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Effects of environmental and anthropogenic landscape features on mule deer harvest in Nebraska

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Understanding the habitat use of wildlife species is important for effective management. Nebraska has a variety of habitat types, with the majority being covered by rangeland and cropland. These habitat types likely influence the harvest of mule deer (*Odocoileus hemionus*) in Nebraska, but their specific effects are unknown. We modeled which environmental and anthropogenic landscape features influenced harvest densities. Spatial analysis in a Geographic Information System was used to determine the mean values of environmental and anthropogenic landscape features at the county level. We then used a generalized linear model to determine which of those factors influenced mule deer harvest from 2014-2016. We found that forest habitat, riparian habitat, road density, time integrated NDVI, and terrain roughness influence mule deer harvest in Nebraska. According to our model, mule deer show a significant preference for less forested, more rugged terrain (often rangelands), that are less fragmented and developed, based on harvest density. Understanding increased harvest densities of mule deer in rangeland habitats with increased roughness, decreased road density, and decreased urbanization can be beneficial for wildlife managers, allowing for more efficient allocation of efforts and expenses by managers for population management.
Effects of environmental and anthropogenic landscape features on mule deer harvest in Nebraska

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Abstract

Understanding the habitat use of wildlife species is important for effective management. Nebraska has a variety of habitat types, with the majority being covered by rangeland and cropland. These habitat types likely influence the harvest of mule deer (*Odocoileus hemionus*) in Nebraska, but their specific effects are unknown. We modeled which environmental and anthropogenic landscape features influenced harvest densities. Spatial analysis in a Geographic Information System was used to determine the mean values of environmental and anthropogenic landscape features at the county level. We then used a generalized linear model to determine which of those factors influenced mule deer harvest from 2014-2016. We found that forest habitat, riparian habitat, road density, time integrated NDVI, and terrain roughness influence mule deer harvest in Nebraska. According to our model, mule deer show a significant preference for less forested, more rugged terrain (often rangelands), that are less fragmented and developed, based on harvest density. Understanding increased harvest densities of mule deer in rangeland habitats with increased roughness, decreased road density, and decreased urbanization can be beneficial for wildlife managers, allowing for more efficient allocation of efforts and expenses by managers for population management.
Introduction

Deer hunting has been a tradition in Nebraska since the mid-1900s. The first official deer hunting season was held in 1945 where 275 mule deer (*Odocoileus hemionus*) bucks and 2 white-tail (*Odocoileus virginianus*) bucks were harvested (Nebraska Game and Parks Commission, 2016a). Along with the growing tradition of hunting, deer populations have also grown. During the 2015 hunting season 8,876 mule deer bucks and 28,505 white-tail bucks were harvested (Nebraska Game and Parks Commission, 2016a), a marked increase from 1945. The use of hunting allows for the Nebraska Game and Parks Commission (NGPC) to manage the deer population to help prevent disease, depredation issues, improve public safety, and sustain the population for future generations. Hunting also provides an economic boost for the state. In 2015, hunting contributed $562 million dollars in retail sales and supported over 8,856 jobs (Nebraska Game and Parks Commission, 2016b). The local economic support of hunting in return benefits wildlife from the Pittman-Robertson Act, which places an 11% tax on all hunting and sporting goods. The money is distributed among the states to be used for wildlife habitat improvement, research, education, and other means to support wildlife as well as hunting. This allows for state and federal agencies to better manage wildlife and in return help increase hunter opportunity and success.

Hunter success, however, is complex and involves many variables. Factors, such as road density, habitat type, and hunter effort all play a role in hunter success. Reardon et al. (1978) found a direct positive correlation between the success of hunters and deer density. Additionally, habitat types are variable in quantity and quality, resulting in varying distribution and abundance of deer. Croplands do not provide the necessary amount of cover required by deer during winter, leading to increased home range size (Walter et al., 2009). However, when croplands are
aggregated with forested areas or rangelands deer move less during these winter months. Close aggregation of these lands provides needed cover from forest or rangelands and nutrition from croplands (Williams, Dechen Quinn & Porter, 2012). Woolf & Roseberry (1998) demonstrated that the amount of forest cover had a positive linear relationship with deer densities, and that the limiting factors of the habitat (quality) restricted densities more than the fragmentation of habitat. Additionally, Mackie (1970) found that mule deer prefer slopes greater than 10%, especially during summer months. Preference for steeper slopes and rougher terrains can cause more difficulty for hunters in accessing populations.

