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Original Article

Identifying Migration Corridors of Mule Deer Threatened by Highway Development

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ABSTRACT Highways are hazardous to migratory ungulates world-wide, causing direct and indirect impacts to ungulate survival. Moreover, significant financial costs are incurred in damage from wildlife–vehicle collisions and in building and maintaining wildlife passage structures. Information is needed to link ungulate movements to collision occurrence to prioritize needed construction of wildlife crossings on highways. We simultaneously documented mule deer (*Odocoileus hemionus*) migration corridors and mule deer–vehicle collisions (DVCs) in South-central Oregon, USA, over 6 years (2005–2011). We calculated Brownian Bridge Movement Models for 359 migrating mule deer equipped with Global Positioning System technology. We modeled DVC counts as functions of probability of use during migration, annual average daily traffic (AADT), and habitat characteristics. Probability of use during migration was the strongest predictor of where DVCs occurred ($r = 0.93$). Predicted DVCs also increased with AADT but peaked at approximately 8,000 and then decreased. Where AADT was above approximately 8,000, fewer deer attempted to cross the highway and DVCs decreased because, over time, deer either abandoned the migration route or were killed trying to cross this busy highway. Our results suggest that managers should focus on migration corridors or high-density DVC locations to identify where fencing and under/overpasses could be most effective for maintaining migratory corridors when confronting increasing traffic and development that bisect seasonal ranges of mule deer. © 2015 The Wildlife Society.

KEY WORDS Brownian Bridge, corridors, deer–vehicle collisions, migration, mule deer, *Odocoileus hemionus*, Oregon, passage, roads, ungulates.

Wildlife mortality caused by collisions with vehicles and fragmentation of habitat caused by roads is a growing problem worldwide because of the increasing use of motor vehicles for human and material transport (Malo et al. 2004, Epps et al. 2007, Huijser et al. 2008). Animals that migrate may be more vulnerable to wildlife–vehicle collisions than nonmigrating wildlife, and thus be more susceptible to population declines (Bolger et al. 2008) and gene-flow disruptions (Watkinson and Sutherland 1995, Epps et al. 2005, Ascensão et al. 2013). Migration corridors may be abandoned at high traffic volumes despite the natural tendency of ungulates to use the same migration routes yearly (Berger 2004, Sawyer et al. 2009). It is important to use identified migration routes to prioritize conservation actions because migration is critical to maintaining healthy populations (Sawyer et al. 2009), especially in areas where nutritional requirements cannot be met at the same location during all seasons (Bischof et al. 2012). No less important are the substantial loss of property and human injuries and fatalities caused by animal–vehicle collisions, estimated in the United States to cost US$6,126/wildlife–vehicle collision and totaling >US$1 billion annually (Conover et al. 1995, Huijser et al. 2008). Wildlife crossings placed over or under highways reduce vehicle-caused animal mortalities by ≥80%

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(Lehnert and Bissonette 1997, Clevenger et al. 2001, Gagnon et al. 2007*b*, Bissonette and Rosa 2012) and are economical when deer–vehicle collisions (DVCs) are >3/km/year (Huijser et al. 2009). Regardless of the type of crossing structure chosen to reduce wildlife–vehicle collisions and facilitate wildlife passage, managers must have sufficient information on animal behavior to prioritize the placement of wildlife structures.

Mule deer (*Odocoileus hemionus*) are traditional in their migration routes and follow the same path closely each year (Monteith et al. 2011, Sawyer and Kauffman 2011, Lendrum et al. 2013). Spring migration occurs when mule deer leave winter range and travel to summer range; females often stop during spring migration to have their fawns (Sawyer and Kauffman 2011). In autumn, snowfall or daylight length prompt deer to leave their summer range (Monteith et al. 2011). Previous studies of wildlife–vehicle collisions have considered habitat characteristics, such as forest cover or distance to water, in predicting wildlife crossings on roadways (Malo et al. 2004, Seiler 2005, Gunson et al. 2011), but few have incorporated actual migration paths (but see Kramer-Schadt et al. 2004, Neumann et al. 2012). Previous studies have also investigated whether traffic levels influence ungulate–vehicle collisions (Seiler 2005, Gagnon et al. 2007*a,* Bissonette and Kassar 2008, Myers et al. 2008) with varying responses observed. Our goals were to investigate the relationship of DVCs to mule deer migration corridors and identify and evaluate models for predicting where DVCs occur to aid managers in placing wildlife crossing structures.

Figure 1. Extent of year-round distribution of mule deer in South-central Oregon, USA, derived from minimum convex polygon determined by >1 million Global Positioning System locations from 463 deer, 2005–2012. Highway study sections for U.S. Highway 97 (Hwy 97) and State Highway 31 (Hwy 31) are in red. Mule deer capture locations are shown for summer (green triangles) and winter (blue circles). Public land is depicted in diagonal lines and mule deer winter range in solid light blue. Wildlife management units are identified by heavy gray lines and labels.

STUDY AREA

We focused our study on portions of 2 highways in central Oregon, USA, and captured mule deer in the wildlife management units surrounding these study highways (Fig. 1). Our study area included 160 km of U.S. Highway 97 (hereafter, Highway 97) and 80 km of State Highway 31 (hereafter, Highway 31). These segments span both summer and winter ranges of migratory mule deer. Bend, Oregon was the northern terminus of our study section and Highway 97 passed through 4 rural residential areas of La Pine, Gilchrist, Crescent, and Chemult, ending at Chiloquin in the south (Fig. 1). Highway 31 angled southeast from its junction with Highway 97 near La Pine and passed through the rural residential area of Silver Lake (Fig. 1). Annual average daily traffic (AADT) for these segments averaged 6,218 for Highway 97 and 870 for Highway 31 during the study. Sixteen percent of the study section of Highway 97 was within mule deer winter range identified by Oregon Department of Fish and Wildlife, whereas 58% of the study section of Highway 31 bisected winter range (Fig. 1).

Populations of mule deer decreased 40% over 7 years in Upper Deschutes, Paulina, Fort Rock, and Silver Lake wildlife management units, from 36,000 in 2005 to 22,000 in 2011 (Fig. 1; C. Heath, Oregon Department of Fish and Wildlife, unpublished data). Average elevation is 1,462 m (range = 315–3,149 m) and the topography is mostly flat, except for the foothills of the Cascade Mountains on the west and scattered volcanic cinder cones to the east. Climate is strongly influenced by the rain-shadowing effect of the Cascade Mountains on the higher western edge of the study area (Fig. 1), with lower elevations in the east being arid. Winters are cold with snow and summers hot and dry. During the years of the study, mean minimum January and maximum July temperatures ranged from between −8.4 to −1.1 °C and 26.0 to 30.4 °C, respectively (Daly and Bryant 2013). Mean annual precipitation varied from 15.7 cm to 37.3 cm, with most falling as snow in the winter (Daly and Bryant 2013). This area was sparsely populated with an estimated 254,000 people (6.22/km^2) and included 4 urban centers of Bend and Redmond in the north, and Klamath Falls and Lakeview in the south (U.S. Census Bureau 2010). Most of the area consisted of public lands administered by the Bureau of Land Management (24%) or U.S. Forest Service (44%), but private land was dominant in the arable lower elevations (Fig. 1). Vegetation consisted of forests in the west and shrub-steppe in the east (Franklin and Dyrness 1973). Forests were dominated by Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*), whereas shrub-steppe communities were dominated by sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and/or juniper (*Juniperus occidentalis*).

