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Original article

Space use of sympatric deer in a riparian ecosystem in an area where chronic wasting disease is endemic

W. David Walter, David M. Baasch, Scott E. Hygnstrom, Bruce D. Trindle, Andrew J. Tyre, Joshua J. Millspaugh, Charles J. Frost, Justin R. Boner & Kurt C. VerCauteren

Knowledge of movements, range size and spatial overlap of sympatric deer is integral to understanding chronic wasting disease (CWD) in endemic areas and can assist resource managers in modeling the spread of the disease. We radio-collared 70 deer (30 mule deer *Odocoileus hemionus* and 40 white-tailed deer *O. virginianus*) in the North Platte River Valley in western Nebraska, USA, from 2004 to 2007 to document movements, size and spatial overlap of home range and resource selection of these sympatric species of deer. We compared home-range size and overlap and resource selection among male and female mule deer and white-tailed deer to examine relative use of space in order to understand the potential for indirect spread of CWD better. We identified forested, riparian habitats as high selection of use and these habitats could likely contribute to the potential spreading of CWD between sympatric deer that concentrate in these areas. We found that migration, size of home range of female mule deer, and similarities in resource selection could contribute to sustaining or spreading CWD in Nebraska. The role of female mule deer in the spread of CWD coupled with selection for riparian corridors by both species should be investigated further, because these factors may be a primary determinant of disease spread in the historical range of mule deer.

Key words: chronic wasting disease, home range, movements, mule deer, Odocoileus hemionus, O. virginianus, resource selection, space use, sympatry, white-tailed deer

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Chronic wasting disease (CWD) is a fatal, transmissible disease that affects both captive and free ranging cervids (Miller & Wild 2004, Miller & Conner 2005). The disease is endemic to southwestern Wyoming, north-central Colorado (Williams & Young 1980) and western Nebraska, USA. CWD has been observed in free-ranging mule deer *Odocoileus hemionus* and white-tailed deer *O. virginianus* with 133 cases reported in Nebraska since 2000 (Nebraska Game and Parks Commission 2008).

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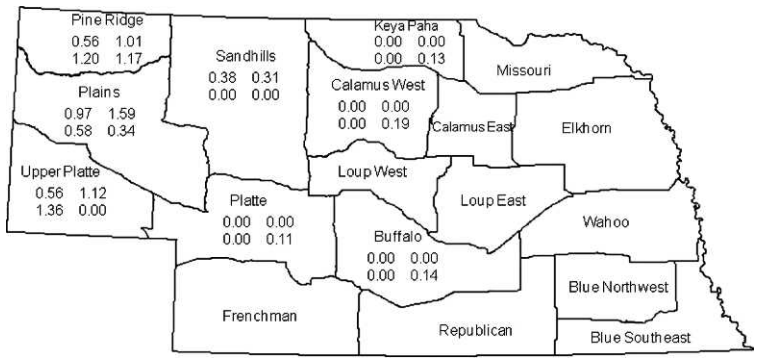


Figure 1. Names of deer management units (DMUs) and prevalence (%) of chronic wasting disease by species and sex from top left hand corner (clockwise): female mule deer, male mule deer, male white-tailed deer and female white-tailed deer in Nebraska, USA, 1997-2006. No prevalence indicated in DMUs show that chronic wasting disease had not been detected.

Distribution of CWD in Nebraska has been in the western deer management units (DMUs; Fig. 1). However, positive samples have recently been collected in central and eastern Nebraska. The highest prevalence of CWD for both species was in the Panhandle region of western Nebraska along the North Platte River (see Fig. 1; J.R. Boner, unpubl. data). The North Platte River in western Nebraska represents the largest river system in the Central Great Plains region and would be comparable to other riparian systems throughout the USA with similar surrounding landscape characteristics. In Nebraska, most effort has been placed on monitoring prevalence and extent of CWD, but ecology of sympatric species of deer in this region has not been examined. Understanding the ecology of sympatric species in areas endemic for CWD was critical for determining the potential spread of the disease.

In areas inhabited by mule deer and white-tailed deer, they typically occupy different habitats and segregate spatially across the landscape (Geist 1998, Lingle 2002). Mule deer in western Nebraska have historically used more rugged and open terrain associated with open range, whereas white-tailed deer which have more recently become established in the region, typically used the more gentle terrain near riparian habitat with forested cover (Severson 1981). The number of white-tailed deer harvested in western Nebraska increased from 11,578 to 57,121 deer from 1980 to 2007, which is evidence of their adaptability and success in this region (Hams & Trindle 2008). Previous studies have measured the topography used by the two species and concluded that when occurring sympatrically, large-scale topographical segregation prevents most competition for food (Martinka 1968, Hudson et al. 1976, Krausman 1978). Both species tolerated a wide range of habitats, however, they also occupied the same ecological niches (Wiggers & Beasom 1986, Whittaker & Lindzey 2004, Brunjes et al. 2006). In areas where both species were sympatric, they used similar foods with some evidence of competition (Anthony & Smith 1977, Krausman 1978). Anthony & Smith (1977) reported an apparent passive-dominance of mule deer over white-tailed deer on feeding grounds.

Data on interactions of deer were difficult to obtain and evidence of indirect transmission (i.e. spread of disease from environment to animal) of CWD among deer is limited. Therefore, several researchers have assessed proxies for indirect transmission of CWD using the overlap of utilization distributions between two radio-collared deer (Schauber et al. 2007, Kjaer et al. 2008). Deer that use overlapping areas have an increased chance of contact, and thus spreading disease, compared to deer using non-overlapping areas. Schauber et al. (2007) suggested that the volume of intersection scores (VIs) could be used to assess indirect spread of disease among deer that were members of the same social group. Resource selection functions (RSFs) have been used to understand species overlap or response to landscape conversion (Millspaugh et al. 2006, Sawyer et al. 2006) with overlap of resource use indicating a potential for indirect transmission of CWD (Schauber et al. 2007). Indirect transmission can occur from deer ingesting the infectious prions for CWD (PrP^{SC}) on contaminated soil, vegetation or carcasses (Miller et al. 2004). However, the fact that no information is available on resource selection and overlap of space use of sympatric mule deer and white-tailed deer in areas with CWD, was the motivation for our research.

Both species of deer in western Nebraska likely used riparian areas of wooded cover more than open areas (Mohler et al. 1951) unlike sympatric confined

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deer in Colorado that exhibited segregation in habitat use (Whittaker & Lindzey 2004). Although CWD prevalence is lower in western Nebraska, CWD is spreading east in habitat conditions (e.g. riparian areas) that are comparable to areas of high CWD prevalence such as Colorado and Wyoming (Farnsworth et al. 2005).

Our objectives were to: 1) compare the size of annual and seasonal home ranges and movements between free-ranging mule deer and white-tailed deer that is not available in the literature for sympatric deer in the CWD endemic area, 2) compare spatial overlap of utilization distributions between sexes and species that are assumed to represent directionality of indirect transmission of CWD (i.e. which species of deer are the most likely environmental source of PrP^{SC}), and 3) develop and assess season- and sex-specific models of RSFs for mule deer and white-tailed deer to document season- and sex-specific avoidance or attraction to resources (i.e. habitats most responsible for environmental source of PrP^{SC}). We assumed that our results for movements, spatial overlap of home ranges and RSFs in sympatric deer could be a proxy for likelihood of indirect transmission (i.e. environmental sources of infection) for CWD in western Nebraska as actual data on indirect transmission is impossible to collect with current diagnostic methods for PrP^{SC}. Our study can assist resource managers in examining movements, space use and habitats to better understand spatial pathways for modeling disease epidemiology.