The accessibility of habitat for hunters is also a key factor. Perhaps counterintuitively, Gratson & Whitman (2000) demonstrated higher hunter success for elk (*Cervus canadensis*) when roads were closed to vehicle access when compared to areas with open roads. Similar results have also been seen with wolves (*Canis lupus*). Both elk and wolves show a distinct avoidance of areas with high human activity. With enough human activity, both elk and wolves will completely avoid the habitat adjacent to the trails and remain at a further distance (Rogala et al., 2011). Sawyer et al. (2007) found that elk habitat use was significantly reduced at road densities as low as 0.17 km/km². Elk avoidance of roads occurs even outside of the hunting season (Ranglack et al., 2016) but successively increases during the archery and rifle hunting season (Ranglack et al., 2017). However, the type of habitat, forested or non-forested, that directly surrounded the roadway was important, as forested roadways allowed for higher road densities before the elk habitat use was affected. Mule deer also show significant change in habitat selection with development, preferring habitats that are farther from roads. (Sawyer et al., 2006).
Here, we investigated the factors that influence the number of mule deer harvested in each county in Nebraska, including habitat type, road density, Normalized Difference Vegetation Index (NDVI), terrain roughness, urbanization, and canopy cover. While each habitat type can be beneficial, the benefits may change depending on the season. For example, the nutritional benefits provided by croplands is year-round, but the cover provided by croplands is seasonal and unable to sustain yearly populations. Increased human activities in agricultural areas is also likely to discourage mule deer use of those areas. Therefore, it is likely that the more rugged and remote rangelands of the state will hold greater populations of mule deer. Consequently, higher populations of mule deer will likely produce higher harvest densities. However, the hunting access in these areas is more difficult, potentially reducing harvest densities.

Materials and Methods

Study Site

Nebraska is divided into 93 counties, which we used as our sampling unit for examining mule deer harvest across the state. In the northwestern portion of the state, the land use is mainly rangeland and the southeastern portion is cropland, with a transition zone between the two. Moving from the northwest to the southeast portion of the state, the land-use slowly transitions towards croplands as the soil type transitions to silt (Nebraska Department of Economic Development, 2016). The main transition point of the state runs diagonal from the southwest corner to the northeast corner along the edge of the Sandhills and the loess mixed grass prairie. The rivers are also segregated on this diagonal plane, with the majority of the rivers being located in the southeast half of the state (University of Nebraska State Museum 2016, Figure 1). Mule deer distribution in Nebraska follows a similar pattern. The majority of mule deer within the state are found in the northwest. However, they can be found throughout the western two-
thirds of the state. Urbanization somewhat follows the same diagonal pattern as seen with the other variables, however, the eastern third of the state is far more populated than any other portion, especially around the Lincoln and Omaha areas (Nebraska Department of Economic Development, 2015).

Data Collection

During the nine-day firearm season, hunters are required to present all harvested deer at one of 119 NGPC check stations across the state. NGPC employees and other check station attendants record the following data for each harvested deer: species (mule deer or white-tailed deer), permit number, county of kill, public or private lands (name of public land parcel), management unit, date of kill, days hunted, weapon type, sex, age (year based on teeth), and antler measurement (more or less 11 inches between main beams). All data recorded was summarized by county. We determined the mean hunter effort for each county as the mean number of days hunted per hunter. Also, using the total area of each county collected from a Geographic Information System (GIS), we determined the harvest density (number of mule deer harvested per 100km$^2$) for each county, to control for differences in county size.

