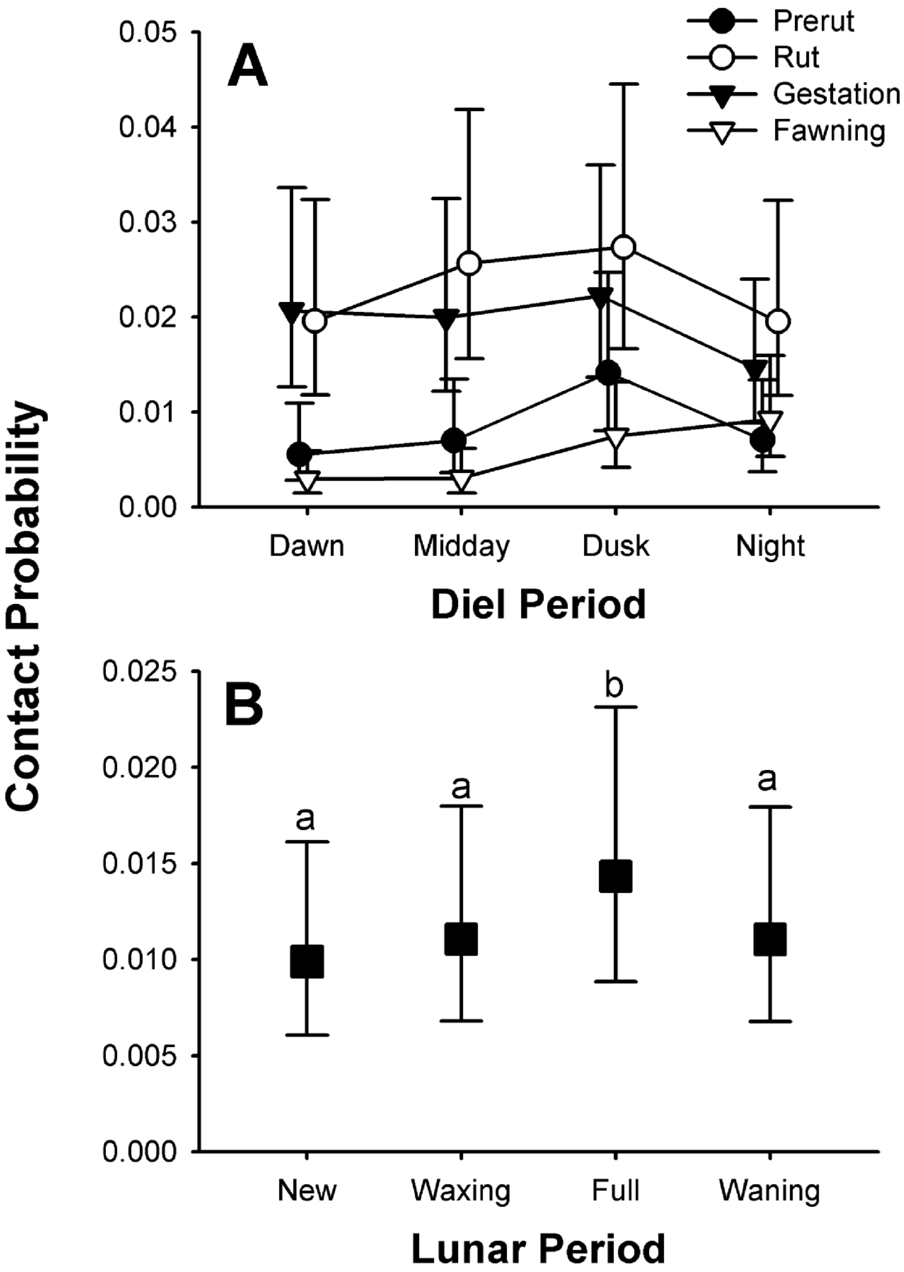
Figure Legends

Figure 1. Log ratios, log(contact landcover/available landcover), for gestation fawning, prerut and rut seasons. 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. In (b), periods sharing a letter did not have statistically different ($\alpha = 0.05$) contact rates based on Tukey's multiple range test.


Gestation
a
b
b
bc
bc
bc
c
Fawning
bc
ab
c
a
c
Prerut
a
a
a
a
Rut
a
b
b
b
b
8
4
0
-4
-8
-12
Log Ratio
Forest
Grassland
Lawn
Agriculture
Urban
Water
Road
Landcover Type

475
476


A
B
Prerut
Rut
Gestation
Fawning
Contact Probability
0.05
0.04
0.03
0.02
0.01
0.00
Dawn
Midday
Dusk
Night
Diel Period
0.025
0.020
0.015
0.010
0.005
0.000
a
a
b
a
New
Waxing
Full
Waning
Lunar Period

477