Methods

Study area

The North Platte River was central to our study area and served as the southern boundary of the Plains DMU. Our study area included the North Platte River Valley from Bayard to Oshkosh, Nebraska and included the Box Butte, Cheyenne, Garden, Morrill and Sheridan counties. Our focal area was in Morrill County in the Plains DMU that had the highest prevalence of CWD in mule deer in Nebraska. Morrill County has a total area of 3,703 km^2 and an elevation of 1,094-1,325 m a.s.l. The climate is semi-arid with occasional extreme variations in temperature and precipitation. Mean, annual summer and winter temperatures were 32.7°C and -9°C, respectively (High Plains Regional Climate Center 2006). Mean, annual precipitation was 415 mm, the majority of which occurred in late spring (High Plains Regional Climate Center 2006). Morrill and its surrounding counties were sparsely populated with human density ranging from 1-4 people/km^2 (U.S. Census Bureau 2000). Major towns in Morrill County included Bridgeport (N = 1,594 inhabitants) and Bayard (N = 1,247 inhabitants; U.S. Census Bureau 2000). The two primary uses of land were farming and livestock ranching. Major irrigated crops included corn *Zea mays*, wheat *Triticum* spp., alfalfa *Medicago sativa* and beans *Phaseolus* spp. Percentage of land cover for Morrill County was: 72% open range, 25% crops, 1% forest, 1% other and < 1% water.

Morrill County was composed of three distinct regions. A mixed hardwood forest was adjacent to the North Platte River and was located centrally throughout the county. Dominant vegetation included cottonwood *Populus deltoides*, red cedar *Juniperus virginiana*, Russian olive *Elaeagnus angustifolia* and American elm *Ulmus americana*. Most irrigated crops were grown within 3 km of the North Platte River. The northern portions of Morrill County were located in the Sandhills, grass-stabilized aeolian sand dunes that contained a variety of native plant communities ranging from upland prairie to wetlands. Predominant vegetation included little bluestem *Schizachyrium scoparium*, blue grama *Bouteloua gracilis* and prairie sandreed *Calamovilfa longifolia*. The southern portion of Morrill County was dominated by short-grass prairie that included blue grama, side-oats grama *B. curtipendula* and buffalograss *B. dactyloides*.

Populations of white-tailed deer and mule deer were of similar size in Morrill County during our study (size ≈ 1,500 deer/species, densities ≈ 0.34 deer/km^2; C.J. Frost, unpubl. data). Fecundity in white-tailed deer (0.95 fawn/female) was higher than mule deer (0.64 fawn/female) and the ratio between males and females was also higher for white-tailed deer than mule deer during our study at 0.4:1.0 and 0.3:1.0, respectively (C.J. Frost, unpubl. data). Sex-specific survival rates for radio-collared deer were similar for both species but females had greater survival rates (0.68) than males (0.38; C.J. Frost, unpubl. data). Mule deer had a higher overall prevalence of CWD (0.61%) than white-tailed deer (0.21%; odds ratio = 2.81, 1.87-4.29, $P < 0.001$) and prevalence was highest in male mule deer (0.63%) and lowest in male white-tailed deer (0.18%; J.R. Boner, unpubl. data).

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Capture and radio-telemetry

We captured deer using netted cage traps (VerCauteren et al. 1999), chemical immobilization with xylazine hydrochloride and Telazol®, and helicopter net-guns (Hawkins & Powers, Greybull, Wyoming, USA). We equipped deer with individualized ear tags and radio-collars with expandable radio-collars for males (150-152 MHz; Advanced Telemetry Systems Inc., Isanti, Minnesota, USA). We classified the age of each deer as fawn (< 12 months old), yearling (≥ 12 to < 24 months old) or adult (≥ 24 months old). However, we did not include age as a variable in our analyses because of limitations in sample size. All capture and handling procedures were approved by the University of Nebraska's Institutional Animal Care and Use Committee (IACUC # 06-07-030C).

We located radio-collared deer using an integrated vehicle-mounted VHF telemetry system and maximum likelihood estimators from Location Of A Signal software (Ecological Software Solutions, Sacramento, California, USA; Gilsdorf et al. 2008). We used aerial telemetry on four occasions to locate deer that dispersed or migrated. We collected 3-6 locations per deer each week at random times throughout the day and night to ensure data included activity influenced by changing diel patterns. Telemetry locations were recorded ≥ 4 hours apart to achieve independence (Swihart & Slade 1985). For each location, we collected 2-4 azimuths consecutively in < 10 min (White & Garrott 1990). Locations that had error ellipses > 10 ha were rejected and bearings were re-collected and solved (Gilsdorf et al. 2008). Random observations of marked deer during field work were digitized on-site using Geographic Information System (GIS) software ArcView 3.2 (ArcView; Environmental System Research Institute (ESRI), Redlands, California, USA) and a 1:24,000 scale United States Geological Survey digital aerial photo.

Movement

We categorized deer as dispersers, migrators or residents based on observed movement patterns (Table 1). We only assigned a movement category to individuals that were tracked during consecutive seasons. We defined dispersal as permanent movement > 4 km away from an established home range to a new area without return or overlap of post-dispersal home range (Marchinton & Hirth 1984). We defined residents as deer that remained in their annual home ranges and had overlapping seasonal ranges throughout the study period. We defined migration as a seasonal movement between established home ranges without overlap (Brown 1992, Nicholson et al. 1997). We defined fall migration as a seasonal movement from summer to winter range and spring migration as movement from winter to summer range. We considered deer obligate migrators if they migrated between established winter and summer ranges during every migration period (Sabine et al. 2002, Brinkman et al. 2005). We modified the definition of a facultative migrator (Nelson 1995, Brinkman et al. 2005) to include deer that failed to migrate to a seasonal range during every migration period, migrated briefly to seasonal range (< 1 month), or made shifts in their home range each season that resulted in non-overlapping areas of use during each season. Dates of dispersal and migration were estimated by using the midpoint of the dates for the last location in the original use area and the first location after dispersal or migration occurred (Sabine et al. 2002). We used the Animal Movement Extension (Hooge & Eichenlaub 2000) in ArcView 3.2 to digitize and measure the route of connecting locations between summer and winter ranges for deer that had dispersed or migrated (Sabine et al. 2002, Sawyer et al. 2005).

Table 1. Movement pattern categories (i.e. resident, disperser and migrator) and sample size by sex for mule deer and white-tailed deer in western Nebraska, USA, 2004-2007. Obligate migrator refers to deer that migrated between established winter and summer ranges during every migration period. Facultative migrator refers to deer that failed to migrate to a seasonal range during every migration period, migrated briefly to seasonal range (< 1 month), or made shifts in their home range each season that resulted in non-overlapping seasonal-use areas. Numbers in parentheses indicate number of deer radio-collared during our study.

			Migratory	
Species	Resident	Disperser	Obligate	Facultative
Mule deer				
Female (19)	12	0	4	3
Male (11)	6	5	0	0
White-tailed deer				
Female (18)	13	1	2	2
Male (22)	10	9	3	0

Home range

Prior to estimating the size of home range, we determined the minimum number of locations needed to reach an asymptote using an area-observation curve (Odum & Kuenzler 1955, Gese et al. 1990), and we excluded mule and white-tailed

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deer with $\leq$ 52 and 42 locations, respectively, from our season- and sex-specific estimates of size of home range. We used the Animal Movement Extension for ArcView 3.2 to construct estimates of overall and seasonal home ranges. We estimated home ranges using a fixed kernel estimator (Worton 1995) with a 95% utilization distribution and smoothing determined by least-squares cross-validation (Seaman et al. 1999). We pooled data across years that were collected throughout the study to estimate a multi-year home range for each deer (overall home range), because we were interested in the size of home range for resident deer for the duration they were tracked. We pooled seasonal data across year, and classified seasonal home ranges as summer (1 May - 31 October) and winter (1 November - 30 April) because the two seasons encompassed the majority of migrations which we documented for mule deer, indicating seasonal changes in forage availability in western Nebraska. We pooled data across years (overall home range) and across years for each season (i.e. summer and winter), because we were interested in comparing home ranges of sympatric deer and not annual or seasonal variation in home range between species. For comparisons to previous research, we determined differences in size of home ranges for overall home range between species and sex with a 2-factor analysis of variance (ANOVA; Zar 1996). We determined differences in size of home ranges among season, species and sex with a 3-factor ANOVA (Zar 1996). We examined all 2- and 3-way interactions and used least-squares means for *post-hoc* comparison of size of home range. We set statistical significance at $P \leq 0.05$ and presented estimates of data as mean $\pm$ SE.