We used GIS layers to assess which factors are influencing mule deer harvest throughout the state, including the NDVI, canopy cover, terrain roughness, urbanization, and road density. Time integrated NDVI and NDVI amplitude both use satellite imagery to produce measures of vegetation ‘greenness’ (USGS, 2015). This provides an approximation of forage availability for ungulates (Pettorelli et al., 2011), particularly in open habitats. With regards to habitat type, mule deer typically prefer areas with open continuous grasslands, therefore, the rangelands are likely to contain more mule deer than croplands. Canopy cover was used to determine the amount of tree cover and as an additional means of measuring riparian habitat within each county (Homer
et al., 2015). Nebraska’s riparian areas are typically wooded, bordered by croplands, and inhabited by white-tailed deer, generally causing low mule deer populations. Additionally, the Pine Ridge, in the northwestern portion of the state, has an abundance of trees, so forested habitat was examined to include this area and others with trees that were not included within the riparian category. Percent development measures the amount of human development on the landscape, which we used to determine the amount of urbanization (Xian et al., 2011). Percent development and urbanization are correlated with road density, which likely indicates an increase in fragmentation and less habitat for mule deer as these covariates increase. To determine differences in the terrain, we used terrain roughness, which analyzes the change in elevation of one point in reference to its neighboring points (Sappington, Longshore & Thompson, 2007). Rougher terrains in the state are typically less fragmented and predominantly rangeland or forested areas. Road density was also assessed to determine if there is a relationship with mule deer harvest density (Hayes, 2011). Road densities are likely higher in areas of increased urbanization and fragmentation. However, increased road density will also allow for increased hunter access, possibly leading to an increase in mule deer harvest. Categorical variables representing forest, rangeland, agriculture, riparian, and urbanization were also included, using the percentage of the county covered by each type. All data was averaged at the individual county scale, to match the finest scale available for the deer harvest data.

**Data Analysis**

We fit multiple generalized linear models using ‘glm’ in R version 3.3.2, to determine the impact of various environmental and anthropogenic landscape features on mule deer harvest densities in Nebraska from 2014-2016. We evaluated 13 covariates thought to influence mule deer harvest densities in Nebraska, representing both landscape and anthropogenic factors (Table 1).
We determined the mean value of each covariate at the county scale using ArcMap 10.4. Given that the relationship between harvest and our covariates may be nonlinear, we evaluated multiple functional forms (linear, quadratic, pseudothreshold) for each continuous covariate in our analysis, unless the most appropriate functional form could be identified \textit{a priori} from the existing literature (Table 1). We fit the pseudothreshold functional form using a natural log transformation (Franklin et al., 2000). Additionally, we standardized all continuous covariates by subtracting the mean and dividing by 2 times the standard deviation (Gelman, 2008; Lele, 2009) to allow for direct comparison of the relative importance of each covariate in our models.

We used a multi-tiered approach to model selection (Franklin et al., 2000) to reduce the number of competing models (Burnham & Anderson, 2002). Tier one was an exploratory analysis of the selected functional forms (linear, quadratic, and/or pseudothreshold) for each covariate. We ranked the resulting models for each covariate using AIC$_c$ and advanced those functional forms that were within 2 AIC$_c$ of the top functional form to the next tier, following Ranglack et al. (2017). In tier two, we combined the top functional form of each covariate in all possible combinations to determine the best-supported model for mule deer harvest in Nebraska. As this was the first step where we included multiple covariates in a single model, we screened all covariates for multi-collinearity using Pearson’s correlations coefficients, using $|0.6|$ as a basis of determining correlation. Therefore, any covariates that were found to be collinear were not included in the same model. We removed uninformative covariates following the recommendations Arnold (2010), when necessary. Finally, we ranked the resulting models using AIC$_c$ to determine the most supported model predicting mule deer harvest in Nebraska.

We validated our top model of mule deer harvest in Nebraska using a $k$-fold temporal cross-validation, to determine the temporal predictability of the model (Boyce et al., 2002; Wiens...
et al., 2008). We used two of the three years to train the model and predict mule deer harvest of the remaining year. This was repeated such that each year was predicted by the other two. We then used Spearman’s rank correlation with 10 equal area bins (Boyce et al., 2002) to compare the predicted and actual harvest densities for each temporal fold and used the average Spearman’s rank correlation to determine overall model validity.

With our top model covariate estimates we were able to create a prediction map of mule deer harvest in ArcGIS using a raster calculator (Figure 2). We multiplied each covariate estimate with its raster in the appropriate functional form from the top model, and added all covariates together. For this, we used a pixel size of 1,500 m\(^2\), which is the average home range size of a mule deer doe (Kufeld, Bowden & Schrupp, 1988). Each pixel was assigned a single point value for the mean of the pixel, with raster to point. Kernel density was used to extrapolate between points and create a continuous scale and allow for any interconnectivity or isolations of mule deer populations in Nebraska to be seen.

