Pronghorn abundance and habitat selection in North Dakota

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Executive Summary

Pronghorn (*Antilocapra americana*) are associated with sagebrush-steppe ecosystems of the Great Plains of North America. At the northern edge of their range in North Dakota, pronghorn have been exposed to a suite of changing conditions including severe winter weather, drought, predation, harvest, and rapid oil and gas development. Adult pronghorn counts in North Dakota have fluctuated over the past 40 years, with an increasing trend from 1974 - 2007, followed by a rapid decline from 2008 – 2012. This decline coincided with significant oil and gas development in pronghorn range, and several severe winters with cold temperatures and/or deep snow. Our primary objectives were to determine what factors were responsible for fluctuations in pronghorn abundance, and to identify key habitat features selected by adult female pronghorn. We were interested in whether increasing densities of well pads resulted in declines in abundance, and whether pronghorn avoided roads or well pads.

In Chapter 1, we identified the key factors that influenced pronghorn abundance in western North Dakota over a 40-year period. We used Bayesian mixed-effects models to test for correlations between an index of pronghorn abundance and different environmental covariates. Bayesian models allowed us to estimate the effects of various parameters with appropriate levels of uncertainty despite missing data for certain years and units. We analyzed variation in annual population count data relative to weather conditions, coyote populations, oil and gas development, human harvest, and agricultural practices. We found that lower indices of abundance corresponded with heavy snowfall and low winter temperatures, suggesting that the large observed decline starting in 2008 was primarily

due to severe winter weather conditions. In addition, our pronghorn abundance index was negatively correlated with road and well density, of which the latter increased exponentially during the last decade. In contrast, we found little evidence that coyote populations, drought, or human harvest were responsible for the observed population declines. These findings indicate that pronghorn abundance in North Dakota is strongly influenced by winter weather conditions, and we expect that the anticipated increase in winter storm frequency due to climate change will have a negative impact on pronghorn. However, warmer winter temperatures may counteract this effect. Our results also indicate that continued oil and gas development will negatively influence pronghorn populations. Movement corridors, which are necessary for pronghorn to escape extreme winter conditions, will likely continue to be impeded by roads, fences, and development.

In chapter 2, we used resource selection functions (RSF) to quantify patterns of habitat selection by pronghorn in two different years (2006 and 2014) with contrasting pronghorn density. In 2006, pronghorn abundance was near its peak (approximately 9329 animals), whereas in 2014, estimates of abundance had declined to 4886 animals. Meanwhile, oil development doubled from 1122 active oil wells in 2006 to 2688 wells in 2014. By comparing known locations of pronghorn to random locations throughout their range in western North Dakota, we sought to identify key environmental attributes (including oil wells) selected or avoided by pronghorn, and whether selected habitats conferred fitness benefits in the form of high fawn: doe ratios. We also sought to determine whether selection was stronger when pronghorn were at low versus high densities, as observed with other species. We found that pronghorn selected habitats with low NDVI and the

presence of sagebrush, but avoided developed areas, roads, forests, and wetlands. Pronghorn selected habitats close to oil wells, which was likely due to the fact that wells were located in high-value habitats such as native grassland and sagebrush-steppe ecosystems (this was quantified in a separate analysis). Selection was stronger in the year with low pronghorn densities for 8 out of 10 parameters estimated, which was consistent with current resource selection theory. We found a positive relationship between fawn production and NDVI, contrasting with observed patterns of resource selection. This appears to be due to the tendency of high biomass areas to produce high fawn: doe ratios, and may reflect a tradeoff between early predator detection (favoring open habitats) and concealment of young from predators (favoring high biomass areas). Our finding that pronghorn were associated with sagebrush steppe habitat and avoided developed areas, densely-roaded areas, and major highways highlights the importance of preserving sagebrush steppe habitat in southwestern North Dakota. Furthermore, our analysis of oil well locations indicates that oil and gas development removes habitat that would otherwise be valuable for this species.

Acknowledgements

Chapter 1: Long-term changes in pronghorn abundance index linked to climate and oil development in North Dakota

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Abstract

The interacting effects of climate change and habitat fragmentation on wildlife are of global conservation concern. Over the past four decades, pronghorn (*Antilocapra americana*) populations in North Dakota have been exposed to severe winter weather, drought, predation, harvest, and rapid oil and gas development. Adult pronghorn counts in North Dakota fluctuated over time with an increasing trend from 1974 - 2007, followed by a rapid decline from 2008 – 2012. Our primary objective was to identify key drivers of an index of pronghorn abundance in western North Dakota over this period to inform conservation and management. Despite missing data, Bayesian mixed-effects models allowed us to analyze variation in annual population count data relative to weather conditions, coyote populations, oil and gas development, human harvest, and agricultural practices. We found that lower indices of abundance corresponded with heavy snowfall and low winter temperatures, suggesting that the large observed decline starting in 2008 was primarily due to severe winter weather conditions. We also found that the abundance index was negatively correlated with road and oil/gas well density, of which the latter increased exponentially during the last decade. In contrast, we found little evidence that coyote populations, drought, or human harvest were major drivers of observed population declines. Based on these findings, we expect that pronghorn populations will be negatively influenced by the anticipated increase in winter storm frequency and continued expansion of oil and gas development. Roads, fences, and development may impede pronghorn movement to more hospitable areas during winter storms, thereby hindering their ability to escape extreme conditions.

Introduction

   Understanding the interacting effects of climate and human disturbance (e.g., habitat
fragmentation) on wildlife populations is critical for successful conservation and
management (McCarty, 2001). Long-term studies that allow identification of major drivers
of population change are rare, despite the fact that intensive monitoring has long been
recommended for high-risk ecosystems and species (Noss, 1990). Recent climate change
already has resulted in changes to species' distributions (Parmesan et al., 1999; Thomas
and Lennon, 1999), and these changes are likely to increase as the magnitude of climate
change intensifies (IPCC, 2013). Climate extremes, which are expected to increase in
frequency and magnitude (IPCC, 2013), can have detrimental effects on wildlife
populations (Boyce et al., 2006). For example, precipitation in the form of snow can
prevent browsing and grazing animals from accessing their food source and escaping
predators (Forchhamnmer and Boertmann, 1993; Post and Stenseth, 1999), while drought
can reduce the availability and nutrition of forage plants (Owen-Smith, 2000; Georgiadis et
al., 2003).

   In addition to climate extremes, wildlife populations also are susceptible to habitat
fragmentation caused by the harvest of natural resources, industrial infrastructure,
urbanization, roads, and the conversion of land for agriculture. For example, many species
of birds and mammals actively avoid oil and gas infrastructure (Sawyer et al., 2002;
Johnson et al., 2005; Sawyer et al., 2006; Benítez-López et al., 2010; Beckmann et al., 2012;
Ciuti et al. 2015). Furthermore, the intensification of agriculture has caused declines in

wildlife populations worldwide (Sotherton, 1998; Fuhlendorf et al., 2002; Naughton-Treves et al., 2003).

Pronghorn (*Antilocapra americana)* inhabiting the Great Plains of North America are vulnerable to climate extremes, as well as landscape fragmentation and habitat loss. Pronghorn are sensitive to deep snow, which restricts access to forage and results in adult malnutrition and low fawn recruitment (O'Gara and Yoakum, 2004). In addition, extended cold periods may negatively influence pronghorn by increasing energy expenditure for thermoregulation. Severe winters, characterized by low temperatures accompanied by frequent blizzards, have been associated with large-scale mortality events of both adults and fawns (O'Gara and Yoakum, 2004). Mortalities were most often attributed to loss of access to shrubs and were exacerbated by fences and roads, which prevented migration to more hospitable areas (O'Gara and Yoakum, 2004). Pronghorn also experience declines in abundance following years of severe drought, likely due to reduced fawn recruitment in years of low forage quality and productivity (Simpson et al., 2007; White et al., 2007). Therefore, increases in the frequency or severity of extreme weather events could have major implications for pronghorn conservation and management.