Resource selection

To assess resource selection, we used discrete-choice models because we can define resource availability separately for each location of deer in a hierarchical structure all included in a single analytical framework (McCracken et al. 1998, Cooper & Millspaugh 2001). To identify resources available to deer, we obtained a land cover map of Morrill County that consisted of 25 land-cover classes created using multi-date Landsat 5 satellite imagery, scaled at 1:100,000 with a ground resolution of 28.5 m (CALMIT 2005). To be consistent with the pixel-size of other geospatial data layers, we used digital image processing to generate a 30×30 m raster with 25 classes of land cover. We combined classes of land cover with low frequency of occurrence with a class deemed to provide a similar utility for deer, which resulted in six classes: alfalfa, corn, beans (soybeans *Glycine max* and edible beans), other agricultural land (potato *Solanum tuberosum*, oat *Avena sativa*, sorghum *sorghum bicolor*, sugar beet *Beta vulgaris*, sunflower *Helianthus annuus* and wheat), forested cover and open range. Due to presumed similarity of use by deer, we combined irrigated and non-irrigated croplands in the same category. We reclassified all land cover identified as barren ground, open water, road, urban or wetland to the nearest adjacent land cover, because they covered such a small proportion of the total area ($<$ 3% combined).

For used locations, we filtered data to include only one location per deer per day to remove temporal correlation and only included locations within Morrill County. As with other analyses, we divided the data to measure seasonal differences in resource selection (i.e. summer and winter). We did not generate RSFs based on behavioural seasons for deer (e.g. breeding and parturition) because RSFs by behavioural season were similar for species and sex (Baasch 2008).

For random locations, we considered Morrill County, except urban areas, a suitable habitat for both species of deer. To determine resources available to deer, we calculated the average daily displacement distances between consecutive locations for each deer. We used these distances to determine the outer buffer when generating random locations for resource selection analyses. We generated five random locations per use location and stratified random locations with their respective use location (McFadden 1978). We did not generate random locations within 180 m of the use location to ensure these locations did not fall within the maximum acceptable error polygon (10 ha) associated with each use location.

We classified used and random locations by land cover using the Intersect Point Tool located in Hawth's Analysis Tools within the GIS software ArcGIS 9.2 (ArcMap; ESRI, Redlands, California). We used the Nearest Feature extension in ArcView to calculate Euclidian distance of each used and random location to nearest forested area, any agricultural crop (i.e. alfalfa, bean, corn and other agricultural land) and to each of the respective agricultural crops from the land cover layer. We assigned a value of 0.0 m to all locations that occurred within their respective classes of land cover.

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We selected habitat variables to be included in discrete-choice models on information specific to mule deer and white-tailed deer and on habitat components found in western Nebraska. We tested covariates in order to include them in the set of discrete-choice models for correlation among variables (pair-wise $|r| < 0.60$; McDonald et al. 2006) and determined that all variables were independent ($|r| \leq 0.13$). We constructed an *a priori* set of 14 models with variables: land cover (alfalfa, bean, corn, other agricultural crop, open range and forested area; reference category = corn), distance to forested area, and either distance to any agricultural crop or distance to alfalfa, bean, corn and other agricultural crop (Table 2). We also included an interaction between distance to forested area and distance to any agricultural crop to discern differences in selection of resources by mule deer and white-tailed deer within areas that contained both high quality forage (crop) and cover (forest), areas with high quality forage or cover and areas with neither high quality forage nor cover for deer (open range). We included land cover as a categorical variable in all models to evaluate seasonal differences in selection of classes of land cover by male and female mule deer and white-tailed deer. We normalized data for all continuous variables (mean = 0.0, SE = 1.0) and pooled data across years prior to dividing them into the eight season-, species- and sex-specific subsets to allow for model convergence and in order to be able to make direct comparisons of the level of effect for each variable across seasons and classes of deer.

Table 2. *A priori* models used in discrete-choice analyses of resource selection by male and female mule deer and white-tailed deer in Morrill County, Nebraska, USA, 2004-2007. Land cover was a categorical variable with six levels: alfalfa field (irrigated and non-irrigated), bean field (irrigated and non-irrigated soybean or edible bean), corn field (irrigated and non-irrigated), other agricultural field (irrigated and non-irrigated potato, milo, oat, sorghum, sugar beet, summer fallow, sunflower and wheat), forested area and open range. Distance measures represent the shortest distance (m) from each use location or random location to specific features across the landscape and were normalized prior to analysis (mean = 0, SE = 1). Distance measures include: distance to any crop field, distance to alfalfa field, distance to bean field, distance to corn field, distance to other agricultural field, distance to forested area and an interaction term (crop*forested area (distance to any crop field*distance to forested area)).

Model #	Habitat variables in model
1	land cover + distance to forested area
2	land cover
3	land cover + distance to any crop field + distance to forested area + crop*forested area
4	land cover + distance to any crop field + distance to forested area
5	land cover + distance to any crop field
6	land cover + distance to forested area + distance to corn field
7	land cover + distance to corn field
8	land cover + distance to forested area + distance to alfalfa field
9	land cover + distance to alfalfa field
10	land cover + distance to forested area + distance to bean field
11	land cover + distance to bean field
12	land cover + distance to forested area + distance to other agricultural field
13	land cover + distance to other agricultural field
14	null

For discrete-choice models, we used Cox proportional hazards regression to develop the eight season-, species- and sex-specific discrete-choice models in survival package of Program R (R Foundation for Statistical Computing, Vienna, Austria; Cooper & Millspaugh 1999, McDonald et al. 2006). We used information-theoretic methods with Bayesian Information Criterion (BIC) to rank the 14 models (see Table 2; Gelfand & Dey 1994, Hoeting et al. 1999). We calculated BIC scores, BIC values and BIC weights to determine weight-of-evidence for each model in the set. We considered a model a candidate if it had a $\Delta BIC \leq 6.0$ and we recorded coefficients and standard errors for the most parsimonious candidate models (Richards 2008). We calculated selection ratios and confidence intervals for each class of the categorical variable (land cover) in the final models (Baasch 2008). An underlying assumption in the interpretation of selection ratios is that relative comparisons between ratios are made while holding other variables in the model constant. Selection ratios range from 0 to ∞ with values < 1 indicating avoidance and values > 1 indicating selection. Confidence intervals that contain 1 indicate that there is no difference in selection. To test goodness-of-fit of models, we generated resource selection probability functions (RSPFs) across our study area for final models. We used simple linear regression to compare observed use with predicted selection, and used the slope of regression models as a measure of predictive ability of discrete-choice models (Howlin et al. 2004). We provided plots of regression lines to demonstrate the goodness-of-fit of data to predictions and to illustrate effects of leverage that outer

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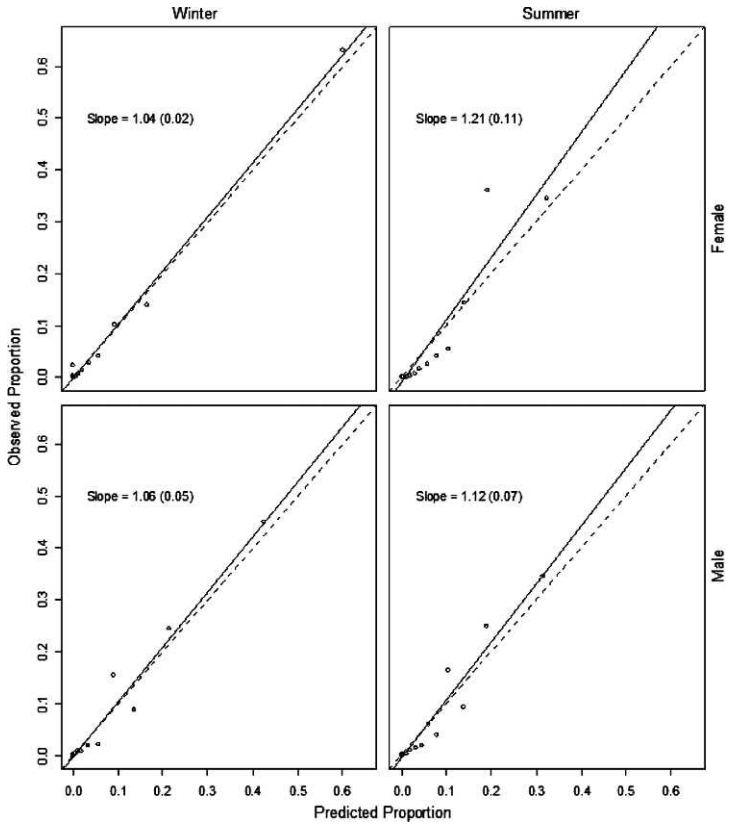


Figure 2. Goodness-of-fit regressions predicting observed selection with predictive resource selection function (RSF) models generated for female and male mule deer during summer (1 May - 31 October) and winter (1 November - 30 April) in western Nebraska, USA, 2004-2007. Plots include observed vs predicted proportions of resource selection (points), a regression of proportions (solid line), X = Y-line (dashed line) and slope of regression line with standard error in parenthesis. A slope of 1.0 indicates a 1:1 relationship between observed and predicted proportions of resource selection (i.e. good fit of RSF to locations of female or male mule deer in Morrill County, Nebraska, USA).

bins can have on fit of regression lines (Figs. 2 and 3; Howlin et al. 2004).