METHODS

From 2005 to 2011, we captured adult female mule deer on winter ranges in proportion to wintering densities of all mule deer (approx. 1 collar/150 deer was attempted) using net guns fired from a helicopter (Jacques et al. 2009) or Clover traps (Clover 1954) baited with alfalfa. Our strategy was to sample in proportion to wintering densities to obtain a representative sample of the entire population of mule deer in South-central Oregon. Some deer were captured on summer range to boost the number of autumn migrations represented in our sample. For summer captures, we used drugs administered by projectile darts fired from tree stands (Kreeger et al. 2002). Summer capture methods differed from winter because deer are widely dispersed in forested areas during summer, whereas they are concentrated in open areas during winter. For each deer, we recorded gender, age class (fawn, yearling, ad), and physical characteristics including total length, girth, neck diameter, and condition based on fat index (Kistner et al. 1980). We considered deer that were ≥2 years old as adults. We fitted deer with Global Positioning System (GPS) collars (Lotek model 3300S and 4400S, Lotek Wireless Inc., Newmarket, ON, Canada; ATS model G2110D, ATS, Inc., Isanti, MN; Tellus Basic GPS collars, Omnia Ecological Services, Calgary, AB, Canada, and Followit AB, Lindesberg, Sweden) programmed to record a location every 4 hr and self-release after 52–72 weeks. Battery life of a collar was 1.5 years, so winter captures were likely to produce 2 spring and 1 autumn migration, whereas summer captures could potentially result in 2 autumn and 1 spring migration. Collars were equipped with mortality sensors that doubled the very high frequency signal pulse rate when a collar was stationary for >4 hr. We monitored collared deer from a fixed-wing airplane twice weekly for mortality signals, locating the collar and investigating for cause of death. All deer were handled in accordance with protocols approved by Oregon Department of Fish and Wildlife for safe capture and handling and following recommendations of the American Society of Mammalogists (Sikes et al. 2011).

We imported GPS collar locations for each deer into a Geographic Information System (GIS; ArcMap, Version 10.0). We eliminated obvious erroneous GPS locations (sequential locations too distant for a deer to travel in 4 hr). We then selected and classified locations as spring or autumn migration using the following procedures. We displayed the locations for a single deer, year, and season, and identified the midpoint of an apparent spring or autumn migration (characterized by a linear sequence of locations spanning winter and summer areas). Those locations were then examined chronologically forward and backward until the distance between consecutive locations indicated a seasonal range characterized by a cluster of locations 1–3 km in diameter. In addition, we included location data 24 hr prior to or after the beginning or end of an identified migration sequence, respectively, to ensure that we identified all migration locations. If a deer exhibited multimigration sequences (i.e., left a seasonal range, started to migrate only to return to the original seasonal range), we included only the final series of locations to the destination range to reduce bias in calculating probability of use during migration (described below). In some instances, deer used stopover areas (indicated by clusters of locations) during migration. If a cluster was within 3 km of its summer or winter range and used for ≥5 sequential days, the locations were not included in the analysis. We chose these criteria based on the typical width of a seasonal range (3 km) and typical duration of migration (5 days). Deer that did not migrate were not used in our analysis.

Brownian Bridge Movement Models

We fit a Brownian Bridge Movement Model (BBMM) to each migration sequence for each adult female migratory deer (Horne et al. 2007, Sawyer et al. 2009) using the "BBMM" package (Nielson et al. 2011) in R (R Core Team 2012). This approach used time-specific location data to quantify the spatial probability of use during a migration sequence, and accounted for the uncertainty in an animal's location between known locations and inherent error in recorded GPS locations (Sawyer et al. 2009). The BBMM provided a probabilistic estimate of a migration route, known as a utilization distribution (UD). This method is generally preferred over connecting sequential GPS locations (Sawyer et al. 2005), which ignores the uncertainty in both the recorded locations and the trajectory of movement, and offers no means for characterizing the population-level route network.

Missing observations, or fix-rate bias (Sawyer et al. 2009), was a concern in our analysis because fix-rates of collars varied from 52% to 100%. Although the BBMM could account for missing locations, multiple missing locations in a sequence could artificially inflate the Brownian motion variance (Horne et al. 2007) or result in convergence problems during model estimation. To prevent these issues, we restricted the BBMM to where no 2 sequential locations were >8 hr apart. In addition, we limited the modeling to migration bouts with >10 GPS recorded locations to ensure that we had a sufficient sample size for modeling. If a migration sequence had ≥2 consecutive missing locations, then 2 BBMMs were estimated—1 before and 1 after the event of ≥2 consecutive missing locations. To estimate the standard deviation of location error in the GPS records, we placed GPS radiocollars used on deer in representative habitats and used the maximum amount of variation as input in the BBMM.

We excluded migrations with an estimated Brownian motion variance >20,000. Tortuous migration sequences with fewer locations and a lower fix-rate success tend to have larger Brownian motion variances, which can increase the error in the estimated UD in an exponential fashion. Based on our experience applying BBMMs to dozens of sampled ungulate populations, Brownian motion variances >20,000 are rare and usually are associated with poor-quality location data. Although our imposed limit of 20,000 is somewhat arbitrary, we believed it would improve estimation of the overall migration routes for each herd and the entire sampled population. We estimated probability of use during each migration bout for each 50-m × 50-m cell in a grid overlaying the minimum convex polygon of year-round mule deer locations to provide high-resolution mapping while maintaining a reasonable processing time.

We estimated a UD for each migration of each deer. For deer that had >1 migration recorded, we summed the cell values of all their UDs and then rescaled their cumulative cell values to sum to 1, such that all migratory routes for each deer were represented by one UD. We then followed this same rescaling procedure to estimate migration routes for each herd (groups of deer using the same winter and summer ranges), and then again to estimate the overall population-level UD. The resulting surface grid provided an estimate of the relative amount of use per 50-m × 50-m cell within the minimum convex polygon during migration by the average deer, referred to hereafter as the "migration UD." We ranked grid cells (3,566 rows × 7,075 columns) and placed cells into 20 equal-area quantiles based on the estimated UD, which we hereafter refer to as "migration UD class." We also calculated the number of highway crossings by intersecting lines created from migration locations of deer used in the UD analysis with the study segments of the highways.