In North Dakota, at the north-eastern fringe of pronghorn range, approximately 90% of the land area is owned by farmers and ranchers. Therefore, land-use decisions made by private land owners have the potential to profoundly affect pronghorn populations. Pronghorn are adapted to native sagebrush and grassland habitats, but will use agricultural areas such as wheat fields, alfalfa fields, and pasture for cattle (Yoakum, 2004; Kolar, 2009;

Hoffman et al., 2010). Changes in the proportions of wheat, alfalfa, and pastureland versus non-preferred crops (e.g. vegetable, corn, soy, and other crops) may influence the distribution of pronghorn across time and space. In addition, rapid increases in oil and gas development, accompanied by increasing human activity and vehicle traffic, has fragmented portions of the North Dakota pronghorn range over the past several decades. Over a 5-year period of increasing gas development in Wyoming, pronghorn abandoned areas with large gas-field infrastructure footprints (Beckmann et al., 2012). In addition to avoiding gas well infrastructure, pronghorn are known to avoid primary and secondary roads (Kolar, 2009). This suggests that land-use decisions also could be important drivers of pronghorn populations in North Dakota.

Pronghorn populations throughout North America are heavily managed and actively harvested. In North Dakota, managers generally restrict the harvest to no more than 15% of the population, and close the season when the number of pronghorn licenses for a unit falls below 100. Human harvest can account for up to 58% of adult mortalities in North Dakota (Kolar et al., 2012), suggesting that harvest could influence the population trajectory. In addition to harvest, predation (O'Gara and Shaw, 2004) and density dependence (Kohlmann, 2004) are known to influence pronghorn numbers. Coyotes prey upon pronghorn fawns, and their abundance was inversely related to pronghorn productivity in Utah and Wyoming (Brown and Conover, 2011). Pronghorn have been shown to undergo an Allee effect at low densities (Hoffman et al., 2010), but can exhibit irruptive population dynamics when released from hunting pressure, predation, or food scarcity (White et al., 2007).

With the goal of identifying the primary drivers of pronghorn population dynamics in North Dakota, we analyzed 40 years of pronghorn count data collected between 1974 and 2013. We conducted a comprehensive analysis to quantify the relative effects of climate, agricultural change, oil development, harvest, predation, and prior year abundance index on pronghorn counts. Our primary objectives were to identify important factors associated with observed variation in population size, and to assess the relative importance of land-use decisions, particularly oil and gas development, on pronghorn populations.

Methods

Study Area

Our study area is in western North Dakota and consists primarily of grasslands, but includes the rugged Little Missouri badlands in the southwestern corner. Elevations range from 230 – 1069 m above sea level (Bluemle, 1977). Most of the region is part of the Great Plains ecotype; the native mixed- and short-grass prairie is dominated by grasses, forbs, and sagebrush (*Artemisia* spp*.,* Johnson and Larson, 1999; Seabloom, 2011). Although some native prairie and sagebrush habitat still remains in the state, much of North Dakota (90%) is privately owned and cultivated either for crops such as wheat, alfalfa, and corn, or managed for cattle ranching. Depending on the county and year, between 1-7% of the land area is classified as Conservation Reserve Program (CRP) land, which includes native grassland and sagebrush habitats, and between 7-67% of the land is allocated to pastureland and rangeland (NASS, 2014).

The region is characterized by long, dry summers and cold winters, with dramatic fluctuations in temperatures. Over the study period (1974 -2013), the maximum summer temperature was 44.4°C and the minimum winter temperature was -42.2°C (NOAA, 2015). Maximum snow depth varied from 178 to 1575 mm, with an average maximum snow depth of 490 mm.

Pronghorn survey protocol

Standardized aerial surveys of pronghorn were conducted annually between 25 June and 17 July, from 1974-2013. Pronghorn range was divided into 50 survey units with boundaries based on major roads, waterways, and county lines. These survey units reflected hunting units and were originally delineated based on major highways, county lines, and ecoregion boundaries. Each year, only a subset of the units (approximately 20 out of 50) was surveyed, and most units were surveyed approximately every three years, with the exception of one unit at the southwestern corner of the survey area that was surveyed every year due to consistently high densities of pronghorn. Surveys were conducted from small fixed-wing aircraft such as Piper Supercub (Piper Aircraft, Vero Beach, FL) or Scout (American Champion Aircraft Corporation, Rochester, WI). Each tier of 1 square mile sections (1.6 km²) was flown, and the aircraft followed the center line of the tier (½ mile line of each tier between section lines within a survey unit) at 1.6 km intervals. The pilot and observer acted as a team and surveyed a 0.8 km strip on either side of the plane. Surveys were flown at an altitude of 76 - 106 m, with an average speed of 129 kph, and detection probability was assumed to be constant across years and units. In the rougher badlands terrain, the aircraft followed terrain contours as needed to ensure full visual

coverage of the survey unit. When pronghorn were detected, the location, age (young vs. adult), and sex of each individual were recorded. This survey protocol was followed consistently throughout the duration of the study and only trained or experienced pilots and observers conducted counts.

Covariates

Weather

We obtained data on winter weather conditions from weather stations in the study area (Minot, Williston, Hettinger, Bowman, Bismarck, Grassy Butte, Dunn Center, Medora, Fairfield). For each survey unit, weather data were used from the nearest weather station. The original data were obtained from NOAA's National Climatic Center and consisted of daily minimum temperatures and snow depths from November through April from 1974-2014. As indices of winter severity, we calculated the number of "snow days" - the number of days with snow depth≥ 36 cm, and the number of "cold days," which was the number of days with minimum temperatures ≤ -7°C. These cutoff values were developed by Brinkman et al. (2005) for white-tailed deer (*Odocoileus virginianus*), and reflect adverse conditions for pronghorn (Pyle, 1972; Yoakum, 2004). Palmer hydrological drought index (PHDI) data were obtained from the National Climatic Data Center. We obtained indices from 1973-2014 for the northwest, northcentral, westcentral, southwest, southcentral, and central divisions within the state of North Dakota. The index from the division encompassing each pronghorn survey unit was used. The average PHDI value from April – August was calculated for each summer prior to pronghorn surveys, and small PHDI values indicated drought conditions. We converted weather covariates to levels representing extreme

versus average conditions. Years in the 90th percentile for cold and snow days (> 37 days where snow depth exceeded 36 cm, and > 120 days with minimum temperatures ≤ -7°C) were considered to have been severe winters. Years in the 10th percentile (with PHDI values ≤ -3.3) for PHDI were considered drought years.

Land use

We used data from the National Agricultural Statistics Service (NASS) to calculate the proportion of land area devoted to alfalfa, wheat, or pasture in each county in each year (NASS, 2014), and expected pronghorn to be positively associated with these land-use categories. We combined lands used for pasture or grazing with lands enrolled in CRP into the category "pasture" and adjusted the data based on the proportion of the county that fell within each pronghorn survey unit using GIS (ArcMap 10.2.2, ESRI 2014). We calculated the proportion of each survey unit classified as "sagebrush-steppe" habitat according to the USGS GAP land cover data set (USGS, 2011), which is based on Landsat TM satellite imagery. Data from the Department of Mineral Resources (DMR) were used to calculate the density of active oil wells (wells per 100 km^2) in each pronghorn survey unit in each year. We included well types that were considered high or moderate use according to DMR, and these were oil and gas, salt water disposal, water supply, and injection wells. We calculated the density of primary and secondary roads (km roads per 100 km^2; North Dakota Department of Transportation) for each survey unit using GIS, with the knowledge that pronghorn are known to avoid these types of roads (Kolar, 2009).