Spatial overlap

We compared utilization distributions of home range and from RSPFs to determine spatial overlap between species and sex. We used VIs to assess spatial overlap with values ranging from 0.0 (no spatial overlap) to 1.0 (complete overlap of utilization distributions; Millspaugh et al. 2004). We determined VIs in ArcMacro Language using an iterative code for VIs. We only used VIs > 0.1 between deer to assess spatial overlap of home ranges and RSFs to avoid incidental overlap being included in our analyses. We tested all home-range VIs for normality and performed log transformation to correct skewed data prior to all statistical analyses.

We assessed whether basic factors (e.g. season, species and sex) were correlated with VI of home range for both species of deer using linear regression. We used BIC to select the most parsimonious model among a suite of models. We included a species-sex variable to represent spatial overlap between species-sex groups (N = 9) instead of an interaction term to prevent over-parameterization of the model (Burnham & Anderson 2002). We assessed a global model that included season and species-sex as categorical variables and three additional models, including an intercept-only model.

Use of RSPFs allows for predictive space use based on the probability of a resource unit being used as a function of the values that the unit possesses for certain variables measured. We used RSPFs as a broad-scale assessment of units used to predict space use of deer throughout the study site with greater overlap indicating greater probability of indirect spread. We used the 'mvrnorm' function located in the MASS package of program R where μ = coefficients of the final models and σ = variance-covariance matrix for each model to generate 1,000 models for each season-, species- and sex-specific class of deer, which resulted in 28,000 RSPFs. We used the RSPFs to calculate 1,000 VIs for each of the 28 possible season-, species- and sex-specific combinations of deer. We reported the mean VIs and 0.025 and 0.975 quantiles (95% confidence limits) from the 1,000 bootstrap simulations.

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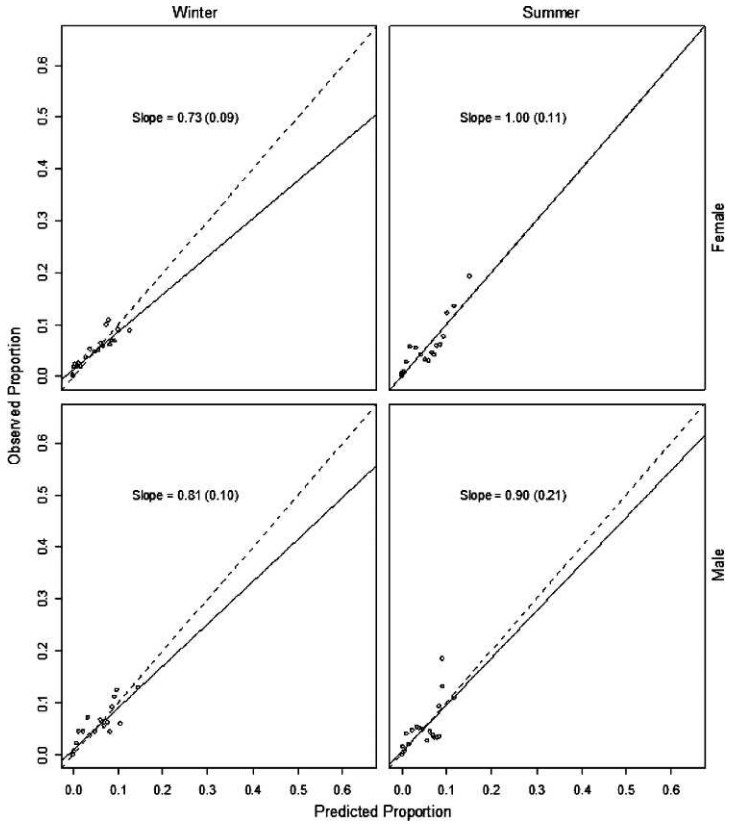


Figure 3. Goodness-of-fit regressions predicting observed selection with predictive resource selection function (RSF) models generated for female and male white-tailed deer during summer (1 May - 31 October) and winter (1 November - 30 April) in western Nebraska, USA, 2004-2007. Plots include observed vs predicted proportions of resource selection (points), a regression of proportions (solid line), X = Y-line (dashed line) and slope of regression line with standard error in parenthesis. A slope of 1.0 indicates a 1:1 relationship between observed and predicted proportions of resource selection.

Results

Capture and radio-telemetry

We captured and radio-collared 43 mule deer (22 males and 21 females) and 48 white-tailed deer (27 males and 21 females) between March 2004 and September 2006. We tracked 42 females for an average of 601 days (SE = 47.2; range: 49-928 days). We tracked 49 males with expandable radio-collars for an average of 272 days (SE = 20.4; range: 17-623 days). We tracked 67% and 20% of radio-collared females and males, respectively, for a period > 1 year. The primary causes for shorter tracking periods of males were dropped collars (38%) and hunter-induced mortalities (35%).

We generated 16,545 useable locations on 91 radio-collared deer from March 2004 to June 2007 to classify individuals as residents, migrators or dispersers (direct observations accounted for 11% of all locations). The distribution of locations by time was: 03:00-09:00 (14%), 09:00-15:00 (35%), 15:00-21:00 (30%) and 21:00-03:00 (21%). Telemetry system tests from true and estimated bearings resulted in an average angular error of 2.63 ± 12.1° (SD) and mean location error distance of 128 ± 91.3 m (SD; Gilsdorf et al. 2008). The minimum and maximum daily displacements for radio-collared mule deer were 1 m (median = 15 m; range: 1-111 m) and 33,672 m (median = 4,313 m; range: 731-33,672 m), respectively. The minimum and maximum daily displacements for radio-collared white-tailed deer were 0 m (median = 14 m; range: 0-39 m) and 41,035 m (median = 3,787 m; range: 1,651-41,035 m), respectively. We found that 87% and 86% of radio-collared mule deer and white-tailed deer, respectively, travelled distances > 2,000 m in a 24-hour period and assumed the others could have as well. We used 2,000 m as our outer buffer when generating random locations for resource selection analyses.

Movements

We identified movement patterns for 70 of 91 radio-collared deer (see Table 1), of which 41 deer (59%) had overlapping seasonal use areas and were classified as residents (see Table 1). Of radio-collared deer, 21% dispersed, and more dispersed in the spring (N = 9) than fall (N = 6). Of dispersing

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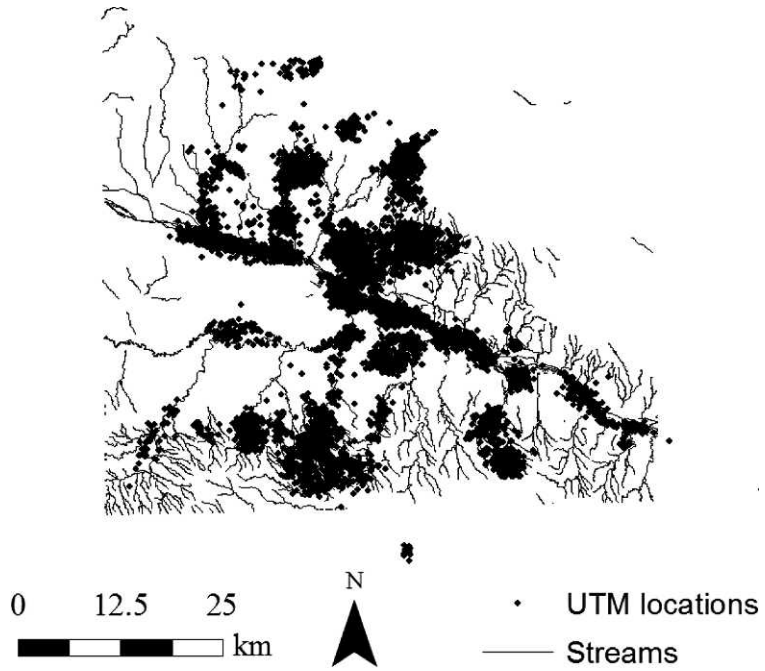