Highway Surveys

From 2005 to 2010, we surveyed our highway study sections by vehicle on a near-daily basis for evidence of deer–vehicle collisions. We examined carcasses within 24 hr of discovery for cause and estimated date of death, sex, number of fetuses, and characteristics of the roadway. Carcass locations were recorded using a handheld GPS device and carcasses were removed from the roadway to avoid double counting. This represented the minimum number of actual DVCs because some mortally wounded deer likely moved out of sight of the highway before dying and were not detected in our surveys. These data are hereafter referred to as the "intensive DVC data set."

From 1995 to 2006, Oregon Department of Transportation maintenance personnel and State highway patrol officers reported and cleared roadway hazards, including mule deer killed by vehicles. Locations of DVCs were estimated by highway personnel to the nearest mile marker (1.6-km precision). Animal carcasses were considered a road hazard, but were not consistently reported. These data are hereafter referred to as the "dispatch DVC data set."

DVC Density

On each study highway, we used the intensive DVC data set to estimate kernel density of DVCs that occurred during peak periods of spring and autumn mule deer migration (Apr–Jun and Oct–Dec). We used a network kernel density function (Okabe and Sugihara 2012) within ArcGIS at a 50-m resolution. Kernel density is a nonparametric technique that fits a specified probability curve over each DVC location using a distance band as criteria for the geographic spread of each curve and results in a probability surface (Worton 1989). Network kernel density assumes events occur on linear segments, producing an estimated density of DVCs along a 1-dimensional linear space (Xia and Yan 2008). We used a distance band of 500 m for kernel estimates based on half the width of the top 5 migration UD class polygons where they crossed the highways, which we hypothesized to be influencing DVCs.

Correlation of DVC density to migration UD.—We spatially intersected DVC kernel density linear segments with migration UD class polygons. We compared DVC kernel density with migration UD class by calculating Pearson's correlation coefficient (*r*) for mean DVC kernel density within each migration UD class. We repeated this analysis using the dispatch DVC data set. We also compared the intensive DVC data set to the dispatch DVC data set using Pearson's correlation coefficient. We calculated mean DVC kernel density across 1.6-km highway segments because the location accuracy of the dispatch DVC data set was relatively coarse (1.6-km positional precision).

DVC Landscape Models

We developed spatial covariates on a 30-m grid within the minimum convex polygon, including tree canopy cover, topographic curvature, distance to development, probability of use during migration, distance to water, and traffic volume. Tree canopy cover (U.S. Department of the Interior 2008) represented vertically projected percent live-canopy layer present in 2008. Some removal of trees along the highway occurred 2008–2012, but we did not account for this in our models. Topographic curvature (Zevenbergen and Thorne 1987) was calculated in ArcGIS from a digital elevation model (Oregon State University 2014) using elevation values of neighboring cells to calculate convexity of terrain surrounding a grid cell. Development zones (Oregon State University 2014) represented existing residential and urban development in 2009. We measured distance to development to the closest development zone. Water sources were stream courses and water bodies (U.S. Department of the Interior 2013), and wildlife "guzzlers" (structures that collect and store rainwater for wildlife use; P. K. Coe, unpublished data). We measured distance to water to the closest water source. Traffic volume was AADT for 2011 (Oregon Department of Transportation 2013). We used AADT with its square to account for an apparent quadratic relationship in which DVCs increased and then leveled off or decreased as AADT increased.

Model development.—Highway 97 and Highway 31 have different habitat and traffic characteristics. Highway 97 bisects summer habitat and is a major north–south highway between California and Washington (USA), whereas Highway 31 is largely winter habitat and is less traveled by vehicles. We therefore built separate models for each highway study section. We used negative binomial regression (Hilbe 2011) to model DVC counts for 500-m highway segments using the intensive DVC data set. We selected 500 m as the segment length to continue the same scale of analysis we used in calculating DVC kernel density. Mean migration UD within 500-m segments was highly skewed, so we log-transformed (base *e*) this covariate to allow for a more linear relationship between it and DVC values, hereafter referred to as Log (UD) (Hooten et al. 2013). Covariates

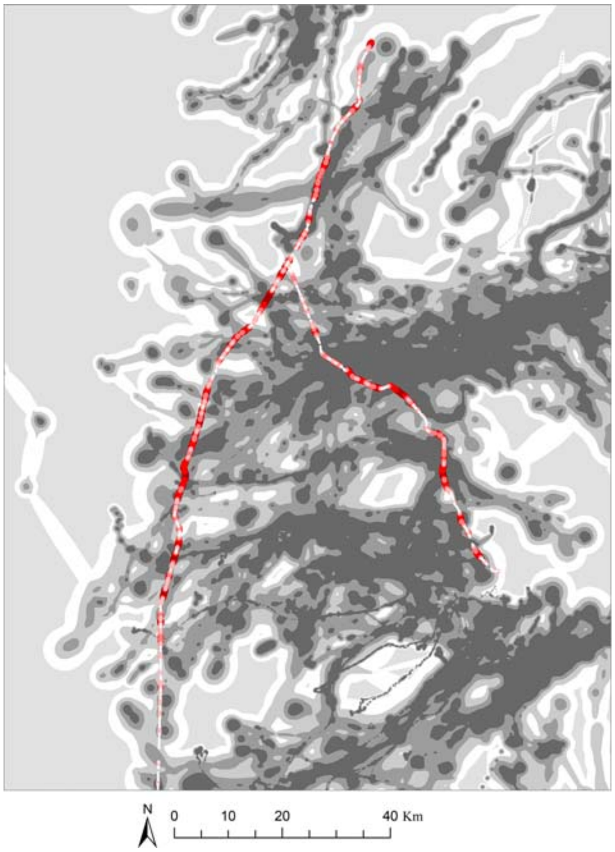

Figure 2. Relative risk of mule deer–vehicle collision (DVC; light pink to dark red = low to high risk of DVC) and probability of use during migration (gray to black = low to high probability of use) on U.S. Highway 97 and State Highway 31 in South-central Oregon, USA. Risk of DVC was calculated from 1,269 spring and autumn DVCs recorded 2005–2010, using a network kernel density estimator. Migration utilization distribution class was equal area classes of cumulative probabilities of use derived from Brownian Bridge Movement Models constructed from 787 migrations (326 autumn, 461 spring) of mule deer ($n = 359$) in South-central Oregon, USA, 2005–2012.

were averaged at 100, 200, and 400 m surrounding each road segment, resulting in 18 covariates (6 covariates at 3 scales). To reduce this set prior to model construction, we analyzed each covariate separately for each buffer class to evaluate the best scale to bring forward for consideration for the multicovariate models. We did not include all possible model combinations, but rather hypothesized *a priori* several plausible model sets. We evaluated competing models using Akaike's Information Criterion adjusted for small sample size (AIC$_c$; Burnham and Anderson 2002). A model was considered competitive if it was within 2 AIC$_c$ units of the top model (lowest AIC$_c$). We calculated Akaike weights (Burnham and Anderson 2002) to assess the relative ranking and significance of each model. We estimated standardized coefficients (Zar 1999) to compare the relative importance of each covariate in predicting DVC counts.