Results

Our dataset contained a total of 26,255 harvested mule deer from three rifle deer seasons (2014 - 2016). Most counties (82 of 93) reported mule deer harvest during the three-year period. The mean harvest density for the 82 counties was 3.79 mule deer harvested / 100 km\(^2\), with a range of 0 – 22.60 mule deer harvested / 100 km\(^2\) (Figure 3 and Table S1).

Tier one of our analysis determined our top functional forms for each covariate (Table 1). The top model produced during the second tier of our analysis consisted of the covariates: percent forested habitat, mean road density, mean time integrated NDVI, percent riparian habitat, and mean terrain roughness (Table 2). Percent forested habitat showed a negative relationship
with harvest density (Figure 4). Mean time integrated NDVI and mean road density both produced concave quadratic relationships with mule deer harvest densities. Optimal harvest was achieved in areas where time integrated NDVI was ~30, and areas where road density was 3,250 m/km$^2$ (Figure 4). In contrast, a convex quadratic relationship was produced for the relationship of mule deer harvest and terrain roughness. However, this relationship is only slightly convex and closely resembles a positive linear relationship (Figure 4). A pseudothreshold relationship was most supported for riparian habitat, and the greatest harvest densities were recorded when percent riparian habitat was lowest (Figure 4). During the validation of our model, we recorded a mean rho value = 0.928, and a mean p-value < 0.001 (Table 3). Our top model predicted higher harvest densities than were observed (Figures 3 & 5), with harvest predicted in 92 counties, a mean of 14.66 mule deer harvested / 100 km$^2$, and a range of 0.0 – 136.31 mule deer harvested / 100 km$^2$.

**Discussion**

Our results suggest that resources for mule deer management should be focused on areas of decreasing forest and riparian habitats, increasing terrain roughness, road densities between 3,000 and 3,500 m/km$^2$, and integrated NDVI values around 30 (Figure 4). The decrease in harvest densities as forested habitat increase is likely due to influences on the hunters’ ability to access and locate deer, rather than habitat quality. Forested areas are likely to have lower fragmentation, making hunter accessibility more difficult; therefore, the ability of hunters to navigate through the terrain likely decreases, along with visibility, which in return decreases harvest (Brinkman et al., 2009). Alternatively, mule deer in Nebraska may avoid forested areas for other reasons, leading to lower harvest in those areas. Further research on mule deer habitat selection is needed to qualify the importance of this covariate.
The decreases in harvest due to riparian habitats is likely due to whitetail deer and disturbance. The majority of riparian habitat in Nebraska is surrounded by agriculture and urbanization or development. These fragmented agricultural habitats generally support high densities of whitetail populations (Lingle, 2002), which prefer gentle terrains generally consisting of agricultural lands. Mackie (1970) found that mule deer prefer areas with increased slope and terrain roughness, which are not likely to be urbanized or developed and consequently more likely to be rangeland dominant. This likely contributes to the increased harvest density of mule deer as terrain roughness increases.

As an index of forage quality, NDVI has become a very useful tool in wildlife ecology and management (Pettorelli et al., 2011), though additional field data is often required to fully understand the relationship between forage quality and NDVI (Borowik et al., 2013). The time integrated NDVI value of 30 roughly correlates with rangeland habitat, with agricultural and forested lands showing significantly higher NDVI values due to higher water availability. Additionally, harvest increased with increased terrain roughness, which also correlate with rangeland. Therefore, rangeland habitat in Nebraska is important for mule deer, as shown by both NDVI and terrain roughness.

Our road density value is a factor of accessibility and disturbance. Between 3,000 and 3,500 m/km² which indicates there are enough roads to allow hunters the access needed to find and get to the deer, while not causing enough disturbance to deter deer from using the area. Areas with lower road densities are likely to have just as good or better mule deer habitat, but do not allow enough access for hunters to be as successful in harvesting mule, and harvest density is what we were modeling. However, areas with higher road densities are likely poor-quality
habitats due to the increased amount of disturbance and fragmentation (Sawyer et al., 2006, 2007; Rogala et al., 2011).