Figure 4. Locations of mule deer and white-tailed deer in a riparian ecosystem along the North Platte River Valley in western Nebraska, USA, 2004-2007.

deer, 93% (N = 14) were males and yearlings dispersed most of any age class for mule deer (N=4) and white-tailed deer (N = 6). One adult female white-tailed deer dispersed 17 km during the first week of July but no female mule deer dispersed. Males dispersed on average 19.4 ± 4.9 km (range: 8.9-43.3 km) in the spring and 18.5 ± 6.1 km (range: 4.5-38.9 km) in the fall. Average dates of spring and fall dispersal for males were 25 May (SE = 9 days; range: 7 April - 19 June) and 25 October (SE = 1.4 days; range: 22 October - 30 October), respectively. Plotted relocations showed that dispersers tended to follow streams and forested riparian corridors when transitioning to new seasonal ranges (Fig. 4).

We classified 14 (20%) radio-collared deer as migrators (see Table 1). Females migrated shorter distances (mean = 9.3 ± 1.8 km; range: 5.4-19 km) than males (mean = 21.4 ± 7.5 km; range: 12.7-36.4 km) during the spring migration period. Mean distance migrated between seasonal ranges in the fall for females was 7.1 ± 2.0 km (range: 3.8-18.7 km) and for males it was 22.5 ± 8.1 km (range: 12.2-38.4 km). Four female mule deer were obligate migrators because they were captured in the same location and migrated together 92-96 km between similar winter and summer ranges (see Table 1 and Fig. 5). Females showed more variability in dates of departure to winter range (SE = 15 days; range: 1 September - 29 December) than to summer range (SE = 4 days; range: 24 April - 31 May). Males had similar variability in dates of departure to summer (SE = 5.5; range: 25 June - 12 July) and winter range (SE = 3.8; range: 24 October - 6 November). Although some facultative migrators used forested riparian corridors as paths for migration, routes of migration for four female mule deer were perpendicular to North Platte River Valley and occurred across agricultural fields or open range (see Fig. 5).

Home range

We documented a species-sex interaction ($F_{3, 37} = 8.26$, $P < 0.001$) for the overall size of home range for resident deer. We found no differences in size of overall home range for female mule deer, male mule deer and male white-tailed deer (Fig. 6). The size of home range for female white-tailed deer was similar to male white-tailed deer, but smaller than female and male mule deer. We found a species-sex ($F_{1, 59} = 9.22$, $P = 0.004$) and a sex-season ($F_{1, 59} = 5.38$, $P = 0.024$) interaction for size of seasonal home range for resident deer. The size of home range for female mule deer was largest during winter, but the size of home range was smallest for female white-tailed deer during summer and male mule deer during winter (see Fig. 6). Seasonal differences in the size of home range were smallest in summer among female mule deer, male mule deer and male white-tailed deer. The size of home range during winter was

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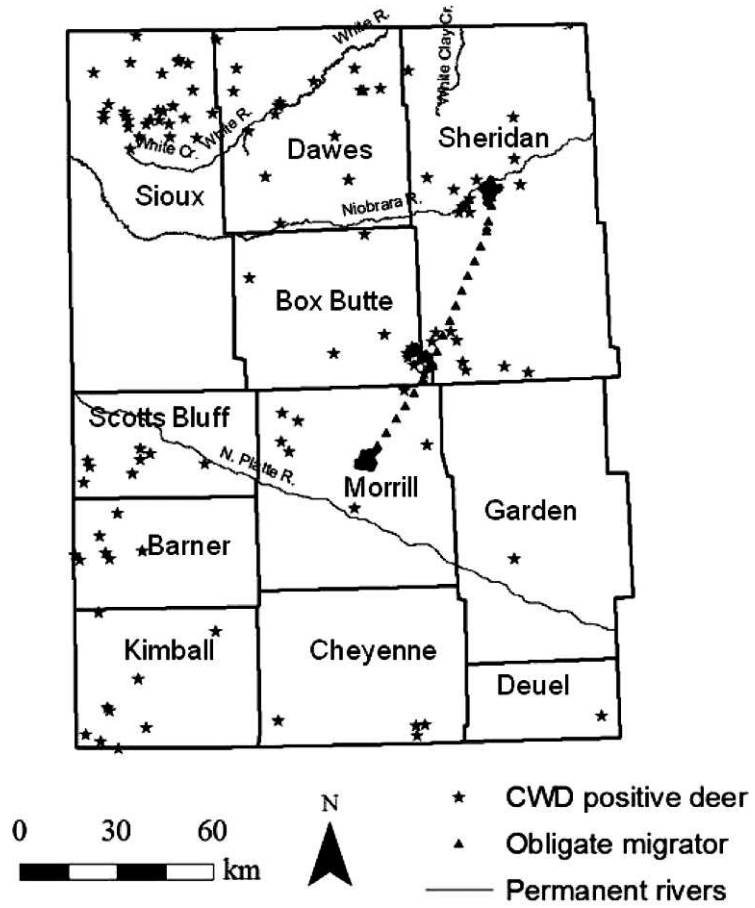


Figure 5. Spatial pathway of migration of four mule deer (▲) from Morrill County (winter range) to Sheridan County (summer range), Nebraska, USA, for two consecutive years (2004-2006). Locations of deer that tested positive for chronic wasting disease (CWD) from 2000 to 2006 are indicated by stars.

similar between male white-tailed deer and female white-tailed deer (see Fig. 6).

Resource selection

Land cover and juxtaposition of crops and forested cover influenced the selection of resources by male mule deer during winter. However, distance to crop fields was not important during summer (see Table 2 and Appendix I). The top-ranked model for female mule deer during summer included an interaction between distance to crop and forested cover, but we chose the more parsimonious candidate model without the interaction term (Howlin et al. 2004). Male and female mule deer selected resources positioned near forested areas during all seasons (Appendix II). Both sexes of mule deer selected forested areas over corn fields during both seasons, however, the effect was not important for female mule deer during summer ($\hat{\beta} \pm 1.96 \times SE = 0$; Fig. 7). Male mule deer were $\geq 142\%$ more likely to select any land cover class other than corn during winter, but showed little selection for any class of land cover during summer (see Appendix II). Female mule deer selected open range over corn fields during winter, but selected corn fields over alfalfa and bean fields. Female mule deer were $\geq 47\%$ more likely to select corn fields than open range and other agricultural crop fields during summer.

Land cover and distance to corn influenced selection of resources by male white-tailed deer during both seasons and female white-tailed deer during summer (see Table 2 and Appendix III). Similar to mule deer, resource selection by male and female white-tailed deer was most related to proximity to forested cover during summer and winter, and this relationship was most pronounced during winter (see Appendix II). Similar to mule deer, female and male white-tailed deer selected resources positioned near corn fields during summer. However, distance to corn fields only influenced selection of resources by males during winter. Among other effects, land cover influenced the selection of resources by both

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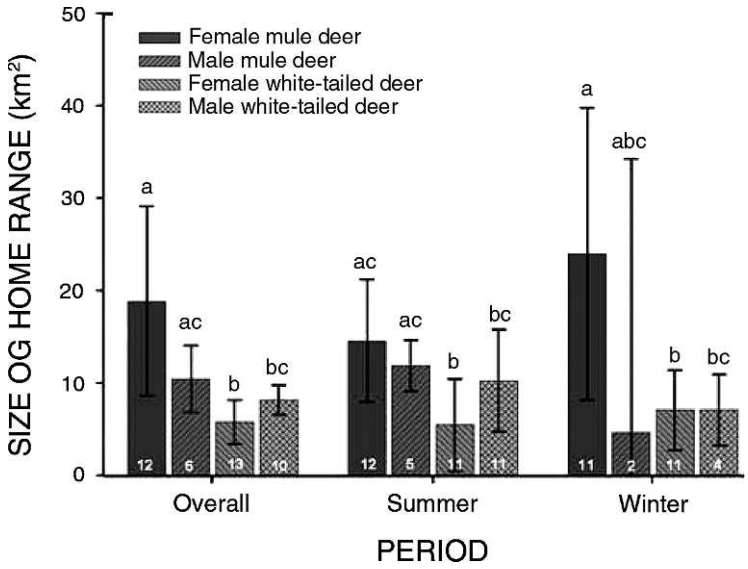