We estimated the spatial autocorrelation in the residuals from the full model (all covariates included) for each highway using Moran's I. If Moran's I was consistently and substantially >0 out to some spatial lag, then standard errors, and thus 90% confidence intervals, of model coefficients could be underestimated (Legendre 1993). Moran's I test of the residuals of the full model for Highway 97 indicated spatial autocorrelation was present but small (correlation <0.3) for pairs of segments up to 30 km apart. There was no evidence of spatial autocorrelation for road segments on Highway 31. Spatial autocorrelation was small or did not exist, so we only report standard CIs for both models.

To assess how well models developed for Highway 97 predicted DVCs, we conducted validation tests using a method outlined by Johnson et al. (2006). This method creates ordinal classes (ranked bins) from predicted values and compares them to observed counts within those same bins. Number of bins used was subjective and we chose 15 bins (10 highway segments/bin). We departed from Johnson et al. (2006) by using a different data set than was used for model-building for a more robust validation, instead of using withheld data. We made predictions for Highway 31 using the 2 highest-ranked models for Highway 97. We sorted predicted use for each 500-m highway segment from low to high and summed observed DVC counts within the 15 sorted predicted use bins. We calculated Spearman's rank correlation coefficients for each model, comparing median predicted DVCs to summed observed DVCs within bins.

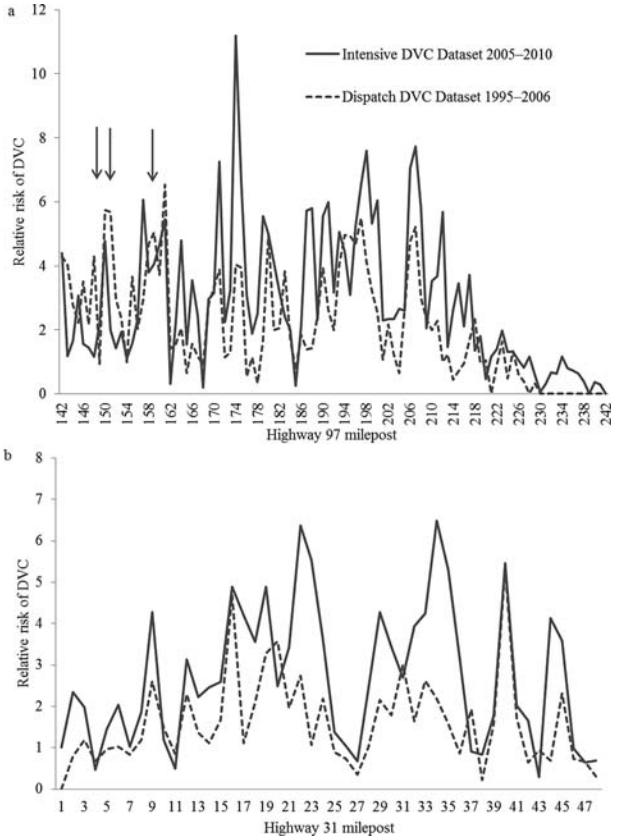

Figure 3. Relative risk of mule deer–vehicle collision (DVC) on 1,600-m (1-mi) highway segments in South-central Oregon, USA, comparing intensive DCV data set (2005–2010, solid lines) and dispatch DVC data set (1995–2006, dashed lines). Highway mileposts are for (a) U.S. Highway 97, and (b) State Highway 31. Arrows indicate where DVC density was higher 1995–2006 than 2005–2010.

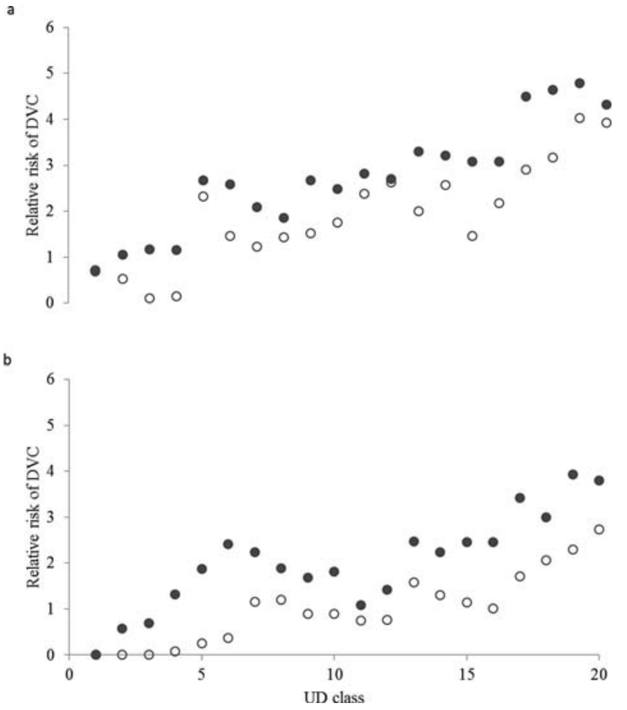

Figure 4. Relationship between utilization distribution class and relative risk of mule deer–vehicle collision (DVC) in South-central Oregon, USA, for (a) U.S. Highway 97, and (b) State Highway 31. Solid circles represent the intensive DVC data (2005–2010, $n = 1{,}269$) and open circles the dispatch DVC data (1995–2006, $n = 897$). Pearson correlation coefficients for intensive and dispatch data sets, respectively, were 0.93 and 0.87 for U.S. Highway 97, and 0.85 and 0.91 for State Highway 31. Utilization distribution (UD) class was relative probability of use during migration calculated from 787 mule deer migrations 2005–2012 using Brownian Bridge Movement Modeling.

We used the same method to evaluate goodness-of-fit of the best model(s) for each highway, comparing predicted to observed DVC counts for Highway 97 based the best model(s) for Highway 97, and predicted versus observed for Highway 31 based on the best model(s) for Highway 31.