Predators and harvest

Annual aerial surveys conducted by NDGF in the spring for mule deer (*O. hemionus*) recorded incidental observations of coyote (*Canis latrans*). Mule deer survey areas overlapped 13 pronghorn survey units, and annual estimates of coyote density from the badlands were used as an index of coyote densities in the entire pronghorn survey area for each year. Data on hunter harvest were obtained from annual hunter harvest questionnaires. The total number of pronghorn killed in each unit was estimated by multiplying the total number of permits issued by the percent of hunters who hunted, and then by the hunter success rate. Gun harvest data were available for every year of the study; however, bow-hunting data were available for 1986, 1996, 1999, and 2001 – 2013 only. Therefore, in years when bow hunting data were missing, we estimated the number of bow-hunted pronghorn based on years when bow-hunting data were available. For each survey unit, we calculated the mean proportion of bow-hunted versus rifle-hunted pronghorn (bow hunters harvested between 3-37% of the rifle harvest). We then multiplied this ratio by the rifle-harvest data to obtain the number of bow-hunted pronghorn for that year.

Analysis

For purposes of this study, we restricted our analysis to counts of adults only because we expected that detection of adults would be more consistent through time compared with fawns, due to variation in survey dates in relation to mean parturition dates. The aerial survey protocol from 1974-2013 precluded calculation of detection probability; therefore, we assume that detection probability was <100%, but constant across years and sites. We

believe this is a safe assumption because a) there was very little turnover of observers from year to year, and extensive training ensured stringent adherence to standardized survey methods, and b) the landscape of western North Dakota is open and fairly homogeneous, facilitating constant detection over a wide spatial scale. Nevertheless, the estimates of abundance presented in this study are indices of abundance rather than true abundance of pronghorn. We assessed the following covariates on abundance index: year, $year^2$ (allowing for the estimation of a non-linear trend), snow days, cold days, $PHDI_{t-1}$, % sagebrush, % wheat, % alfalfa, % pasture, coyote index, harvest, well density, and road density. We also included the variable $pronghorn_{t-1}$ to assess the influence of pronghorn counts the previous year on the current index of abundance. This covariate was created using a function in the model statement that used the count data from the previous year. We checked for correlation among our covariates prior to fitting models with the Pearson's correlation test, using a threshold of r = 0.7 (Dormann et al., 2013). Prior to analysis, continuous covariates were scaled to have mean = 0 and a standard deviation = 1. Due to the fact that not every survey unit was surveyed every year, we had missing data for the response variable (adult count at time t), and the covariate $pronghorn_{t-1}$. We therefore conducted the analysis in a Bayesian framework, using Markov-chain Monte Carlo methods (MCMC). This method assumed an underlying model for the missing data and accounted for uncertainty of the missing values (King et al., 2009), thereby providing inference to all sites and years. This approach also allowed us to more easily incorporate random effects for site and year, thereby helping to account for site-level and annual variation that was not addressed by our suite of covariates (Bolker et al., 2014; Kery and Schaub, 2012). MCMC simulations were performed in JAGS (Plummer, 2003) through the R2JAGS interface (Su

and Yajima, 2009). The model structure was as follows: Count$\sim$dpois(exp($\beta_1\chi_1$ + $\beta_2\chi_2$ ... + $\beta_n\chi_n$ +α_{year}+ε_{site})), where β represents fixed effects, α_{year} represents the random effect for year and ε_{site} represents the random effect for site. We used vague, normally distributed priors with a mean of 0 and a standard deviation of 100 for all fixed and random effects, and uniform priors for the standard deviation of the random effects (year effects: α_{year} $\sim$dnorm(0, σ_1^2), $\sigma \sim$ unif(0, 100), site effects: $\varepsilon_{site} \sim$ dnorm(0, σ_2^2), $\sigma \sim$ unif(0,100)). We ran three independent Markov chains for 100,000 iterations with a burn-in of 50,000 iterations and subsequently thinned values by 6 to reduce autocorrelation and storage requirements. We assessed convergence using the Brooks-Gelman-Rubin test statistic (Brooks and Gelman, 1998) and by visually inspecting chains.

Results

Correlations and model fit

Pronghorn density at time t-1 was highly correlated (r = 0.89) with harvest, because harvest quotas were determined largely based on pronghorn counts in the previous year. When we ran two models including each of these covariates separately (together with all other covariates), credible intervals for harvest, but not pronghorn$_{t-1}$ overlapped 0. Therefore, we kept pronghorn$_{t-1}$ and excluded harvest from the model. The 95% credible intervals for coyote density and sagebrush overlapped 0, indicating high uncertainty about their correlation with pronghorn abundance index (Fig. 1). We therefore do not make strong inferences from these covariates. Estimates of predicted abundance from this model were similar to the observed abundance index (r^2 = 0.85, $p < 0.001$).

General spatial and temporal trends

Pronghorn density was greatest in the southwestern portion of the state, and declined markedly in the northern and eastern parts of the study area (Fig. 2). Estimates of the effects of year and year^2 indicated that pronghorn experienced a non-linear population trajectory over time (Fig. 1, 3). Since 1974, pronghorn populations experienced peaks in abundance index in 1983, 1993, 2005, and 2007, with the highest peak in 2007, followed by a precipitous decline over the next five years (Fig. 3).

Weather

Our index of pronghorn abundance was inversely related to snow days (Fig. 1), and low abundance was observed after extremely snowy winters (1977-78, 1985-86, 1993-94, 2008-09, 2009-10, 2010-11; Fig. 3). Cold winters (November-April) also had a negative effect on the index of pronghorn abundance (Fig. 1), and extremely cold winters occurred in 1973-74, 1974-75, 1978-79, 1979-80, 1995-96, 1996-97, 2007-08, 2008-09, and 2012-13. The combined effects of cold and snow reduced the pronghorn abundance index to a greater degree (32% annually) than each covariate on its own (23% and 12% for cold and snow, respectively; Fig. 4). A large portion of the observed decrease in the pronghorn abundance index from 2008 – 2012 can be explained by winter weather. The winter of 2007-08 was extremely cold, 2008-09 was both cold and snowy, and heavy snowfall occurred in 2009-10 and 2010-11. According to our model, these conditions alone would result in a 60% decrease in the pronghorn abundance index from 2007 - 2012. In reality, we observed a 73% decrease in the abundance index during this period. In addition to adverse winter conditions, we predicted that pronghorn would be negatively affected by

extremely dry summers. Contrary to predictions, drought conditions the prior summer

corresponded with a relatively high pronghorn abundance index the following July (Fig. 1).

Agricultural land-use and sagebrush

   The index of pronghorn abundance was positively related to the proportion of wheat in

survey units, and negatively related to both alfalfa and pasture, although the effect of

pasture was small (Fig. 1, Fig. 5). The average amount of land in wheat production

increased over time from 16 – 20% in western North Dakota, whereas the amount of land

in alfalfa stayed relatively constant, at 4%. Although land enrolled in the CRP declined

during the study, the total amount of land in our "pasture" category (which included both

rangeland used for cattle grazing and CRP land) remained constant at about 41%.

Agricultural land use varied spatially, with most of the alfalfa and pasture occurring in the

southeast and southcentral parts of the study area. Wheat production was focused in the

north in the 1970's, but by 2013 had spread to the southwestern part of the survey area.

Sagebrush was positively correlated with the abundance index, but credible intervals were

wide and overlapped 0, indicating high uncertainty as to dependence by pronghorn on this

habitat feature at the time of surveys (Fig. 1).

Oil well and road density

   Oil development in the study area occurred gradually for the first three decades of the

study, and then increased rapidly from 2004-2013 (Fig. 6). The index of pronghorn

abundance was negatively related to oil well density (Fig. 1, Fig. 6), with large declines

occurring from 2008-2012 at a time when density of active oil wells increased

exponentially (Fig. 7). Our model predicted that oil development was associated with 8% of the 73% decline that occurred between 2008 and 2012 (the remainder being primarily due to winter conditions). When we mapped population growth rates ($\ln(N_{t+1}/N_t)$) for different survey units averaged over each decade of the study, growth rates were positive or stable for the first 30 years, but became negative for the last decade of the study (Fig. 7). The lowest growth rates at this time were in northern and eastern survey units, which corresponded to areas of intense oil development but also un-developed areas. The abundance index was negatively correlated with the density of primary and secondary roads, although wide credible intervals reflected considerable uncertainty about the magnitude of this effect (Fig. 1, Fig. 6). Our measure of road density did not change over time; therefore, this effect indicates spatial trends, such that abundance tended to be greater in units with low road densities.