Figure 6. Mean ± CI size (km^2) for overall and seasonal home range for resident mule deer and white-tailed deer radio-collared in western Nebraska, USA, 2004-2007. Numbers inside bars indicate sample size. Different letters above confidence interval bars indicate least-squared means differences at $P < 0.05$.

sexes of white-tailed deer during both seasons (see Appendix II). Male white-tailed deer were 82% and 79% more likely to select forested cover over corn fields during winter and summer, respectively (see Fig. 7). Similar to males, female white-tailed deer were 27% and 166% more likely to select forested areas than corn fields during winter and summer, respectively. Female white-tailed deer also selected corn fields during winter, but open range, alfalfa and other agricultural crop fields were selected over corn fields during summer. All season-specific models provided reasonable predictions of resource selection by male and female mule deer and white-tailed deer (see Figs. 2 and 3, respectively).

Spatial overlap

Mean spatial overlap of home ranges varied by season and was lowest for interspecific or intersexual comparisons. Spatial overlap of home range was from 0.1 (i.e. minimal spatial overlap) among several individuals of both species and sex to 0.953 (nearly complete spatial overlap) between female mule deer and other females presumed to be in their social group. Weights for BIC indicated that models

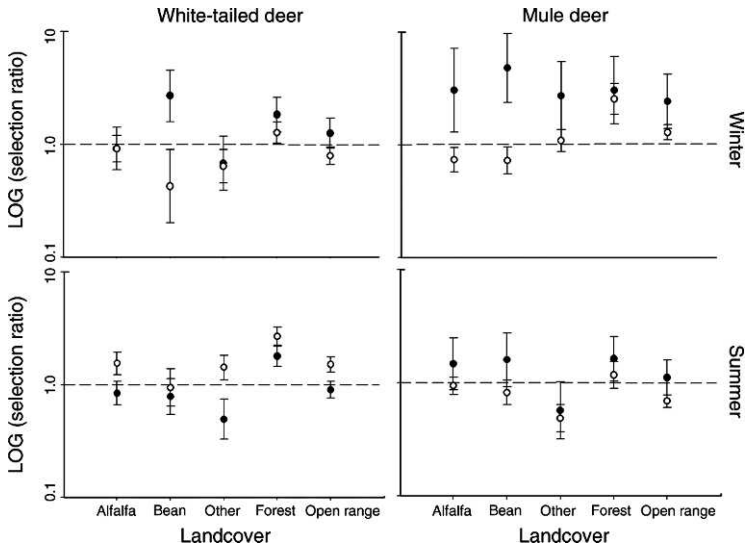


Figure 7. Selection ratios and 95% confidence limits for the categorical variable, land cover, in model averaged discrete-choice models used to estimate the relative probability of male (●) and female (○) mule deer and white-tailed deer selecting 30 × 30 m resource units in Morrill County, Nebraska, USA during summer (1 May - 31 October) and winter (1 November - 30 April), 2004-2007. Confidence intervals were computed as exp(coefficient ± 1.96 × coefficient standard error). Interpretation of selection ratios were in comparison to corn field (reference category) and assume all distance measures included in final models were held at their respective scaled and centered mean distance of 0.0 m.

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Table 3. Ranks of four *a priori* models using Bayesian information criterion (BIC) for variables that influenced volume of intersection scores as measure of spatial overlap between mule deer and white-tailed deer by sex in western Nebraska, USA, 2004-2007. Model rankings based on number of parameters (K), BIC, BIC differences (ΔBIC) and BIC weights (Weight). Species-sex refers to spatial overlap between all possible combinations of species and sex (N = 9).

Model	BIC	K	ΔBIC	Weight
Species-sex + season	174.55	10	0.000	0.913
Species-sex	179.26	9	4.705	0.087
Season	198.76	2	24.206	< 0.001
Intercept	200.27	1	25.714	< 0.001

which included the season and species-sex variables had the strongest support (BIC weight = 0.931; Table 3; Burnham & Anderson 2004). Mean VI for home range was three times higher between female mule deer and twice as high between female white-tailed deer than any other species and sex overlap (Table 4). Home-range VIs were only slightly higher during summer than winter (see Table 3).

Mean inter- and intraspecific overlap in RSPFs within season tended to be twice as high during summer than winter (Appendix IV). Greater overlap of RSPFs during summer occurred for both species compared to winter. The RSPFs for female mule deer and male white-tailed deer were more similar during winter and summer than their conspecifics. Intersexual, interspecific overlap in RSPFs was also nearly twice as high during summer than winter. Furthermore, overlap between male white-tailed deer and female mule deer RSPFs tended to be higher than overlap between female white-tailed deer and male mule deer during both seasons (see Appendix IV).

Discussion

Movement and home range

Movement by both species was documented as 41% of deer dispersed or migrated seasonally from areas of capture and were not classified as year-round residents of our study site. Furthermore, female mule deer exhibited larger size of home ranges than female white-tailed deer in all seasons, which has not been documented in the literature. Male deer are considered the primary mode of CWD spread, however, because their large home ranges and high dispersal rates presumably result in greater contact rates with conspecifics (Farnsworth et al. 2005, Skuldt et al. 2008, but see Conner & Miller 2004). Although behaviour of male deer would suggest greater interactions with conspecifics (Hawkins & Klimstra 1970, Hirth 1977, Marchinton & Hirth 1984), males that typically have greater dispersal rates exhibited home ranges of comparable size to those of females for both species in western Nebraska. Male deer in older age classes incur greater mortality from hunting than females and yearling males which were less likely to be infected with disease (O'Brien et al. 2002, Miller & Conner 2005). The size of home ranges for female mule deer were comparable to male deer of both species, suggesting that female mule deer may play a more predominate role in the spread of PrP^{SC} in the environment than previously proposed.

Routes of dispersal and migrations indicated that

Table 4. Mean volume of intersection scores (VI), parameter estimates (Estimate), P-values for the Wald χ^2 statistic, and 95% confidence intervals for parameters in the best model to determine spatial overlap of home ranges between sexes of mule deer and white-tailed deer in western Nebraska, USA, 2004-2007. Sympatric = spatial overlap between mule deer and white-tailed deer. Intersexual = spatial overlap between male and female deer.

Parameter	Mean VI (SE)	Estimate (SE)	P-value	95% Lower CI	95% Upper CI
Sympatric-Intersexual	0.12 (0.01)	-0.475 (0.29)	0.103	-1.046	0.096
Sympatric-Female	0.17 (0.02)	-0.029 (0.26)	0.911	-0.539	0.481
ympatric-Male	0.17 (0.04)	-0.189 (0.27)	0.485	-0.720	0.341
Mule deer-Intersexual	0.23 (0.03)	0.064 (0.20)	0.746	-0.324	0.452
Mule deer-Female	0.36 (0.04)	0.528 (0.18)	0.004	0.168	0.888
Mule deer-Male	0.26 (0.12)	-0.115 (0.25)	0.650	-0.611	0.381
White-tailed deer-Intersexual	0.24 (0.02)	-0.184 (0.18)	0.336	-0.184	0.539
White-tailed deer-Female	0.23 (0.03)	0.184 (0.20)	0.366	-0.216	0.584
White-tailed deer-Male	0.23 (0.04)	0.000		0.000	0.000
Summer	0.27 (0.02)	0.231 (0.11)	0.029	0.024	0.438

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mule deer and white-tailed deer may contribute to disease spread differently as mule deer moved across open range, but white-tailed deer moved along forested, riparian areas. Although 81% of females were year-round residents in North Platte River Valley, six female deer (four mule deer and two white-tailed deer) were obligate migrators with seasonal ranges ≥ 92 km away from our study area for female mule deer. Migrations of this magnitude could be responsible for moving CWD throughout Nebraska via direct or indirect transmission (Miller et al. 2004). The nearest counties in Colorado, Wyoming and South Dakota that have known cervids positive for CWD were about 69, 85 and 142 km, respectively, from the western extent of our study area with no known dispersals to Sheridan County, Nebraska, from adjacent states. Dispersal by CWD-infected mule deer from South Dakota was not documented (Schuler 2006), and is unlikely, and positive counties in Wyoming were > 132 km from the location in Sheridan County, Nebraska, that our four female mule deer occupied seasonally. The female mule deer that migrated to Sheridan County moved perpendicular to the riparian corridor, while female white-tailed deer traveled along the North Platte River during migrations. Furthermore, two male white-tailed deer that were harvested, and tested positive for CWD, could have come from western Nebraska and could have followed North Platte River east for 193 km to Hall County, Nebraska. Statewide testing has occurred since 2002, so sampling and testing was likely sufficient to detect CWD in deer in eastern Nebraska. Although deer in North Platte River Valley concentrated in the riparian areas, spread of CWD throughout Nebraska could occur across open range or along riparian areas further complicating CWD epidemiology in areas with sympatric deer.

