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Source: Wildlife Biology, 21(2) : 80-87

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00043
How does variation in winter weather affect deer–vehicle collision rates?

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Understanding how deer (Cervidae) move in relationship to roads is critical for wildlife and transportation management, because deer frequently are involved in vehicle collisions throughout much of the developed world (Groot Bruinderink and Hazebrrok 1996, Conover 2001, Noro 2010). In the United States alone there are 1–2 million vehicle collisions with large animals annually, resulting in more than 8 billion dollars in economic costs; the majority of these accidents involve deer (Huijser et al. 2008). Deer–vehicle collisions (DVCs) not only can cause vehicle damage (Bissonette et al. 2008), but occasionally vehicle occupants are injured and in rare cases killed (Conover et al. 1995, Langley et al. 2006). Vehicle collisions are nearly always fatal for the deer (Allen and McCullough 1976).

Mule deer *Odocoileus hemionus* occur throughout much of western North America and are commonly involved in vehicle collisions (Reed 1981, Peterson and Messmer 2011, Bissonette and Rosa 2012). In temperate climates, most mule deer populations are migratory (Gruell and Papez 1963, Kucera 1992, Sawyer et al. 2009) and have distinct seasonal movement patterns that can affect their spatial distribution in relationship to roads (Stewart et al. 2010). For example in summer, deer typically use high elevation ranges with abundant resources (Boecker et al. 1972) that generally are farther from high-volume roads (Stewart et al. 2010). In early to late fall, mule deer generally move from high elevation summer ranges, largely in response to seasonally declining resource quality and snow accumulations that inhibit movement and decrease forage availability (Parker et al. 1984). Mule deer winter ranges are usually lower in elevation and occur on southern aspects that have lower snow accumulations (Gilbert et al. 1970, Garrott et al. 1987). Many roads are located on or near deer winter ranges, and deer may be closer to high-volume roads during winter in some landscapes (Reed 1981).

Variation in the seasonal and annual movement patterns of deer can produce marked changes in DVCs (Mysterud 2004, Sullivan 2011). A common seasonal pattern that has been observed for both mule deer and white-tailed deer *Odocoileus virginianus* is a rise in DVCs during spring and fall when deer transition between summer and winter ranges (Case 1978, Biggs et al. 2004, Grovenburg et al. 2008). Additionally, Reed and Woodard (1981) observed that DVC rates for mule deer appeared to vary annually in response to changes in winter conditions. Mule deer typically exhibit a high degree of fidelity to summer ranges (Thomas and Irby
1990, Kucera 1992), but the use of winter ranges may vary between years depending on winter conditions (Garrott et al. 1987, Brown 1992). For example, in southern Idaho during a mild winter only 52% of deer returned to the same winter range they used the previous year (Brown 1992). The use of different wintering areas between years may cause variation in the exposure of deer to high-volume roads.

Deer–vehicle collision rates are not only affected by movement patterns but also by deer abundance and traffic volumes on roads (Jahn 1959, Sullivan 2011, Rolandsen et al. 2011). Additionally, speed limit and road edge clearance have been implicated for cervids (Meisingset et al. 2014), while anthropogenic activity appears to influence elk Cervus elaphus activity patterns in North America but not mule deer (Barruetot et al. 2014). Collision rates have been shown to be associated with abundance for both red deer Cervus elaphus and mule deer (Romin and Bissonette 1996b, Mysterud 2004). For white-tailed deer, DeNicola and Williams (2008) observed a proportional decrease in DVCs by experimentally reducing deer abundance. DVC rates are also affected by traffic volume on roads (Romin and Bissonette 1996b, Ng et al. 2008). Collision models have indicated that traffic volume is one of the most important predictors of DVCs (Litvaitis and Tash 2008), and high DVC rates have been reported on roads with high traffic volumes (Romin and Bissonette 1996b). Alternatively, roads with low traffic volumes appear to have a limited effect on deer survival, even if they frequently cross these roads (Hansen et al. 2012). Consequently, it is important to consider the type of road and its traffic volume when examining effects on deer movements and collision rates (Neumann et al. 2012, Sawyer et al. 2013).