Predation, harvest, and density dependence

Our analysis suggested that neither the index of coyote abundance nor human harvest had strong effects on pronghorn abundance (Fig. 1). The abundance index was positively correlated with counts the previous year, although the magnitude of this effect was small (Fig. 1).

Discussion

Pronghorn populations in North Dakota, while variable over the short-term, generally increased in abundance through the first three decades of the study, followed by a pronounced decline from 2008-2012 (Fig. 3). Much of the observed temporal variation

could be explained by winter weather conditions and changes in land-use related to oil and gas development. The combined effects of severe cold and snow were related to large reductions in pronghorn numbers, suggesting that severe winters were a primary factor in the decline that occurred during 2008-2012. Oil and gas development increased rapidly in the later years of the study and was negatively correlated with the pronghorn abundance index. We found little evidence that other factors such as coyote index and human harvest were strongly correlated with the abundance index. With more heavy precipitation events occurring in the winter (IPCC, 2013), pronghorn populations could experience more frequent or more pronounced declines, and continued energy development could exacerbate these effects. Alternatively, warmer winters under future climate scenarios (IPCC, 2013, Kunkel et al. 2013) might improve conditions for pronghorn in the state.

Effects of weather conditions

Pronghorn are poorly adapted to foraging and moving through snow (Telfer and Kelsall, 1984), and a lack of access to food, in combination with increased energetic demands during extended cold periods, can cause mass mortality events in this species (O'Gara and Yoakum, 2004). Pronghorn declines usually corresponded with periods of low temperatures and extreme snow. For example, the precipitous decline in pronghorn from 2008 – 2012 occurred during a period with an annual mean of 108 cold days and 31 snow days, whereas the increase in abundance that occurred from 1998-2005 corresponded with an annual mean of 94 cold days and 5 snow days. Winter weather patterns in the Great Plains are in large part dictated by large-scale climatic events such as the North Pacific Oscillation NPO and El Niño Southern Oscillation (Linkin and Nigam, 2008), and

these indices have been linked to wildlife population dynamics (Hegel et al., 2010; Hebblewhite, 2005; Ciuti et al. 2015). In North Dakota, the El Niño Southern Oscillation and Pacific Decadal Oscillation are positively correlated with warm, dry winters, whereas the North Pacific Index (NPI) is correlated with cold, snowy winters (Ciuti et al. 2015). The decline in pronghorn that occurred from 2008-2012 corresponded with positive NPI values in all years except for 2010 (Hurrell et al. 2015). Predictions of large-scale climate patterns may help managers to anticipate severe winters, and to set harvest objectives accordingly.

Contrary to predictions, pronghorn populations in our study area were not adversely affected by summer drought and in fact were positively correlated with drought conditions. This contrasts with studies by Brown et al. (2006), Simpson et al. (2007), and White et al. (2007) showing declines in abundance, fawn production, or doe survival after severe drought in New Mexico, Texas, and Wyoming. The influence of drought on pronghorn is likely to be strongest in regions where annual precipitation is low and highly variable such as the Chihuahuan Desert (Simpson et al., 2007). Our results suggest that pronghorn in North Dakota might be adapted to the range of drought conditions that occurred in the state from 1974-2013, but are limited to a greater extent by winter severity. The positive relationship we observed between abundance and drought conditions may have been an artifact of the relationship between PHDI and underlying weather systems (such as the El Nino Southern Oscillation) that drive large-scale patterns of precipitation (Kurtzman and Scanlon, 2007). Dry summers often follow winters with little snow, the latter having a positive effect on pronghorn, thereby potentially causing a spurious correlation with PHDI.

Spatial patterns of abundance

Pronghorn in North Dakota reach the highest densities in the southwestern corner of the state. This region represents the core of pronghorn range in North Dakota, and overlaps the northern part of the sagebrush steppe ecoregion (Bryce and Clark, 1996). Marginal habitats in northwestern and central North Dakota likely experience more pronounced population fluctuations than optimal habitats and may serve as population sinks (Kohlmann, 2004). The negative population growth rates observed in the northern and eastern parts of our study area lend support to this idea (Figure 7). These fluctuations in marginal habitats are a result of emigration, mortality, and reduced fawn recruitment during population declines (Jacques et al., 2009; Kohlmann, 2004), and may be linked to a lack of sufficient grasses, forbs and woody shrubs available above the snow, especially during severe winters (Bruns, 1977; Barret, 1982; Sievers, 2004) .

Agricultural land-use and sagebrush

Although many forms of agriculture reduce the amount of suitable habitat for pronghorn, some agricultural land types (such as wheat, alfalfa, and rangeland used by cattle) are extensively used by pronghorn during the summer months (Kolar, 2009). Surprisingly, pronghorn counts were negatively related to alfalfa and pasture in our study, although effect sizes were small. The amount of land allocated to pasture and alfalfa stayed relatively stable over time, and correlations may therefore be due to coarse-scale geographic patterns of land use and abundance, such that alfalfa and pasture were concentrated in southeast and southcentral regions, where the abundance index was relatively low. Furthermore, seasonal patterns of habitat use may explain the negative

correlations with alfalfa. Pronghorn are known to forage in wheat fields in both summer (Griffin, 1991) and winter (Torbit et al. 1993), whereas the use of alfalfa tends to be greatest in the early spring and fall (Griffin, 1991). As expected based on their association with native grassland and sagebrush-dominated ecosystems, we found a positive correlation between pronghorn abundance index and the proportion of sagebrush in the survey unit, although credible intervals were wide for this parameter. Pronghorn are more heavily dependent on shrubs like sagebrush for food during the winter months, at which time snow impedes access to other food sources (Griffin, 1991; Yoakum, 2004).

Effects of oil and gas development and roads

Our results support previous conclusions that pronghorn are negatively affected by oil and gas infrastructure (Kolar, 2009; Beckmann et al., 2012). The observed inverse relationship between the index of pronghorn abundance and oil well density is likely due to a combination of increased vehicle traffic and habitat fragmentation associated with oil development. Parts of North Dakota with high oil-well densities have extremely high traffic volume, thereby posing a barrier to seasonal movements as well as a source of additional mortality (O'Gara and Yoakum, 2004; Beckmann et al. 2012). Negative population growth rates in the last decade of the study occurred both in areas of intense oil development *and* un-developed areas, indicating that other factors (e.g. climate) were responsible for the majority of the population crash from 2008-2012. Nevertheless, oil and gas infrastructure reduces the net primary productivity of forage plants (Allred et al., 2015) and is projected to reduce sagebrush and grassland habitat by 3.7 and 1.1 million hectares, respectively, over the next 20 years in the US Intermountain West (Copeland et al., 2009). This will

restrict resource availability for pronghorn during the summer and winter months. High

densities of wells were located in the southwestern part of the survey area, overlapping

valuable sage-steppe habitat that represented the core of pronghorn range in North

Dakota. Our results indicate that in addition to oil-well density, road density was negatively

correlated with pronghorn abundance. High-traffic roads, often flanked by impenetrable

fences, can restrict the ability of pronghorn to migrate between foraging areas (Gates et al.,

2012; O'Gara and Yoakum, 2004).

The interactive effects of severe winters and increased fragmentation of the landscape by

well pads and associated roads may be significant, and are cause for concern for

pronghorn. In winters with heavy snowfall or extreme temperatures, pronghorn

populations are buffered by their tendency to migrate to areas with more accessible forage,

warmer temperatures, and/or less snow (O'Gara and Yoakum, 2004). However, in areas

with high densities of wells and roads, their migration may be impeded and the total area

of winter habitat available to them is reduced (Copeland et al., 2009).