Similar to previous research, we used VIs as a proxy for indirect spread of PrP^{SC} between species and sexes during our study (Schauber et al. 2007). We documented spatial overlap of home range for female mule deer as high as 0.95 (nearly complete spatial overlap) and 0.67 for male mule deer with conspecifics. The VIs for female and male white-tailed deer never exceeded 0.56, suggesting less overlap of white-tailed deer with conspecifics. Less overlap in home ranges of conspecifics for white-tailed deer than mule deer may be a result of larger and more stable group dynamics for mule deer than white-tailed deer (Bowyer et al. 2001, Lingle 2003). No home-range VIs for sympatric species of mixed sex were > 0.32, which suggests that overlap occurred more between conspecifics than between sympatric species. Greater contact rates and overlap of home range have been suggested for conspecifics than for intraspecific comparisons of both deer species, although these variables have not been investigated in areas of sympatry (Miller & Conner 2005, Schauber et al. 2007).

Home ranges of deer in North Platte River Valley were along a riparian corridor that contained forested land cover and associated intermittent streams that were surrounded by an agricultural matrix. Forested land cover along riparian habitats have been used by mule deer and white-tailed deer because they provide a mixture of cover, forage and water (Compton et al. 1988, Nicholson et al. 1997, Whittaker & Lindzey 2004). As indicated in our discrete-choice models, deer in our study area selected for these forested, riparian areas likely because the areas provided preferred forage and security cover in all seasons. Extensive grazing by cattle on open range in the surrounding landscape or the lack of forested cover outside of riparian areas resulted in limited habitat for deer outside of the riparian areas. Several studies have documented little overlap in sympatric mule deer and white-tailed deer in more heterogeneously forested landscapes (Martinka 1968, Whittaker & Lindzey 2004, Brunjes et al. 2006), but overlap was more prominent in homogeneous landscapes (e.g. patch sizes of equal size and shape) or areas with less suitable forage (Anthony & Smith 1977, Hornbeck & Mahoney 2000). Overlap among sympatric deer in western Nebraska was likely due to the congregation of both species in forested, riparian areas in the absence of suitable open range habitat similar to findings in previous research (Anthony & Smith 1977, Wiggers & Beasom 1986, Hornbeck & Mahoney 2000). Riparian corridors in the Great Plains could act to concentrate sympatric species of deer and result in higher rates of interaction and deposition of PrP^{SC} (e.g. feces, urine and decaying carcasses) compared to habitats in more heterogeneous landscapes (e.g. winter range at low elevations; Farnsworth et al. 2005).

A notable difference between the species was the specificity in selection of resources, thus this could infer the directionality of spread of the disease. Mule deer of both sexes selected resources more uniformly (i.e. less specificity) across the landscape than white-tailed deer, suggesting that white-tailed deer may be primarily responsible for depositing

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PrP^{SC} in riparian corridors along the North Platte River. Specificity in resource selection was lowest for white-tailed deer during summer months and highest during winter months, which was probably related to increased availability of cover (e.g. corn fields) during summer months (VerCauteren & Hygnstrom 1998). Especially during winter months, white-tailed deer also selected areas of rugged terrain and open range, which were historically occupied by mule deer (Mohler et al. 1951). This further suggests that contamination of mule deer habitat with PrP^{SC} may be occurring by populations of white-tailed deer occupying historic mule deer range. Much of this movement away from riparian habitats was believed to be in response to the appearance of patches of trees within bluffs along North Platte River Valley, and an increase in the size of the population of white-tailed deer (Hams & Trindle 2008). Female mule deer were more selective of resources during summer, presumably during fawning and lactation, while male mule deer were less selective of resources during summer. However, mule deer have greater prevalence of CWD in western Nebraska, so directionality of indirect spread (i.e. white-tailed deer to mule deer) can only be inferred until better analytical methods are developed to detect PrP^{SC} in the environment.

Populations of mule deer in Nebraska and other parts of North America have declined in recent years (Clements & Young 1997, Unsworth et al. 1999, Robinson et al. 2002). In many areas of North America, mule deer had an insular pattern of distribution and typically segregated from related species, which reduced the likelihood of interspecific competition (Kramer 1973, Wasley 2004, Whittaker & Lindzey 2004). In western Nebraska, however, we observed overlap in space-use by the two species, suggesting indirect transmission of prions for CWD as a plausible mechanism to spread of disease as previously proposed in captive deer (Miller et al. 2006, but see Miller et al. 2004). In 2004, our study site was positioned on the eastern edge of the core endemic area for CWD. CWD has since spread from west to east across the Panhandle of Nebraska, and by 2007 it had been reported in every county within this region (Nebraska Game and Park Commission 2008). The continued presence of CWD in our study area, and the fact that it has spread to other regions of Nebraska, could be from direct contact of infected deer or indirect contact with PrP^{SC} in the environment, but current methods prevent accurate assessment of causal mechanisms (Miller et al. 2004, Johnson et al. 2006). The prolonged drought in the area and overlap in relative use of space of sympatric populations of deer may have played a prominent role in the indirect spread and transmission of CWD.

Conclusions

Management of deer populations that are infected with CWD is a complex issue that requires managing sympatric species that differ in migratory behaviour, size of home range, seasonal resource selection and sex-age-specific prevalence for CWD. With the reduction of habitat resulting from land-use changes (e.g. biofuel production) and global climate change (Joyce & Birdsey 2000, Millar et al. 2007), interactions among sympatric deer in various ecosystems throughout North America are likely to continue or increase. Mule deer selected resources more uniformly distributed across the landscape than white-tailed deer, but we observed considerable overlap along North Platte River Valley. Selection of riparian, forested habitat by mule deer, generally considered an open-range species, would result in continued sharing of resources with an increasing population of white-tailed deer in western Nebraska. Direct competition for resources (Anthony & Smith 1977), in combination with mortality from CWD, could contribute to a decline in mule deer populations throughout the range of mule deer, which is counter-productive to management of mule deer populations. Therefore, a reduction in the number of white-tailed deer, specifically around riparian corridors of major river systems, would seem to be a feasible initial step in containing CWD or decreasing the spread of CWD and, potentially, competition for resources.

Low sample size of known-aged deer precluded our understanding of age-specific prevalence of CWD, but sex-specific prevalence of CWD varied by species (see Fig. 1). Sex- and age-specific prevalence of CWD and the probability of infection has been documented previously for both species of deer (Miller & Conner 2005, Grear et al. 2006). We found that female mule deer exhibited longer migrations (i.e. > 90 km) and larger size and overlap of home ranges than female white-tailed deer. Spread of diseases within species or matrilineal groups is likely, but our data suggested that migratory behaviour of female mule deer may also contribute to inter-corridor spread of CWD. Combined with

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the high prevalence of CWD found in female white-tailed deer in western Nebraska, relative to other sexes and species we studied, managers should consider reductions in females of both species in management of CWD. Future research on the influence of altering sex ratios of both species on prevalence of CWD could be initiated in populations of deer experiencing high prevalence of CWD such as those in central Wisconsin and north-central Colorado (Miller & Conner 2005, Grear et al. 2006).