An understanding of how deer move in response to annual changes in weather is key to understanding variation in DVC rates in temperate climates (Rolandsen et al. 2011). In this paper, we analyzed mule deer movements during two consecutive winters with vastly different conditions to determine what effect weather had on DVC rates. We predicted that DVC rates would rise when precipitation and snow depth increased, because deep snow restricts deer movements to low elevation habitats that may increase exposure to high volume roads. We monitored deer movements to document road crossing rates, distance of deer to roads and elevation use during both winters. We used meteorological data to describe temperature, precipitation and snow depth in the study area. We also documented changes in deer abundance and traffic volumes, which were potentially confounding variables.

Methods

Study area

The study area (8278 km²) was located on the western edge of the Rocky Mountains in central Utah (Fig. 1). Topography in this area was mountainous and highly variable (1463–3415 m). The climate was temperate; typical summer temperatures were > 22°C and winter temperatures were < 0°C (UCCW 2013). Precipitation occurred during all months of the year, but during most years, peaks in precipitation occurred during spring and fall. Total precipitation (203–406 mm) was variable between years (UCCW 2009, 2013). The majority of the study area consisted of the Wasatch Mountains ecoregion, but its eastern edge encompassed a small portion of the Colorado Plateau (Griffith and Omernik 2011). A variety of land cover types (> 40) existed within the study area, but aspen Populus tremuloides, Gambel oak Quercus gambelii and sagebrush Artemisia spp. were relatively common (Lowry et al. 2005). Mule deer, elk and a limited number of moose Alces alces occurred within the study area (Bernales et al. 2011).

Roads were common throughout the rural study area (Fig. 1), but most had low (< 500 vehicles day⁻¹) traffic volumes (UDOT 2012). However, there were a few roads with higher traffic volumes. For example US 6, a major east–west route in Utah, bisected the center of the study area (Fig. 1). Traffic volumes on US 6 within the study area were ∼9000 vehicles day⁻¹ and speed limits varied between 72–105 km h⁻¹ (UDOT 2012). In 2005, data showed that US 6 had the sixth highest number of DVCs in the state (Kassar and Bissonette 2005). To improve safety for motorists and deer, four wildlife crossing structures and 26 km of intermittent, exclusionary fencing (2.4 m high) were installed in 2008–2009 on US 6 within the study area. While most mitigation was in place prior to this study, one wildlife crossing structure (MP 204) and ∼6 km of wildlife fencing were installed in 2011 during the study. Prior to installation, 6–7% of deer carcasses reported during winter occurred within that section of highway (MP 202-205). Consequently, the project may have had a minor impact on the results reported in this paper, but was likely not the major driver of the pattern we observed.

Winter conditions

Precipitation and temperature often are used to describe weather conditions (i.e. short-term patterns) and climate (i.e. long-term averages or normals) of areas (NOAA 2014). To document weather and climate during winter, we obtained temperature, precipitation, and snow depth data from weather stations that were located throughout the study area (Fig. 1). Temperature and precipitation data were provided by the National Climatic Data Center (NCDC 2013), and snow depth data were provided by the National Water and Climate Center (NWCC 2013). We defined the winter season as 1 December–31 March. We calculated temperature and precipitation normals by averaging annual winter data for 1981–2012, which was the range available for most weather stations in the study area. The snow depth normal represented a shorter temporal range (2003–2012) due to the limited data available for that variable. Temperature data were reported as the mean monthly temperature and precipitation data were reported as total precipitation for the winter season. Snow depth data represented the mean daily snow depth for the winter season.

We compared temperature, precipitation, and snow depth between winters using paired t-tests (α = 0.05). When data did not meet the assumptions of the parametric t-test, we used the nonparametric Wilcoxon rank-sum test. We used the same approach for all comparisons in the paper, except for DVC data. When we compared differences in DVC
data between winters, we used $\chi^2$-tests. All statistical tests were performed in R ver. 2.14 (<www.r-project.org/>) and were purposely kept uncomplicated to increase the clarity of the results, as recommended by Guthery (2008).