Temporal auto-correlation and density dependence

  The index of pronghorn abundance was positively correlated with counts the previous

year, indicating temporal auto-correlation among counts, although the magnitude of this

effect was small. Similar to populations in Wyoming (White et al. 2007), pronghorn in

North Dakota may exhibit density-dependent fluctuations in abundance such that at

maximum carrying capacity (K), population declines occur. *K* likely fluctuates within and

among years depending on snow fall, such that many of the shrubs that pronghorn depend

upon in the winter are inaccessible in years with heavy snow fall, and lower densities of

animals can be supported at these times. Detection of density dependence can be difficult

unless substantial perturbations reduce abundance so that the approach to carrying

capacity can be monitored (Fowler et al., 2006). Accordingly, the population crash that

occurred during 2008-2012 might have been worsened by high population densities in the

study area. Pronghorn exhibited similarly irruptive population dynamics in Wyoming,

where a release from intensive culling resulted in rapid population growth followed by a

population crash due to degradation of sagebrush habitat on the winter range (White et al.,

2007). Animal populations track seasonal variation in K, and harvest theory has been

advanced to accommodate this (Boyce and Daley, 1980; Boyce et al., 1999; Xu et al., 2005).

For many species, density dependence is usually strongest as populations exceed seasonal

K during severe winters, and harvest may reduce competition for winter forage at this time

(Murton et al., 1974; Boyce et al., 1999; Xu et al. 2005).

Conservation and management implications

  Our results indicate that pronghorn in North Dakota are susceptible to severe winter

weather, similar to other species of ungulate in North America (Hebblewhite, 2005;

Johnston, 2013; Ciuti et al. 2015). The frequency of blizzards has increased over the past

several decades (Schwartz and Shmidilin, 2002), and projected increased winter storm

frequency (IPCC, 2013, Kunkel et al. 2013) may negatively impact pronghorn populations

(Boyce et al., 2006). Whether expected warmer winter temperatures (Kunkel et al. 2013)

might counteract this effect is unknown. Structurally diverse sagebrush and native prairie

habitat may help to buffer the population against winter mortalities by providing adequate

food during times of heavy snowfall (Bruns, 1977; Amstrup, 1978; Sievers, 2004).

Therefore, the long-term maintenance of stable pronghorn populations in the northern

Great Plains requires structurally diverse native prairie. Over the past few decades, native

grassland habitat in the prairies of North America has been converted to agriculture and oil

and gas infrastructure at an unprecedented rate. Increased demand for biofuel production,

in conjunction with restrictions on allowable hectares enrolled in CRP land has reduced the

amount of land set aside for conservation, as well as land devoted to small grain production

(Fargione et al., 2009; Wright and Wimberley, 2012; Johnston, 2013). Similarly, oil and gas

development has resulted in the widespread conversion of land otherwise devoted to

agriculture, cattle grazing, and conservation, resulting in a loss of net primary productivity

equivalent to 10 Tg of dry biomass in central North America since 2000 (Allred et al.,

2015). These threats to native prairie can be mitigated by prioritizing the conservation of

important habitat for wildlife, for example by placing new developments in disturbed areas

and using existing oil and gas infrastructure for further development (Dyke et al., 2010).

   In the mixed- and short-grass prairie region of North Dakota, only 27% remained in its

native state as of the late 1990's (Jensen, 2001; Seabloom, 2011). With recent increases in

commodity prices, particularly corn, native prairie that was once considered marginal

farmland is now being converted to crop production at a steadily increasing rate (Stephens

et al., 2008; Doherty et al., 2013; Lark et al., 2015). Additionally, large tracts of grasslands

are being treated mechanically and chemically to remove forbs and shrubs. Judicious use

of these management techniques can benefit both livestock grazing and wildlife on the

Great Plains (Richardson et al., 2001; Autenrieth et al., 2006, Fox et al., 2009). Agricultural

practices are not necessarily incompatible with wildlife conservation, and certain crops

such as wheat can provide important habitat for pronghorn, as we have shown. However,

widespread conversion of native vegetation has been known to reduce avian diversity

(Rodgers and Sexson 1990) and negatively affect threatened species such as such greater

sage-grouse (*Centrocercus urophasianus*; Martin 1970; Wallestad 1975). Historically,

managers have encouraged the removal of 75% or more of the sagebrush to maximize

grass forage production (Hull et al., 1952; Alley, 1956). As a result, much of the historical

sagebrush vegetation has been removed or fragmented (Schlaepfer et al., 2014). Future

research should focus on the regional impacts of changing agricultural practices, the

implications of converting native prairie to cropland, and the subsequent impacts of these

actions on wildlife.

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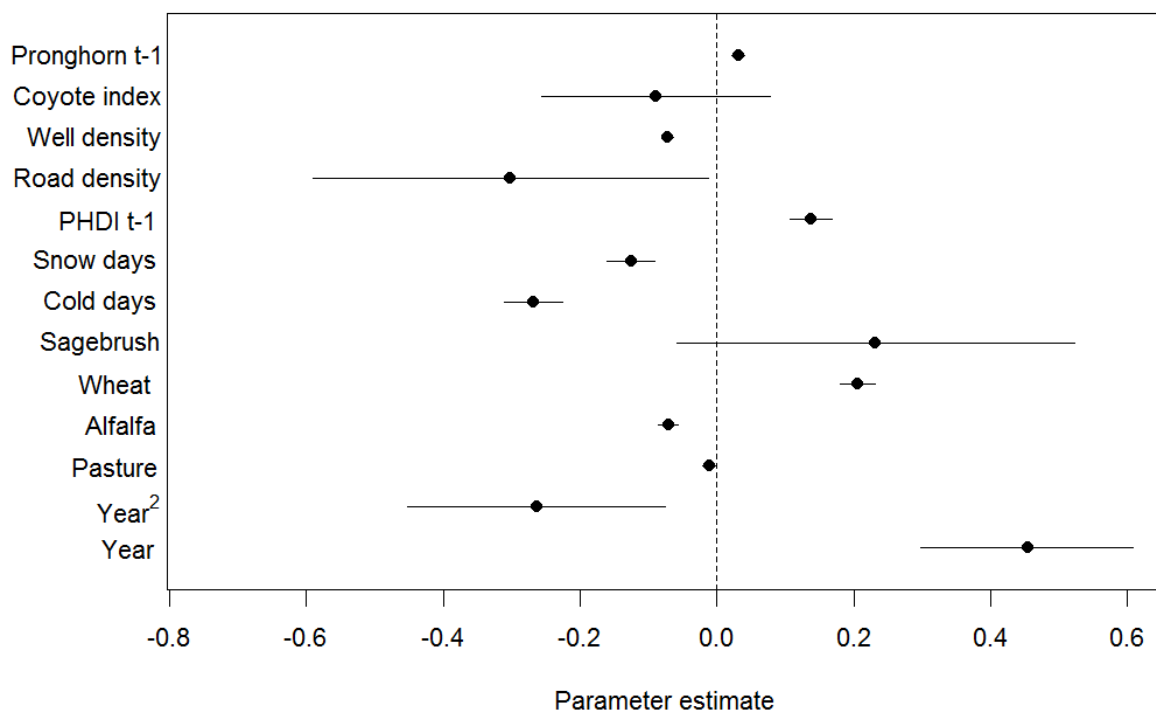
Figures