Our study site was along a riparian corridor of North Platte River that likely concentrated sympatric populations seasonally or throughout the year during extreme droughts and harsh winters. Areas of concentration may have increased rates of direct or indirect disease transmission and could be a focal center in modeling disease epidemiology. Mule deer migrated across open range, while white-tailed deer dispersed along the riparian corridor, indicating that different dispersal or migratory behaviours are responsible for disease transmission through contact or deposition of PrP^{SC} in the environment. Models on epidemiology of CWD should consider that indirect transmission of PrP^{SC} deposited in the environment could differ in populations of sympatric deer that use habitats more uniformly across a region (i.e. mule deer) compared to white-tailed deer that concentrate in riparian corridors. Infectious prions can persist in soil and environment (e.g. vegetation around CWD-positive carcasses) for at least five years (Johnson et al. 2006) and up to 16 years for scrapie (Georgsson et al. 2006), suggesting that, as techniques become more reliable, monitoring of soil and water should be conducted in riparian corridors to understand the influence of indirect transmission of PrP^{SC} in epidemiology of CWD in endemic areas.

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Appendices

Appendix I. Top four discrete-choice models used to estimate probability of male and female mule deer selecting 30 × 30 m resource units, number of parameters in model (K), Bayesian information criteria (BIC), ΔBIC and BIC weights (Weight) during two seasons in Morrill County Nebraska, USA, 2004-2007. Winter = 1 November - 30 April and summer = 1 May - 31 October.

	Male					Female				
Season	Model #	K	BIC	ΔBIC	Weight	Model #	K	BIC	ΔBIC	Weight
Winter	3	8	2007.5	0.0	0.99	4	7	10074.2	0.0	0.66
	4	7	2017.0	9.5	0.01	3	8	10075.6	1.4	0.34
	5	6	2023.8	16.3	0.00	12	7	10092.7	18.4	0.00
	10	7	2028.7	21.2	0.00	1	6	10115.6	41.3	0.00
Summer	1	6	4001.6	0.0	0.82	3	8	9713.7	0.0	0.91
	4	7	4007.1	5.5	0.05	4	7	9718.4	4.8	0.09
	10	7	4007.7	6.2	0.04	1	6	9726.6	12.9	0.00
	8	7	4007.8	6.2	0.04	8	7	9734.0	20.3	0.00

Appendix II. Coefficients and standard errors (in parentheses) of discrete-choice models used to estimate the probability of male or female mule deer or white-tailed deer selecting 30 × 30 m resource units within Morrill County, Nebraska, USA, during summer (1 May - 31 October) and winter (1 November - 30 April), 2004-2007. Distance measures represent the shortest Euclidian distance (m) from each use or random location to specific features across the landscape. We normalized distance measures to have a mean of 0.0 and standard deviation of 1.0 prior to analysis. Distance measures include: distance to any crop, distance to bean, distance to corn, distance to forested area (forest), and an interaction term (crop*forest (distance to any crop*distance to forested area)). Variables not included in the final model are indicated by '-'. Land cover class was a categorical variable with six levels: alfalfa (irrigated and non-irrigated), bean (irrigated and non-irrigated soybean or edible bean), corn (irrigated and non-irrigated (reference category)), other agricultural crop (irrigated and non-irrigated potato, milo, oat, sorghum, sugar beet, summer fallow, sunflower and wheat), forested area (forest) and open range.

	White-tailed deer				Mule deer			
	Male		Female		Male		Female	
Variables	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Distance								
Any crop	-	-	-	-	-0.22 (0.07)			
Forest	-8.53 (0.53)	-4.31 (0.27)	-7.65 (0.35)	4.04 (0.22)	-0.60 (0.18)	-0.64 (0.12)	-0.56 (0.07)	-0.94 (0.09)
Bean	-	-	0.37 (0.05)	-	-	-	-	-
Corn	-0.37 (0.10)	-0.49 (0.08)		-0.75 (0.07)	-	-	-	-
Crop*forest	-	-	-	-	-0.22 (0.06)	-	-	-
Land cover								
Alfalfa	-0.09 (0.26)	-0.18 (0.12)	-0.09 (0.14)	-0.43 (0.12)	1.11 (0.44)	0.38 (0.27)	-0.31 (0.13)	-0.06 (0.09)
Bean	0.99 (0.27)	-0.25 (0.18)	-0.86 (0.38)	-0.06 (0.19)	1.57 (0.36)	0.46 (0.28)	-0.33 (0.14)	-0.20 (0.13)
Other	-0.39 (0.28)	-0.71 (0.21)	-0.46 (0.17)	0.35 (0.13)	1.00 (0.36)	-0.57 (0.30)	0.08 (0.12)	-0.73 (0.14)
Forest	0.60 (0.18)	0.58 (0.11)	0.24 (0.11)	0.98 (0.10)	1.11 (0.35)	0.48 (0.23)	0.93 (0.16)	0.15 (0.14)
Open range	0.22 (0.16)	-0.11 (0.09)	-0.24 (0.09)	0.41 (0.08)	0.89 (0.28)	0.10 (0.18)	0.25 (0.08)	-0.38 (0.07)

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Appendix III. Top four discrete-choice models used to estimate probability of male and female white-tailed deer selecting 30 × 30 m resource units, number of parameters in model (K), Bayesian information criteria (BIC), ΔBIC and BIC weights (Weight) during two seasons in Morrill County Nebraska, USA, 2004-2007. Winter = 1 November - 30 April and summer = 1 May - 31 October.

	Male					Female				
Season	Model #	K	BIC	ΔBIC	Weight	Model #	K	BIC	ΔBIC	Weight
Winter	6	7	3119.3	0.0	0.95	10	7	7178.1	0.0	1.00
	12	7	3126.9	7.5	0.02	12	7	7200.6	22.5	0.00
	1	6	3127.6	8.2	0.02	8	7	7205.2	27.1	0.00
	8	7	3128.0	8.7	0.01	6	7	7217.8	39.7	0.00
Summer	6	7	5690.5	0.0	0.98	6	7	7676.3	0.0	1.00
	12	7	5698.5	8.0	0.02	10	7	7723.9	47.5	0.00
	3	8	5708.9	18.4	0.00	12	7	7758.1	81.8	0.00
	4	7	5711.8	21.3	0.00	1	6	7795.1	118.8	0.00

Appendix IV. Mean volume of intersection indices (VI × 100) with upper and lower 95% confidence limits (in parentheses) from 1,000 parametric-bootstrap simulations used to determine similarities in seasonal selection of resources between both sexes of mule deer and white-tailed deer in Morrill County, Nebraska, USA, 2004-2007. We used season-, species- and sex-specific locations of deer and discrete-choice resource selection functions to estimate selection distributions. Seasons included summer (1 May - 31 October) and winter (1 November - 30 April). Abbreviations for class of deer and season include: male mule deer during summer (mmds), male mule deer during winter (mmdw), female mule deer during summer (fmds), female mule deer during winter (fmdw), male white-tailed deer during summer (mwtds), male white-tailed deer during winter (mwtdw), female white-tailed deer during summer (fwtds), and female white-tailed deer during winter (fwtdw).

Class	mmds	mmdw	fmds	fmdw	mwtds	mwtdw	fwtds
mmdw	71 (56-84)						
fmds	87 (81-92)[a]	67 (54-80)					
fmdw	85 (81-88)	73 (60-86)[a]	88 (84-92)				
mwtds	61 (56-66)[b]	54 (44-61)	67 (64-71)	63 (60-67)			
mwtdw	49 (45-54)	45 (39-52)[b]	53 (50-57)	49 (46-53)[c]	78 (73-83)		
fwtds	57 (53-62)[c]	57 (50-63)	63 (60-67)[b]	62 (58-65)	87 (82-92)[a]	72 (67-77)	
fwtdw	41 (36-46)	35 (28-41)[c]	43 (37-48)	40 (34-45)[b]	48 (40-56)	55 (46-66)[a]	42 (35-49)

[a] Intraspecific, within-season VI between male and female mule deer or male and female white-tailed deer.
[b] Interspecific, within-season VI between male mule deer and male white-tailed deer or female mule deer and female white-tailed deer.
[c] Interspecific, within-season VI between male mule deer and female white-tailed deer or female mule deer and male white-tailed deer.

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