Traffic volumes and deer abundance

Traffic volume data were obtained from the Utah Department of Transportation (UDOT) for the study area (UDOT 2012). Traffic volumes for roads were reported by UDOT as average annual daily traffic during each calendar year. We categorized roads as US 6, major roads and minor roads. Major roads were defined as having traffic volumes $\geq 500$ vehicles day$^{-1}$. Minor roads were defined as having $< 500$ vehicles day$^{-1}$ or roads that were unmonitored for traffic volume. We considered US 6 separately from other major roads because it had the highest traffic volumes of all roads within the study area, and because it has been the focus of DVC mitigation for several years.

Mule deer abundance was estimated annually by the Utah Division of Wildlife Resources (UDWR). During the study period, the UDWR collected survival, harvest, recruitment, and population structure data and used POP-II to model deer abundance within management units (Bernales et al. 2011). The modeling process did not include estimates of uncertainty. We used management unit totals to estimate the number of mule deer within our study area by weighting totals by the proportion of the management unit area that occurred within the boundaries of our study area.

Deer movements and survival

To document the movements and survival of deer in relationship to roads, 32 adult ($> 2$ years) female mule deer were captured on winter ranges in the US 6 corridor (Fig. 1). Contractors employed by the UDWR captured deer using a standard helicopter and net gun technique.
Using ArcGIS 10.1, we estimated road crossing rates (crossings week$^{-1}$) by overlaying each animal’s movement path on a current road layer obtained from the Utah Automated Geographic Research Center (Utah AGRC 2012). Road crossing rates represent minimum estimates because the interval between locations was long enough that deer could have moved back and forth across roads without being detected.

We also documented elevation use by deer and distance that deer occurred from roads. Elevation for each location was recorded by the GPS collar. We used ArcGIS 10.1 to measure the Euclidean distance between deer locations and roads. When comparing differences between winters, we considered the individual animal as the experimental unit (Sawyer et al. 2006, 2009).

We estimated winter survival rates (1 December – 31 March) for deer using a known-fate analysis in Program Mark 6.1 (Cooch and White 2013). We fit models with crossing rates, distance to roads, and year, and compared them to an intercept-only model using Akaike information criterion (AIC) (Akaike 1973) with a correction for small sample sizes (Burnham and Anderson 2002). When nested models were separated by < 2 AIC, points and differed by only one parameter, we considered the model with an additional parameter as noncompeting and did not report it (Arnold 2010).

Deer–vehicle collisions

To index the number of DVCs that occurred on roads within the study area, we used carcass survey data that were collected by UDOT contractors. Carcass surveys have been conducted in Utah since at least 1998 (Bissonette and Rosa 2012). Surveys were performed using automobiles that were driven at posted speed limits by a single observer. During surveys, contractors were required to remove all carcasses that were detected on the road surface and the road shoulder. Contractors kept detailed records of deer carcass locations using GPS. Double-counting of deer carcasses was unlikely because reported carcasses were also removed from roads and deposited at local landfills. Within our study area, carcass surveys were conducted on US 6 and all major roads, but not on minor roads. DVC estimates from carcass surveys represent minimum estimates, because carcass survey totals have not been corrected for bias (e.g. detection, carcass persistence).

Results

Winter conditions

Data on winter conditions were collected from 12 weather stations throughout the study area (Fig. 1). Mean elevation of weather stations was 2484 m (n = 12, SD = 293). Normal winter temperature for the study area was $-4.9\, ^\circ\text{C}$ (n = 384, SD = 8.4). Normal precipitation was 226 mm (n = 384, SD = 52), and normal snow depth was 891 mm (n = 50, SD = 359). Compared to normal conditions, temperatures during both winters were warmer (Fig. 2). However, precipitation and snow depth were both below normal during 2010–2011, but above normal during 2011–2012. When we compared the two winters to each other, temperature ($t = -11.89$, DF = 10, p = $< 0.001$), precipitation ($t = 3.16$, DF = 7, p = 0.016), and snow depth ($t = 9.76$, DF = 5, p = $< 0.001$) all differed significantly. The extent of the difference in weather conditions between winters was biologically meaningful; temperatures were 28% warmer (+ 1.1$\, ^\circ\text{C}$), precipitation was 50% less (~138 mm), and snow depths were 48% lower (~568 mm) during 2011–2012.