To investigate the quadratic effect of AADT in a retrospective analysis, we calculated the value of AADT at maximum DVC (*max*DVC) in the highest ranked model for Highway 97 and examined DVC kernel density and Log(UD) where AADT exceeded this value. Deer may have avoided crossing the highway or abandoned migration routes that crossed the highway where AADT exceeded the threshold and DVC decreased. This effect should be evident in lower DVC kernel density on sections of the highways where AADT > AADT at *max*DVC compared with where AADT < AADT at *max*DVC. To further investigate a barrier effect of Highway 97, we compared the proportion of radiomarked deer that summered west of Highway 97 (whose winter ranges were E of the highway) with the proportion of available summer range west of the highway. For our summer range estimate, we overlaid mule deer summer range (Black et al. 2004) with the study area minimum convex polygon and then divided the resulting polygon, creating 2 polygons of summer range east and west of Highway 97. We compared area of mule deer summer range west and east of the highway within our study area. We also compared proportion of mortality due to DVCs of deer that summered west of the highway to the overall radiomarked DVC mortality.

RESULTS

We captured and placed GPS collars on 492 mule deer (395 and 97 on winter and summer range, respectively; Fig. 1). Overall adult mortality was 32.9% and, of those, DVC mortalities accounted for 10.0%, which was roughly equivalent to mortality caused by legal hunting (11.0%) and illegal kills (13.0%). Six radiomarked deer were killed by vehicles on Highway 97 and 3 were killed on Highway 31.

Brownian Bridge Movement Models

We identified 359 radiomarked adult female mule deer that migrated from their capture location, and estimated UDs for 787 migration routes (326 autumn, 461 spring). Average fix-rate success was 88% (SD = 0.10) and standard deviation of location error was 37 m. Brownian motion variance was $5{,}622 \pm 4{,}558\ \mathrm{m}^2$ (mean ± SE). We excluded 69 migration sequences on account of sequences either having fewer than 10 locations or Brownian motion variance >20,000. Values for migration UD along the study highways were highest along 13 km of Highway 31 southeast of La Pine where deer concentrated on winter range (Fig. 2). In contrast, migration routes were narrower on Highway 97 where deer dispersed to summer range.

Of the 787 migrations used in the UD analysis, there were 287 crossings by 102 deer of Highway 97 and/or Highway 31

Table 1. Mean number of mule deer–vehicle collisions (DVC) and covariate metrics on 500-m segments of U.S. Highway 97 ($n = 325$) and State Highway 31 ($n = 155$) in South-central Oregon, USA, 2005–2010. "Tree canopy cover" was mean percent live tree cover within 100 m of highway. "Topographic curvature" was mean convexity of terrain within 200 m of the highway. "Distance to development" was mean distance (m) to residential or urban development within 100 m of highway. "Log probability of use" was natural log mean cumulative probability of use by mule deer during spring or autumn migration within 400 m of highway. "Distance to water" was mean distance (m) to stream course, water body, or wildlife guzzler within 100 m of highway. "Annual average daily traffic" was mean annual average count of all vehicles/day.

	DVC count		Tree canopy cover		Topographic curvature		Distance to development		Log probability of use		Distance to water		Annual average daily traffic	
Hwy	**97**	**31**	**97**	**31**	**97**	**31**	**97**	**31**	**97**	**31**	**97**	**31**	**97**	**31**
Mean	2.71	2.51	18.1	9.4	−0.002	−0.003	3,012	11,902	1.00	2.15	1,934	1,392	6,218	870
Min.	0	0.0	0.0	0.0	−0.043	−0.050	0	0	−4.61	−4.61	131	5	1,380	660
Max.	14	8	45.4	31.1	0.052	0.028	12,948	28,239	5.73	5.85	7,944	5,246	19,800	4,225
SD	2.71	2.04	9.90	9.70	0.0086	0.0106	3,240	9,040	1.90	1.91	1,584	1,174	3,862	370

Table 2. Model selection results from an analysis of factors affecting mule deer–vehicle collisions on U.S. Highway 97 and State Highway 31 in South-central Oregon, USA, 2005–2010. Models are ranked 1–8 based on Akaike's Information Criterion with small sample size correction (AIC$_c$). A change of <2.00 AIC$_c$ units indicate competitive models and AIC weights indicate relative strength of models. We report differences between AIC$_c$ and that of the top model (ΔAIC), and Akaike's weight (AIC wt).

	Rank		ΔAIC$_c$		AIC wt	
Model[a]	**97**	**31**	**97**	**31**	**97**	**31**
Cc + Curv + Ddev + Log(UD) + Dwater + AADT + AADT^2	1	1	0.00	0.00	0.746	0.703
Log(UD)	2	2	2.78	2.10	0.185	0.246
Log(UD) + AADT + AADT^2	3	3	4.77	5.25	0.087	0.051
Cc + Curv + Ddev + Dwater	4	5	25.5	21.48	<0.000	<0.000
Ddev + Dwater	5	4	31.4	19.35	<0.000	<0.000
AADT + AADT^2	6	6	32.0	23.78	<0.000	<0.000
Cc + Dwater	7	8	32.1	25.92	<0.000	<0.000
AADT	8	7	34.5	29.46	<0.000	<0.000

[a] Cc = percent canopy cover, Curv = topographic curvature, Ddev = distance to development, Log(UD) = log probability of use during migration, Dwater = distance to water, AADT = annual average daily traffic, AADT^2 = squared term for AADT, indicating a quadratic relationship to deer–vehicle collisions.

study sections. Of those, 48 deer crossed Highway 97 105 times and 82 deer crossed Highway 31 182 times. Twenty-eight deer crossed both highways during a single migration.

Deer–Vehicle Collisions

There were 1,901 DVCs recorded in the intensive DVC data set and 1,369 DVCs recorded in the dispatch data set. Spring and autumn DVCs were 67% of the year-round total DVCs ($n = 1,269$) recorded in the intensive DVC data set and 63% of year-round total ($n = 867$) recorded in the dispatch data set. For the intensive data set, mean spring and autumn DVC counts were 5.5/km and 4.9/km for Highways 97 and 31, respectively. For the dispatch data set, mean total spring and autumn DVC counts were 4.0/km and 2.9/km for Highways 97 and 31, respectively. One DVC was a radiomarked deer used in the UD analysis.

Mean DVC kernel density (relative risk of a DVC occurring) for the intensive data set was 3.4 and 3.0 for Highways 97 and 31, respectively (Fig. 2); and for the dispatch data set, it was 2.2 and 1.7 for Highways 97 and 31, respectively. Inspection of DVC kernel density by highway milepost revealed that dispatch data had lower peaks than did intensive data for both highways, with the exception of mileposts 149, 151, and 159 on Highway 97 (Fig. 3, arrows), where DVC kernel density of the dispatch data was higher.