The difference between our actual and predicted harvest is likely due to limiting factors during harvest. Hunting is difficult, and requires both skill and luck. Our model predicts the number of mule deer that could be harvested based on the environmental and anthropogenic features in that area. Whereas, with the actual harvest there are other constraints such as accessibility to private lands, hunting regulations, skill, and luck. Nebraska is in large part privately owned, and therefore, hunters are not capable of accessing all available land that mule deer prefer, which likely causes a decrease in harvest. Also, hunting regulations may not permit the harvest of that many mule deer in a given area due to management practices or low population numbers.

Our map of predicted mule deer harvest densities (Figure 2), indicates that most of the eastern third of Nebraska has little to no mule deer harvest, which is supported by the actual harvest data from 2014-2016 (Figure 3). The predicted harvest density (Figure 2) likely correlates with the quality of habitat available in the area; therefore, higher densities likely indicate higher quality habitat. However, Figures 3 and 5 also show that many of the counties with large amounts of suitable mule deer habitat in Nebraska (Banner, Custer, Cherry, Dawes, Lincoln, Scotts Bluff, and Sioux), do not have the highest harvest densities. Mule deer habitat appears to be patchily distributed in these counties, except Custer and Lincoln. Therefore, even though these habitat patches are likely of very high quality, they can only support a limited number of deer in these smaller areas. These smaller areas are also more likely to be controlled by a small number of landowners, potentially limiting public access and leading to lower harvest densities.
For the counties of Custer and Cherry, however, suitable habitat is more evenly dispersed. These two counties still do not have overly high harvest densities (Cherry 3.51 deer/100km$^2$ and Custer 11.2 deer/100km$^2$). This is likely because they are both large counties, and have low accessibility due to low road densities (Cherry 560 m/km$^2$ and Custer 831 m/km$^2$) and large parcels of land being owned by a single landowner. Even though these counties are likely supporting large quantities of mule deer, due to the lower road densities and decreased development as preferred by mule deer (Sawyer et al., 2006), hunters are not capable of accessing these lands, leading to low harvest density. The two counties with the highest actual harvest densities, Frontier (22.6 deer/100km$^2$) and Hayes (21.4 deer/100km$^2$), still have modest amounts of average to high quality habitat. This habitat is spread evenly within the counties with a few areas of increased habitat quality densities (Figure 2). The differences in road densities between these two counties and Custer county are minimal, with Hayes actually having a lower density. However, they both still have nearly over 200 m/km$^2$ more roads than Cherry county. Therefore, whereas road densities do have an influence on harvest due to accessibility to habitat, the accessibility of private lands may be a more important factor.

Given that Nebraska is largely a privately-owned state, incentive for landowner conservation may be needed, such as the Grassland Reserve Program (GRP), the Conservation Reserve Program (CRP) (USDA, 2010, 2016), or a community-based wildlife management scheme (Ranglack & du Toit, 2015). Deutsch (2009) showed that the involvement of local communities helps increase the success of rangeland wildlife conservation, which could be very beneficial in areas of the state under high demand for mule deer conservation. Community involvement funds could also be given as local scholarships or for community development or projects (Frost & Bond, 2008).
The understanding of habitat types that lead to higher mule deer harvest density can be beneficial to management, as areas that have higher harvest densities are likely correlated to having higher mule deer populations. This is a key piece of information for wildlife managers for effective resource management. In Nebraska, efforts are being made to increase mule deer populations, and understanding their habitat choices would allow managers to effectively target their management actions. Our results suggest that conservation efforts should be allocated to areas matching the description of our top five covariates (decreasing forested and riparian habitats, increasing terrain roughness, road densities between 3,000 and 3,500 m/km², and integrated NDVI values around 30). These areas have the capabilities for producing the highest harvest densities for mule deer, and likely indicate better quality habitat. This is not likely the best quality habitat for mule deer due to the presence of moderate road densities, but the increasing harvest densities shows that the habitat is suitable for mule deer. The best quality habitat is likely in areas farther from roads (Sawyer et al., 2006, 2007; Rogala et al., 2011; Ranglack et al., 2016), but further research is needed into mule deer habitat selection to fully understand the impacts of our top five covariates on habitat selection. This allows for scientifically informed management of mule deer, their habitat, and their harvest.

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Table 1 (on next page)

The covariates that were included in the analysis of mule deer harvest density in Nebraska, USA, 2014-1016, along with the functional forms considered and included in the final analysis.