Traffic volumes and deer abundance

Traffic volumes on US 6 ($t = 0.11$, DF = 12, p = 0.915) and major roads ($t = -0.32$, DF = 61, p = 0.752) did not differ between years. Mean traffic volume for US 6 was 9216...
vehicles day\(^{-1}\) (\(n = 27\), SD = 1965) and for major roads it was 3625 vehicles day\(^{-1}\) (\(n = 124\), SD = 3214). According to population estimates, mule deer abundance within the study area was 31 145 animals in 2010–2011 and 28 911 animals in 2011–2012, which represented a 7% decrease between years. There was also a marginal decrease (\(-3\%)\) in mule deer abundance throughout the state.

**Deer movements and survival**

To document movements and survival of mule deer, 31 adult female deer were captured in December 2010 and one additional deer was captured in January 2011 (Fig. 1). The mean distance of deer capture locations to US 6 was 3.5 km (\(n = 32\), SD = 3.9 km). GPS collars acquired spatial coordinates on 89\% (\(n = 40 787\)) of programmed attempts (\(n = 40 787\)), and 87\% of locations were 3D, indicating horizontal location error was generally \(< 20\) m (Di Orio et al. 2003, Sawyer et al. 2009). From GPS movement data, we estimated crossing rates of deer on roads within the study area (Fig. 3). Crossings rates deceased 96\% between winters on US 6 (\(\chi^2 = 663\), \(p < 0.001\)). Crossing rates also decreased on major roads (\(-72\%)\) and on minor roads (\(-12\%)\) between winters, but differences were not statistically significant (major roads, \(\chi^2 = 464\), \(p = 0.56\); minor roads, \(\chi^2 = 462.5\), \(p = 0.81\)).

There were also marked changes in habitat use by deer. Elevation use differed between winters (\(t = -8.62\), DF = 29, \(p < 0.001\)). Deer occurred at a mean elevation of 1843 m (\(n = 32\), SD = 224 m) during winter 2010–2011, but moved an average of 302 m (16\%) higher in elevation during winter 2011–2012 to 2145 m (\(n = 32\), SD = 182 m). Deer also occurred 55\% farther from all roads during the second winter, but distance varied by road type. Deer were 213\% (3.8 km) farther from US 6, 21\% (1.6 km) farther from major roads, 42\% (0.3 km) farther from minor roads compared to winter 2011–2012 (Fig. 4). The distance that deer occurred from US 6 (\(W = 112.0\), \(p < 0.001\)) and major roads (\(W = 301.5\), \(p < 0.001\)) differed significantly between winters, but we did not detect a difference for minor roads (\(W = 415.0\), \(p = 0.364\)).

When we modeled survival for road and year effects, we found that crossing rate by deer on US 6 was the top predictor of survival (Table 1). According to model predictions, \(> 1.2\) crossings week\(^{-1}\) began to substantially reduce deer survival (Fig. 4); although there was considerable uncertainty in survival estimates. Crossing rate on minor roads also had limited support (13\% of model weight). However, it is unlikely that crossing minor roads is an actual driver of deer survival, because minor roads have low traffic volumes and few DVCs occur on these roads.

**Deer–vehicle collisions**

The number of deer carcasses reported on roads that were surveyed within the study area decreased 75\% (234 carcasses) between 2010–2011 and 2011–2012. Additionally, the number of carcasses reported on US 6 (\(\chi^2 = 140\), DF = 1, \(p = < 0.001\)) and major roads (\(\chi^2 = 24\), DF = 1, \(p = < 0.001\)) differed significantly between winters. Reported carcasses decreased 91\% (168 carcasses) on US 6 and 52\% (66 carcasses) on major roads (Fig. 3). Furthermore, the number of reported carcasses in Utah differed between winters (\(\chi^2 = 760\), DF = 1, \(p = < 0.001\)), with 73\% (1316 carcasses) fewer carcasses reported during 2011–2012, indicating a statewide trend.