Fig. 1. Parameter estimates and 95% credible intervals from the Bayesian hierarchical model of pronghorn abundance index.
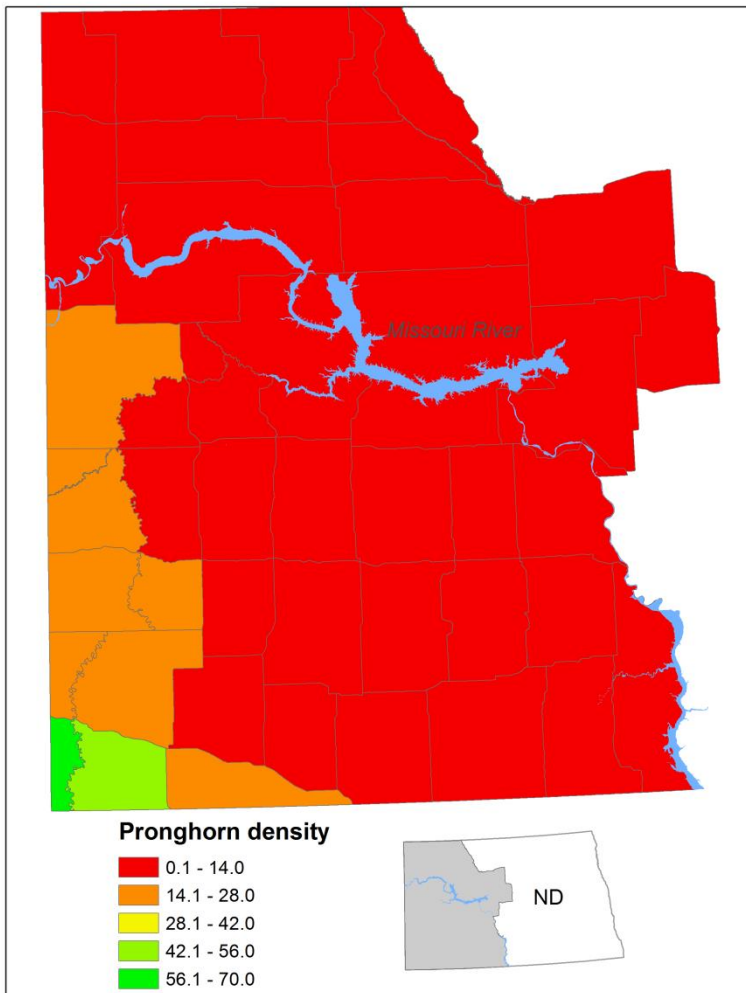
Fig. 2. Pronghorn density (pronghorn per 100 km^2) across western North Dakota. Density was calculated as the mean of each survey unit across all years (1974 – 2013) for which there were survey data for each individual unit. Polygons represent survey units.
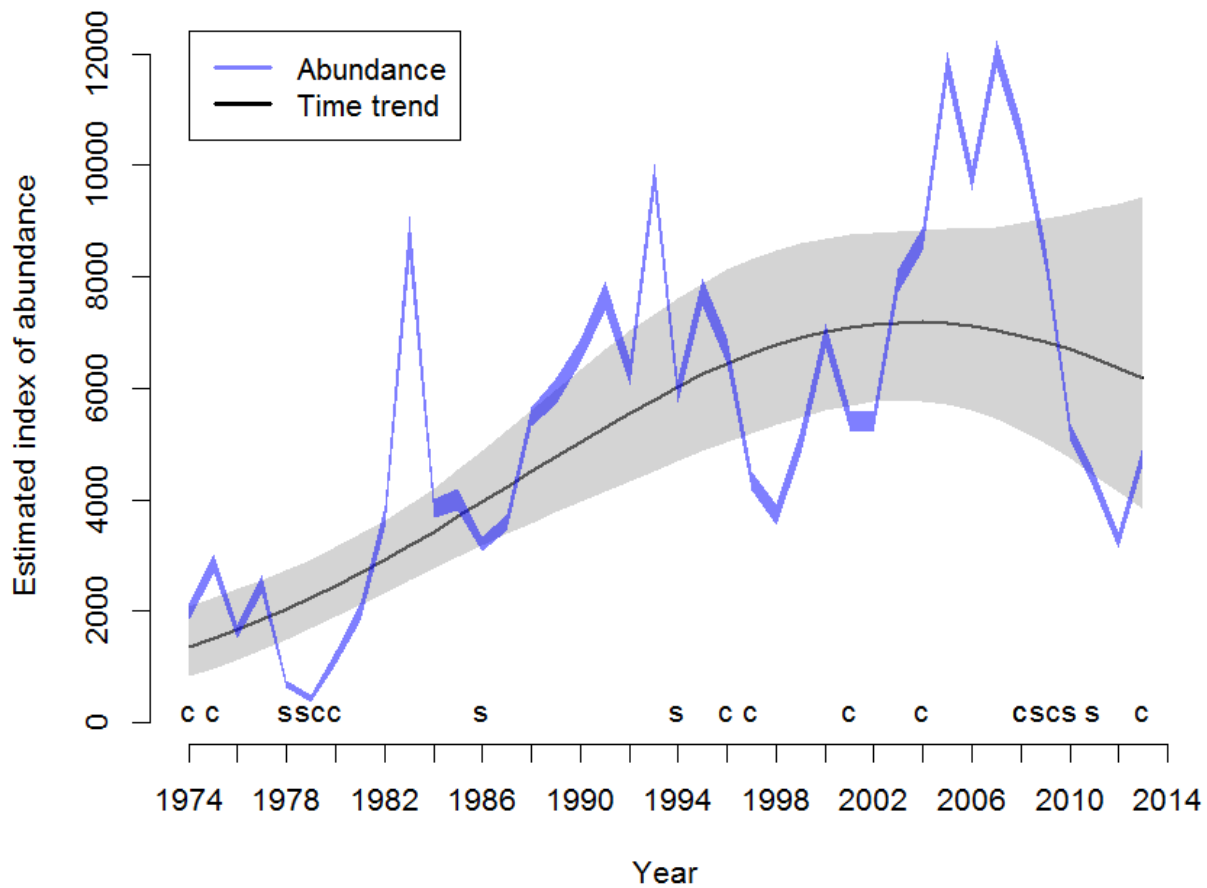
Fig. 3. Estimated index of abundance of pronghorn over time (blue line) with 95% credible intervals (blue shading), totaled across all survey units. The year trend is also shown (black line). Years that met the threshold for cold (more than 120 days with minimum temperatures ≤ -7°C), snow (more than 37 days with snow depth ≥ 36 cm), or both are denoted by "c", "s", and "sc", respectively.
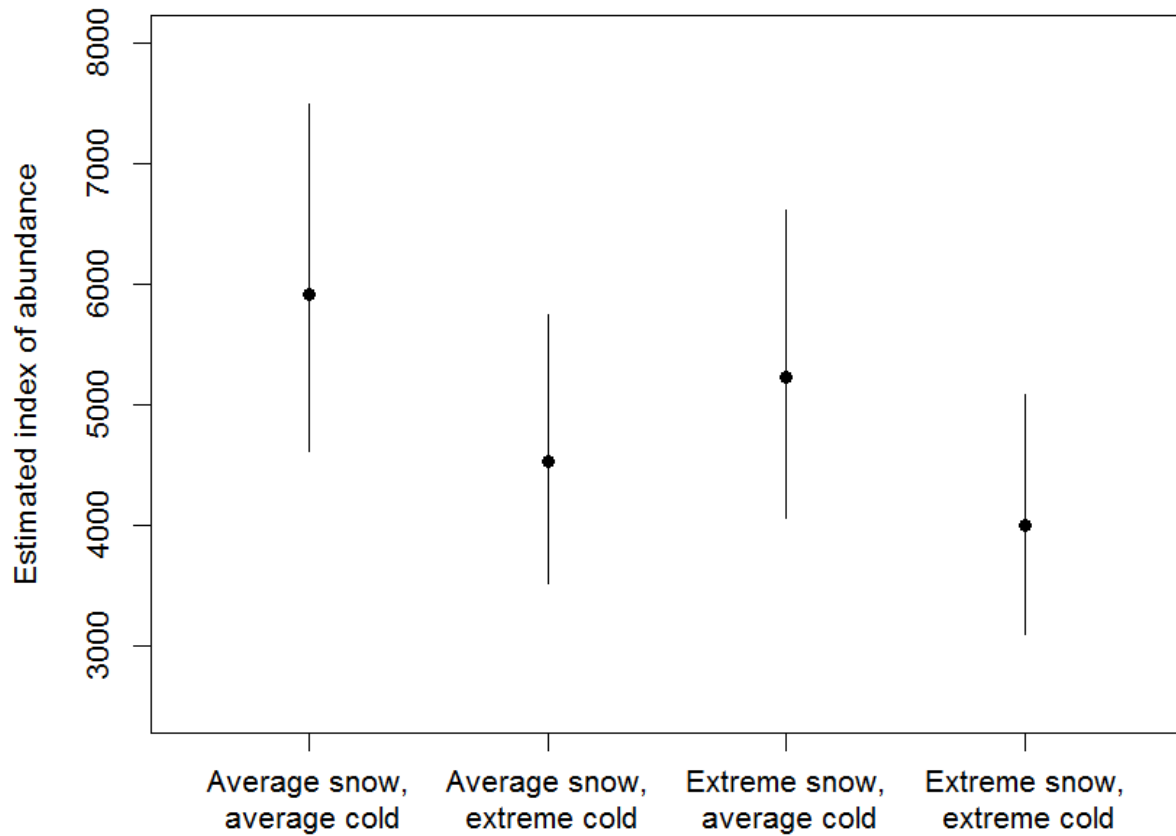