Any forms that were within two AIC$_c$ units of the top form were included in the analysis to determine the top model.
Table 1. The covariates that were included in the analysis of mule deer harvest density (harvest / 100 km²) in Nebraska, USA, 2014-2016, along with the functional forms considered and included in the final analysis. Any forms that were within two AICc units of the top form were included in the analysis to determine the top model.

| Covariates      | Functional Forms Considered           | Functional Forms Included |
|-----------------|--------------------------------------|---------------------------|
| Agriculture     | Linear, Pseudothreshold, Quadratic   | Quadratic                 |
| Canopy Cover    | Linear and Pseudothreshold           | Pseudothreshold           |
| Development     | Linear and Pseudothreshold           | Pseudothreshold           |
| Elevation       | Linear, Pseudothreshold, Quadratic   | Quadratic                 |
| Forest          | Linear and Pseudothreshold           | Linear and Pseudothreshold|
| NDVI Amplitude  | Linear and Pseudothreshold           | Linear                    |
| NDVI Time Integrated | Linear and Pseudothreshold             | Linear and Quadratic       |
| Range           | Linear, Pseudothreshold, Quadratic   | Quadratic                 |
| Riparian        | Linear and Pseudothreshold           | Pseudothreshold           |
| Road Density    | Linear, Pseudothreshold, Quadratic   | Quadratic                 |
| Roughness       | Linear, Pseudothreshold, Quadratic   | Quadratic                 |
| Slope           | Linear, Pseudothreshold, Quadratic   | Linear and Quadratic      |
| Urbanization    | Linear, Pseudothreshold, Quadratic   | Pseudothreshold           |
Table 2 (on next page)

The functional form, standardized coefficient estimate, and standard error of covariates included in top model of mule deer harvest (individuals / 100 km²) in Nebraska, 2014-2016.
Table 2. The functional form, standardized coefficient estimate, and standard error of covariates included in top model of mule deer harvest (individuals / 100 km²) in Nebraska, 2014-2016.

| Covariate            | Function Form | Estimate | Std. Error |
|----------------------|---------------|----------|------------|
| Intercept            |               | 4.2      | 0.32       |
| Forest               | Linear        | -3.04    | 0.43       |
|                      | Linear        | -5.93    | 0.53       |
| Time Integrated NDVI| Quadratic     | -4.90    | 0.88       |
| Riparian             | Pseudothreshold | -1.93  | 0.37       |
|                      | Linear        | 4.12     | 0.48       |
| Roughness            | Quadratic     | 2.54     | 0.66       |
|                      | Linear        | 2.75     | 0.75       |
| Roads                | Quadratic     | -1.07    | 0.31       |
Table 3 (on next page)

Spearman rank correlation coefficient and p-values from the temporal k-folds cross validation of our top model of mule deer harvest in Nebraska, USA, 2014-2016.

The data presented indicate which year was being used as a validation dataset.
Table 3. Spearman rank correlation coefficient and p-values from the temporal $k$-folds cross validation of our top model of mule deer harvest in Nebraska, USA, 2014-2016. The data presented indicate which year was being used as a validation dataset.

| Test          | 2014 | 2015 | 2016 | Mean |
|---------------|------|------|------|------|
| Spearman Rank | 0.884| 0.954| 0.947| 0.928|
| p-value       | <0.01| <0.01| <0.01| <0.01|
Figure 1 (on next page)

Nebraska landscape features
**Figure 2** (on next page)

Map of the predicted mule deer harvest density (harvest / 100 km$^2$) from the top model of mule deer harvest in Nebraska, USA, 2014-2016.

Pixels were created at 1500m$^2$, which represents the mean home range size of a mule deer doe (Kufeld, Bowden & Schrupp, 1988).
Figure 3 (on next page)

Mean actual mule deer harvest density (harvest / 100 km$^2$) from 2014-2016 in Nebraska, USA by county.
Figure 4 (on next page)

Plots of the five covariates included in the top model of mule deer harvest density (harvest / 100 km$^2$) in Nebraska, USA, 2014-2016, on the original, non-standardized scale.

The black lines represent the coefficient estimate and the shaded areas represent the 95% confidence interval across the available range of each covariate, while the other covariates were held at their mean value.
Figure 5 (on next page)

Mean predicted mule deer harvest density (harvest/ 100 km$^2$) in Nebraska, USA by county.