**Discussion**

Deer–vehicle collisions are a significant management and conservation challenge in landscapes that have been altered...
by humans (Neumann et al. 2012). The rate at which DVCs occur is spatially and temporally variable (Biggs et al. 2004, Kassar and Bissonette 2005), and understanding the source of this variation is the key to effective mitigation that will enhance driver safety and reduce deer mortality. Our purpose in conducting this study was to examine how natural variation in weather during winter influenced deer distribution, movement patterns and DVC rates.

The study encompassed two consecutive winters during which weather conditions differed considerably. During the first winter, the study area was slightly warmer than average but had above average precipitation and snow depths. Alternatively during the second winter, precipitation and snow depth were below average, and temperatures were even warmer. This created a stark contrast in the amount of snow cover on the landscape, because on average snow depths were higher during that period compared to the previous winter.

Table 1. Results of model selection (AICc and ΔAICc), model weights (wi), and number of estimated parameters (K) for models of mule deer survival in relation to various road-related covariates during the winters of 2010–2011 and 2011–2012 in central Utah, USA. Deer crossing rate on US 6 was the highest supported model. Crossing rate on minor roads also had support but was likely not a substantial driver of deer survival, because minor roads had low traffic volumes and few deer–vehicle collisions.

| Model structure                  | AICc  | ΔAICc | wi  | K  |
|----------------------------------|-------|-------|-----|----|
| Crossing US 6                    | 23.72 | 0.00  | 0.28| 2  |
| Crossing minor roads             | 25.27 | 1.55  | 0.13| 2  |
| Distance to major roads          | 26.89 | 3.17  | 0.06| 2  |
| Crossing US 6 + Distance to US 6 + Year | 26.99 | 3.28  | 0.05| 4  |
| Distance to minor roads          | 27.44 | 3.72  | 0.04| 2  |
| Distance to US 6                 | 28.58 | 4.86  | 0.02| 2  |
| Year                             | 29.13 | 5.41  | 0.02| 2  |
| Intercept                        | 29.88 | 6.16  | 0.01| 1  |
| Crossing major roads             | 31.69 | 7.97  | 0.01| 2  |

Figure 4. A known-fate model describing the relationship between mule deer survival and road crossing rates on US 6 in central Utah, USA. Model estimates indicate that crossing rates as low as 1.2 crossings week⁻¹ can begin to substantially lower deer survival; however error bars indicate there is considerable uncertainty in model estimates.

Variation in survival is influenced by minor roads with low traffic volumes and US 6 with high traffic volumes. Minor roads had lower support than US 6 in the highest supported model. Crossing rate on minor roads also had support but was likely not a substantial driver of deer survival, because minor roads had low traffic volumes and few deer–vehicle collisions.

Given that snow depth is often patchy, especially on south facing slopes, it is conceivable that more resources were available for mule deer use during the second winter. Movement allows deer to adjust to environmental variation in snow depth (Garrott et al. 1987, Brown 1992, van Moorter et al. 2013). In our study, deer wintered at higher elevations during the second winter, most probably because of relatively lower snow accumulations in those areas. As a result, the spatial distribution of deer in relationship to roads was affected, with deer occurring twice as far from US 6 and somewhat farther from major roads. Consequently, deer crossed roads with high traffic volumes less frequently (52–96% decrease) because fewer deer wintered adjacent to roads with high traffic volumes.

In our study area, deer that crossed US 6 less often had higher survival than deer that crossed more frequently. Additionally, relatively low road crossing rates (1.2 crossings week⁻¹) were enough to cause declines in survival; however, there was considerable uncertainty around survival estimates. These results suggest that roads with high traffic volumes pose a significant risk to deer safety and provide support that the reduction in DVCs we observed during the second winter was the result of deer crossing high volume roads less frequently. Additionally, the reduction in road crossings on US 6 between winters was essentially proportional to the reduction in DVCs, providing further support that changes in movement patterns of deer due to climatic variation were driving the observed changes.

While there was considerable support that variation in weather caused much of the difference in DVCs we observed between winters, DVC rates may have also been affected by changes in traffic volumes (Romin and Bissonette 1996a). It is possible that traffic volume decreases could have contributed to a decrease in DVC rates, because as traffic volume declines, roads become safer for deer to cross (Litvaitis and Tash 2008). According to UDOT estimates, however, traffic volumes were essentially unchanged between years; as a result, it is unlikely that variation in traffic volume contributed substantially to the pattern in DVCs we observed.