For the intensive DVC data set, there was a strong, positive correlation between mean DVC kernel density and migration UD class for Highway 97 ($r = 0.93$) and Highway 31 ($r = 0.87$; Fig. 4). For the dispatch DVC data sets, the correlation also was strong for Highway 97 ($r = 0.85$) and Highway 31 ($r = 0.91$; Fig. 4). There was moderate positive correlation between mean DVC kernel density/1,600-m highway segment for the intensive and dispatch DVC data sets for Highway 97 ($r = 0.40$) and for Highway 31 ($r = 0.40$).

DVC Landscape Models

xBased on AICc scores that evaluated buffer distances around highway segments for summarizing landscape covariates, we used 100-m buffers for canopy cover, distance to development, and distance to water; and 400 m for Log(UD); and a 200-m buffer for topographic curvature (Table 1). Deer–vehicle collision counts/500-m highway segment ranged from 0 to 14 ($\sum = 880$ DVCs, $n = 325$ segments) for Highway 97 and 0 to 8 ($\sum = 389$ DVCs, $n = 155$ segments) for Highway 31.

The top 3 models for both highways were the full, Log (UD) only, and Log(UD) plus AADT models (Table 2). The full models received 75% and 70% of model weights for Highway 97 and Highway 31, respectively (Table 2);

Table 3. Nonstandardized and standardized parameter estimates for covariates in the highest-ranked models of factors affecting mule deer–vehicle collisions on U.S. Highway 97 and State Highway 31 in South-central Oregon, USA, 2005–2010. Confidence intervals are for standardized coefficients.

	Highway 97				Highway 31			
Covariate[a]	**Coeff.**	**Standardized coeff.**	**Lower 95%CI**	**Upper 95%CI**	**Coeff.**	**Standardized coeff.**	**Lower 95%CI**	**Upper 95%CI**
Intercept	7.717e − 01				−2.853e + 00			
Cc	5.012e − 03	0.050	−0.069	0.168	−2.410e − 02	−0.234	−0.416	−0.052
Curv	−1.785e + 01	−0.154	−0.261	−0.047	2.362e + 00	0.025	−0.092	0.143
Ddev	−4.160e − 05	−0.135	−0.257	0.012	1.903e − 05	0.175	0.059	0.291
Log(UD)	1.683e − 01	0.340	0.205	0.434	1.994e − 01	0.369	0.206	0.532
Dwater	−6.415e − 05	−0.102	−0.225	0.021	−1.083e − 05	−0.013	−0.149	0.123
AADT	3.922e − 05	0.152	−0.382	0.685	6.549e − 03	1.668	−0.155	3.491
AADT^2	−2.499e − 09	−0.177	−0.707	0.353	−2.928e − 06	−1.557	−3.372	0.259

[a] Cc = canopy cover, Curv = topographic curvature, Ddev = distance to development, Log(UD) = log probability of use during migration, Dwater = distance to water, AADT = annual average daily traffic, AADT^2 = squared term for AADT, indicating a quadratic relationship to deer–vehicle collisions.

however, some covariates influenced DVCs differently for each highway as evidenced by signs of model coefficients (Table 3). Highway 97 DVCs increased with increasing tree canopy cover and concave topography (slope rises from roadside), and decreased as distance to development and water increased. Conversely, Highway 31 DVCs increased as distance to development increased and as convex topography (slope declines from roadside) increased, and DVCs decreased with decreasing tree canopy cover (Table 3). Of the 3 highest-ranked models, 2 included the squared term for AADT, indicating a quadratic relationship to DVCs.

For model validation, Spearman rank correlation coefficients comparing predicted to observed DVC counts indicated that the highest-ranked model for Highway 97 performed poorly when applied to Highway 31 ($r_s = 0.135$; Fig. 5a). However, there was strong positive correlation for the second-ranked Log(UD)-only model ($r_s = 0.904$; Fig. 5b).

Focusing on the barrier effect of traffic on Highway 97, the value of AADT at *max*DVC in the highest ranked Highway 97 model was 7,847 (Table 3) and AADT exceeded this value on Highway 97 between Bend and its intersection with Highway 31 (Fig. 6). Most migration corridors along this section paralleled the eastern side of Highway 97 where deer migration routes were apparently diverted south because of increasing AADT (Fig. 6). Of 298 deer that wintered east of Highway 97, 48 (16.1%) crossed Highway 97 during migration to summer range. However, 45% of available summer habitat was west of Highway 97 (9,000 km^2 of 20,000 km^2; Fig. 7). Of the 359 deer in our migration analysis, 4 died because of DVC (1.1%). Two of these mortalities were deer that summered west of Highway 97 and died because of DVC (4.2%).

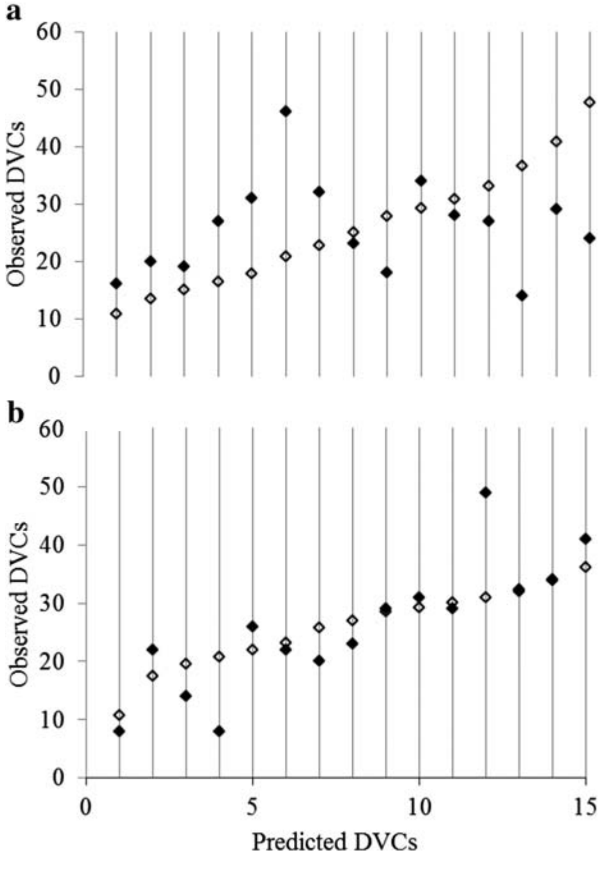

Figure 5. Out-of-sample validation results for 2 highest-ranked mule deer–vehicle collision (DVC) models developed for U.S. Highway 97 and applied to State Highway 31, Oregon, USA. Open symbols are predicted DVCs and closed symbols are observed DVCs within bins of increasing predicted DVCs for (a) highest-ranked full, and (b) Log(UD)-only model (Table 2). Spearman rank correlation coefficients for predicted versus observed DVC densities were 0.135 for the full model and 0.904 for the Log(UD)-only model.