Fig. 4. Estimated index of abundance of pronghorn under different winter weather scenarios, with 95% credible intervals. Mean levels of all other modeled covariates were used in predictions.
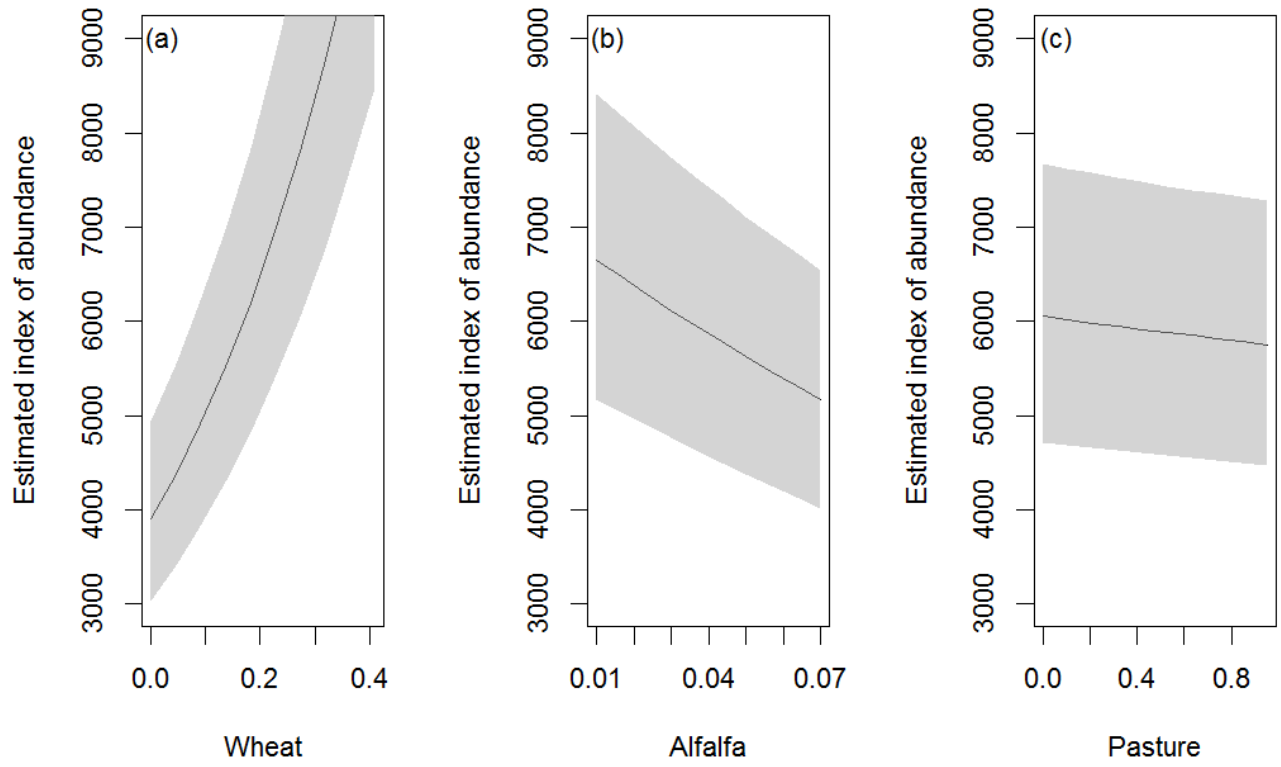
Fig. 5. Estimated index of pronghorn abundance with increasing proportion of wheat (a), alfalfa (b), and pasture (c). 95% credible intervals are shown. Mean levels of all other modeled covariates were used in predictions.
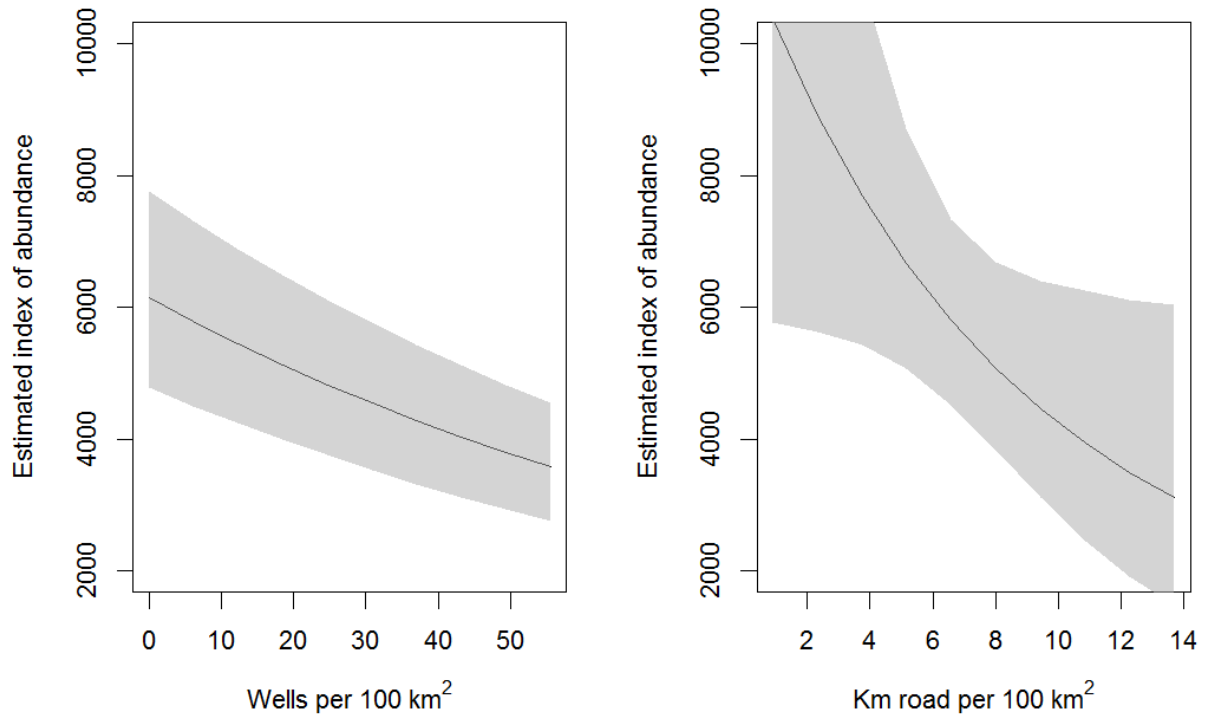
Fig. 6. Estimated index of pronghorn abundance with increasing active well and road density. 95% credible intervals are shown. Mean levels of all other modeled covariates were used in predictions.
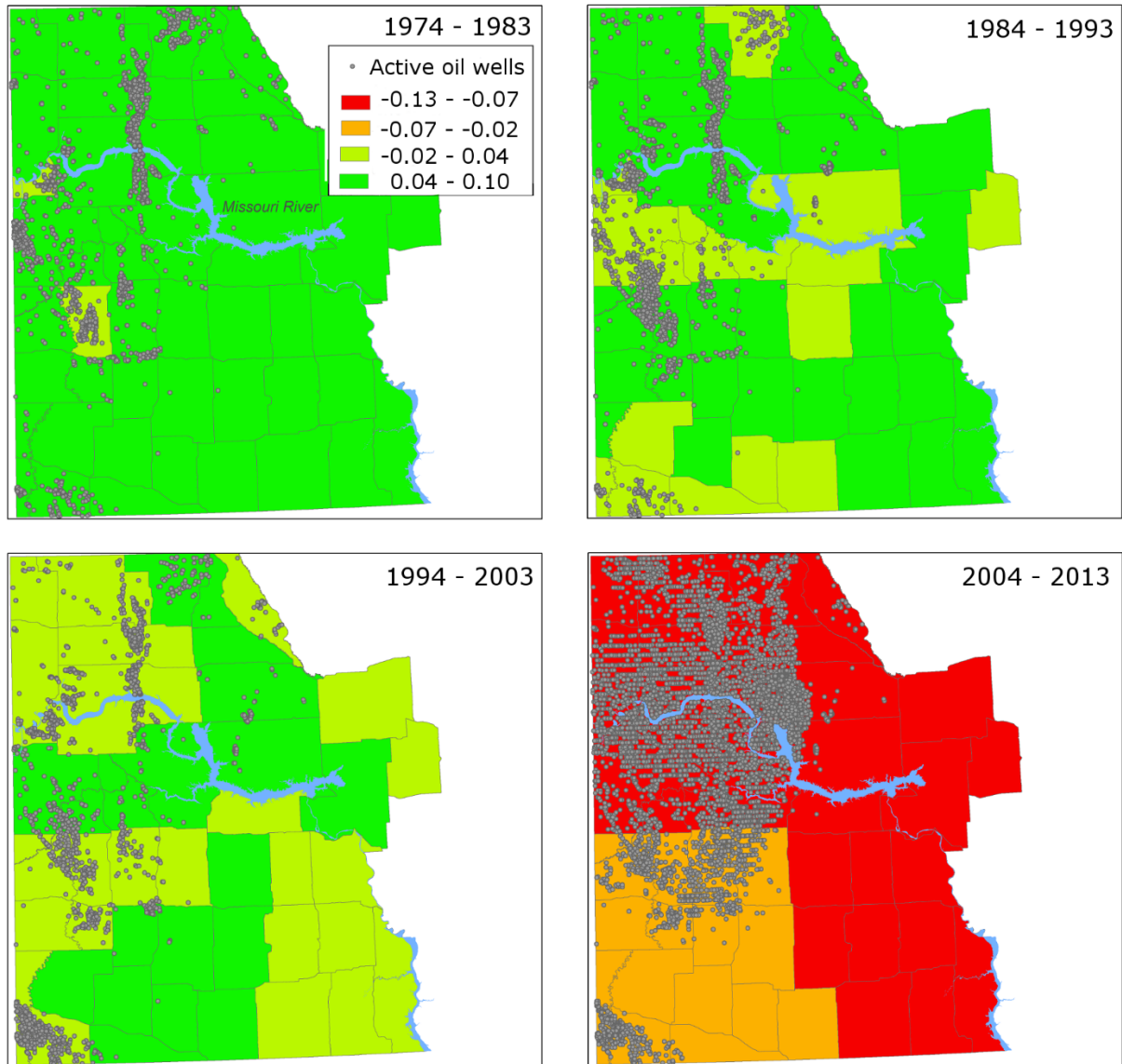
Fig. 7. Maps of decadal population growth rates ($\ln(N_{t+1}/N_t)$) for pronghorn in western North Dakota calculated from model estimates of abundance indices. Positive (green) and negative (red) numbers indicate increasing and decreasing pronghorn populations, respectively. Also shown are active oil wells at the end of each decade.