Variation in deer abundance also can produce marked changes in DVC rates (Jahn 1959, DeNicola and Williams 2008). Mule deer populations are highly variable in Utah (Austin 2010, Bernales et al. 2011) and not surprisingly, deer abundance differed between winters during the study. Deer abundance was higher during the first winter when DVC rates were high and lower during the second winter when DVC rates decreased. A reduction in deer abundance likely contributed some of the variation in DVC rates that was observed between winters. According to UDWR population estimates, however, mule deer abundance only decreased 7% between winters in our study area, which is considerably less than the 52% decrease in DVCs we observed on major roads and the 91% decrease we observed on US 6. Based on the results from current DVC studies (DeNicola and Williams 2008, Rolandsen et al. 2011), we would expect DVCs to decrease proportionally to changes in abundance, which did not occur in our study. Additionally, abundance...
during 2011–2012 may be underestimated and the rate of decrease (−7%) may be even smaller because deer were more dispersed and likely more difficult to detect in surveys during that winter (Habib et al. 2012). Due to these factors, we suggest that changes in deer abundance may have had a marginal effect on DVC rates but was not the major driver of the pattern we observed. However, our study was limited in both temporal and geographic scope. Future research should focus on long-term, broad-scale studies that quantify the relative importance of winter weather and abundance on DVC rates (Rolandsen et al. 2011).

Snow conditions, which can vary considerably between years, are a major factor influencing the movement patterns of mule deer in temperature climates (Garrott et al. 1987). More than 30 years ago, Reed and Woodard (1981) suggested winter weather was likely an important driver of DVC rates. The evidence from our study provides a mechanism by which variation in winter conditions contribute to variation in DVC rates between years. Deer in the study area occurred farther from roads and crossed high traffic volume roads less when snow depths were lower, which resulted in lower DVC rates. Because harvest quotas are often set by management agencies in the spring, these findings may help deer managers adjust harvest quotas annually to account increased vehicle-related mortality that occurs during winters with high precipitation and snow fall.

The response of mule deer to snow conditions may result in an ecological trap for deer during severe winters in landscapes that have roads with high traffic volumes (Schlaepfer et al. 2002). As deer move from areas with high snow accumulations to areas with low snow accumulations, movement and foraging become relatively more efficient, but if deer select habitats near roads with high traffic volumes, then survival and fitness may actually be reduced due to the increased probability of being involved in a vehicle collision. This problem can be mitigated with exclusionary fencing (>2 m) that prevents deer from accessing road ways (McCollister and Van Manen 2010). Exclusionary fencing can reduce DVCs 80–90 % (Huijser et al. 2008), but fencing can be expensive and wildlife crossings, which are also relatively expensive, should be built at frequent intervals (~1.6 km) to retain landscape permeability for deer (Bissonnette and Adair 2008). Researchers also have tried manipulating the spatial distribution of deer in relation to roads with winter feeding stations to decrease DVCs (Wood and Wolfe 1988). By placing feeding stations away from roads, DVC rates were reduced nearly 50%. However, winter feeding has significant economic costs, implications for pathogen transmission, and may degrade vegetation and alter migration patterns of deer (Peterson and Messmer 2007).

Another aspect of DVC mitigation is warning drivers of potentially dangerous situations (Mastro et al. 2008), but the dynamic nature of DVCs can make this a challenge. However, it would seem that the most effective DVC warning systems would be as dynamic as the phenomena they represent. Recent advances in DVC reporting systems have used smartphones to collect and transfer information, which have made current and accurate DVC data readily available for mitigation (Olson et al. 2014). Current DVC information from these databases could be used to create a smartphone-based warning system that would indicate to drivers when they were entering a section of highway that was currently experiencing high rates of DVCs. Warning systems such as these could accurately represent the spatial and temporal variation that occurs in DVC patterns and may prove to be an effective area of research that could improve driver safety and reduce the number of deer killed.

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