DISCUSSION

Predicting DVCs in regions where migratory ungulates exist is critical to planning passage structures for future highway construction (Seidler et al. 2014). We found mule deer migration corridors to be the strongest predictor compared with other biophysical predictors of DVCs on 2 highways in eastern Oregon. We know of no other study linking migration corridors to DVCs in western North America. Our study provides a strong argument for the use of migration corridor data for planning wildlife passage structure sites.

Density of deer–vehicle collisions may be an excellent proxy for identifying high-use mule deer migration corridors that cross existing highways. Our dispatch data set, which represented DVCs recorded during routine traffic maintenance during the 10 years prior to our study, was highly correlated to migration UD class. Snow et al. (2015) found that underreporting of wildlife–vehicle collisions did not hinder predictive models of vehicle collisions for large ungulates. Our dispatch DVC data set was only moderately correlated with the intensive DVC data set, probably because of the coarser resolution of the dispatch data set compared with the intensive data set. Thus, routine highway data may be a suitable estimate of migration corridors, but we suggest collection at a finer scale.

Previous research has recommended wildlife passage structures be spaced regularly at approximately 1-mile (1.61-km) intervals (Bissonette and Adair 2008, Clevenger and Ford 2010). Sawyer et al. (2012) monitored regularly spaced mule deer passage structures in Wyoming, USA, and found disproportionate use by mule deer, and they hypothesized that passage structures with the greatest mule deer use were near migration corridors. Our study supports that hypothesis, and the implications are that passage structures may be spaced irregularly and still be effective, along with being more cost-effective, at least for allowing safe passage for migrating mule deer.

Migratory pathways of mule deer span disparate habitats from high-elevation forested summer range to low-elevation sagebrush steppe (Zalunardo 1965), and consequently landscape attributes at road and highway crossings vary widely, depending upon the habitat. We found that landscape attributes improved models on each highway but were inconsistent in their influence on DVC density between the 2 highways. Some of this inconsistency could

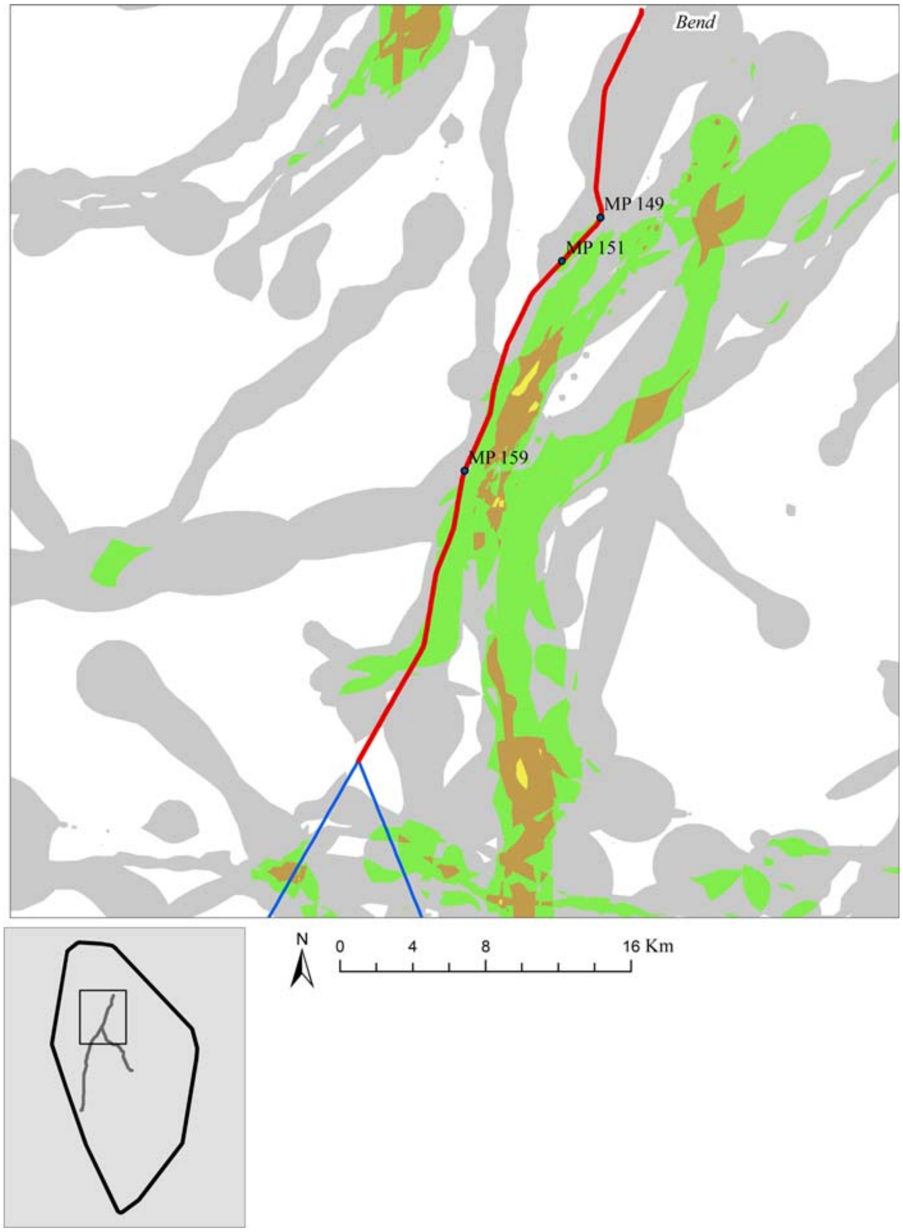

Figure 6. Number of radiomarked mule deer using migration corridors along Highway 97 2005–2012 where annual average daily traffic (AADT) exceeded 8,000 (heavy red line). Colors indicating number of mule deer are gray (1–2), green (3–4), brown (5–6), and yellow (7–8). Mule deer may have diverted from traditional migration paths because of high traffic. Mileposts 149, 151, and 159 are where deer-vehicle collisions (DVCs) were higher 10 years previous to this study, when AADT was below *max*DVC.

have been due to management by the Oregon Department of Transportation that we could not incorporate into our models. For example, from 2008 to 2012, the Oregon Department of Transportation removed trees along parts of both our study highways, which may have resulted in a weaker effect of canopy cover on DVCs. However, virtually all studies that have found roadside landscape predictors useful for predicting DVCs have been for nonmigratory white-tailed (*Odocoileus virginianus*) or roe deer (*Capreolus* spp.) in Europe (Gunson et al. 2011). Migratory mule deer exhibit strong fealty to their migration pathways (Russell 1932, Sawyer et al. 2009), which are determined by larger scale landscape features (Thomas and Irby 1990, Hebblewhite et al. 2008, Sawyer and Kauffman 2011) that may largely eclipse the influence of roadside landscape features.

Ungulate migration pathways could change or be eliminated over time because of changing landscape conditions or increasing traffic (Seidler et al. 2014). We found evidence of redirection of migrating mule deer, probably because of increasing traffic, on Highway 97. First, we found a quadratic effect of AADT on DVCs, indicating a threshold whereby DVCs declined. Previous researchers have found AADT thresholds on animal–vehicle collisions (Wang et al. 2010) and moose (*Alces alces*)–vehicle collisions (Seiler 2005). Second, we observed migration corridors that

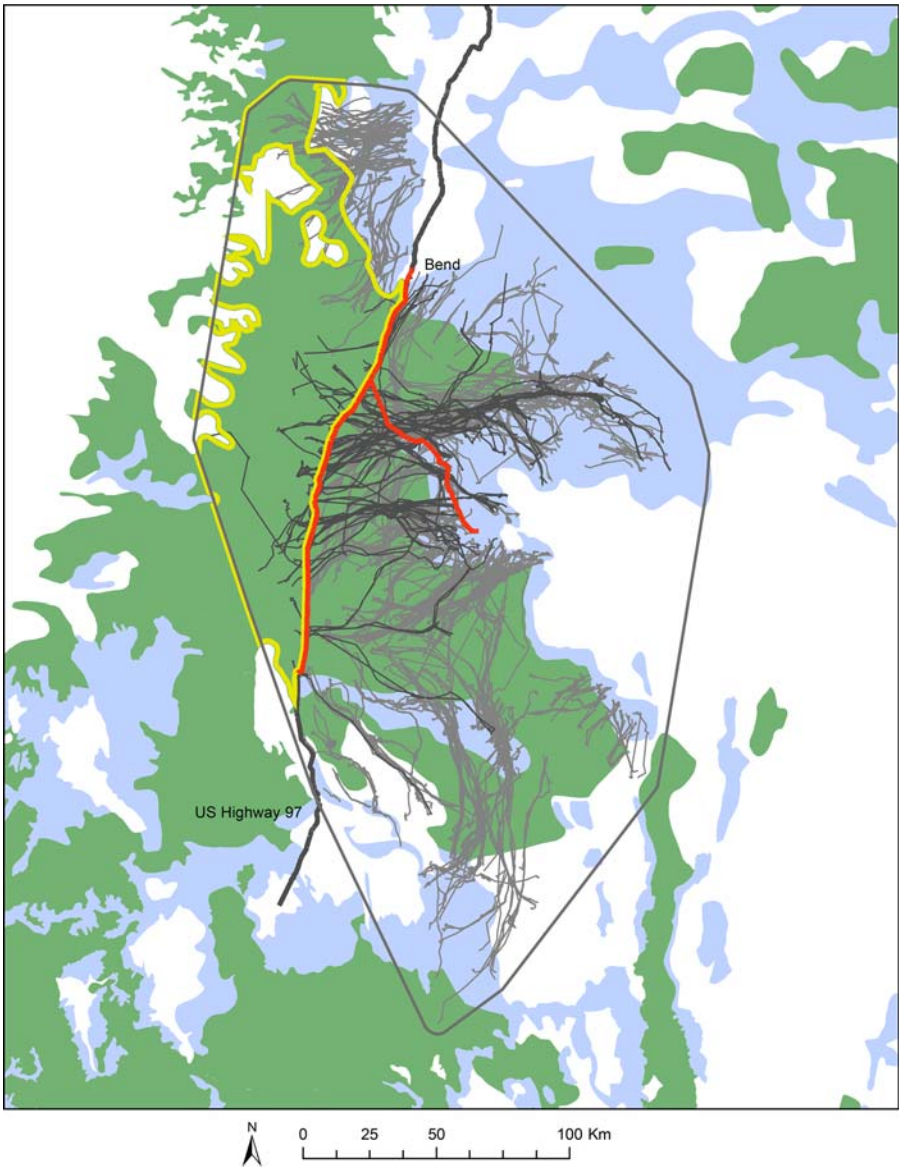

Figure 7. Summer range of mule deer west of U.S. Highway 97 in South-central Oregon, USA (2005–2012), was 45% of total summer range within the minimum convex polygon (yellow highlighted polygon) but only 16.1% of deer whose winter ranges were east of Highway 97 migrated to summer range west of the highway. Migration routes used in our analysis are represented by black (those that crossed Highway 97) and dark grey lines. Winter range is represented in light blue and mule deer summer range in forest green.

paralleled Highway 97 where AADT exceeded *max*DVC, indicating deer were seeking a less busy place to cross. Third, we observed a drop in DVCs from 10 years previous where AADT exceeded *max*DVC. Thus, our study links high traffic levels to changes in migration corridors of mule deer.

In the past, more deer likely successfully migrated to the west of Highway 97 to take advantage of the higher elevation summer habitat in the Cascade Range (Zalunardo 1965, Cupples and Jackson 2014). Mule deer that crossed Highway 97 were at higher risk of direct mortality from a DVC. Our data indicated disproportionate lower use of summer habitat by mule deer west versus east of Highway 97, with substantially fewer deer summering west of Highway 97 than we would expect given the available habitat. We have no evidence to suggest that mule deer summer habitat differed east and west of Highway 97, although large-scale habitat changes have occurred in this region (Peek et al. 2001). Further work is needed to investigate mule deer summer populations east and west of Highway 97.

Studies of migratory animals worldwide are becoming more common because of lower costs of GPS collars and new techniques for analyzing migration data (Bolger et al. 2008, Sawyer et al. 2009). Careful preplanning of animal capture to ensure adequate representation of the entire population is important to ensure a comprehensive migration GIS layer that is highly useful for wildlife planning and management. Our study represented the entire population of mule deer in South-central Oregon and therefore identified the most used migration corridors in the region. Consequently, our migration corridor UD is of high management utility not only for transportation management but for wildlife management across the region.

MANAGEMENT IMPLICATIONS

Societal infrastructure of highways and railroads is being upgraded to handle faster and higher traffic volumes throughout the world. The strong positive correlation of DVCs to mule deer migration corridors is a providential one for managers that helps in the siting of passage structures for both new and existing highways. For new highways, migration corridors may be identified by radiomarking mule deer prior to construction and using our techniques to estimate probability of use by deer of corridors during migration. Managers attempting to maintain migratory corridors on existing highways should focus mitigation measures where DVCs are highest and, secondarily, where AADT is highest. Restoration of lost migration routes across existing highways may require delving into historical records of mule deer migration or DVCs.

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