Chapter 2: Habitat selection and fawn production by pronghorn in a human-altered landscape

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Abstract

Our understanding of fine-scale habitat selection can be enhanced by information on habitat-specific reproductive success. Highly-selected habitats can confer reproductive benefits to animals; however, this is not always the case. We analyzed patterns of female pronghorn (*Antilocapra americana)* habitat selection and fawn production in two years with contrasting pronghorn density and oil production in western North Dakota (2006 and 2014). We quantified resource selection and fawn production relative to proximity to active wells, road density, land cover, development, NDVI (normalized difference vegetation index) and agricultural practices. We also assessed patterns of well placement relative to the same environmental variables. We found that pronghorn selected areas with low NDVI and sagebrush habitats, but avoided developed areas, roads, forests, and wetlands. Pronghorn selected habitats close to oil wells which was likely due to the fact that wells were located in high-value habitats such as native grassland and sagebrush-steppe ecosystems. For the majority of variables tested, selection was stronger when pronghorn density was low, consistent with current resource selection theory. Fawn production was positively correlated with NDVI, in contrast to observed patterns in resource selection. Despite the fact that pronghorn females selected relatively open habitats, high fawn: doe ratios were observed in areas with high vegetation biomass within habitats selected by females. This indicates that tradeoffs exist between early predator detection and concealment of young at time of high fawn vulnerability to predators.

Keywords: *Antilocapra americana,* fitness, fracking, habitat selection, herbivore, oil development, pronghorn, reproductive success, resource selection function, sagebrush

Introduction

Selection of habitats determines animal distributions over space and time, and has consequences for individual fitness, population dynamics, interspecific interactions, and speciation (Morris 2003; Fortin, Morris & McLoughlin 2008). Understanding habitat selection is critical to successfully protect key resources for wildlife on increasingly human-altered landscapes. Habitat selection, however, is not static, and varies over time, space, and with varying levels of predation and competition for resources (McLoughlin *et al.* 2010). For example, selection of highly productive grasslands by feral horses (*Equus ferus caballus*) became weaker as populations approached carrying capacity and many individuals were forced to use low-quality sites (van Beest *et al.* 2014). Habitat selection therefore should be considered as a dynamic phenomenon, dependent upon intrinsic and extrinsic factors that influence a population at any given time.

Information on fine-scale habitat selection can be complemented by data on reproductive success and survival to anticipate the fitness value of selected habitats. Generally, the use of or preference for habitats reflects the quality of resources within that habitat, and in turn relates to habitat-specific fitness outcomes (McLoughlin *et al.* 2006). However, occurrence is not always a good indicator of fitness, and animals can select "sink" habitats that do not confer fitness benefits (Pulliam 1988). This has been known to occur in human-altered environments, where anthropogenic changes happen so quickly that animals are no longer able to make optimal habitat selection decisions (Remes 2000; Bock & Jones 2004). This phenomenon of animals settling and breeding in "ecological traps" has been documented in numerous systems (Dwernychuk & Boag 1972), including passerines that breed in edge

habitat prone to high rates of nest-predation and parasitism (McCollin 1998) and greater

sage-grouse (*Centrocercus urophasianus*) hens that select sink habitats near oil wells,

resulting in low chick survival (Aldridge & Boyce 2007).

The pronghorn (*Antilocapra americana*) is a North American sagebrush-dependent species

that occupies highly fragmented habitats. Pronghorn are adapted to sagebrush and

grasslands, and concerns exist about how roads, oil and gas infrastructure, and expanding

agriculture influence their populations (Rosenzweig 1991; Yoakum 2004; Beckmann *et al.*

2012; Gates *et al.* 2012; Seidler *et al.* 2014). Pronghorn occur in areas with a mixture of

grasses, forbs, and shrubs, and typically avoid steep terrain, forests, and certain types of

crops (Yoakum 2004). During summer pronghorn often are associated with native

grasslands as well as fields of alfalfa, wheat, and hay (Torbit *et al.* 1993; Yoakum 2004;

Kolar 2009). In winter, pronghorn rely heavily on sagebrush and other shrubs; deep snow

in northern parts of their range necessitates seasonal migrations to areas with sufficient

amounts of available forage (Yoakum 2004; Kolar 2011). These seasonal migrations can be

impeded by fences, highways, and heavy snowfall, and bottlenecks can occur adjacent to

roads and fences in the winter where there can be heavy mortality (O'Gara 2004; Seidler *et

al.* 2014). Placement of oil wells in pronghorn habitats further fragments the landscape,

reduces net primary productivity, and can contribute substantially to the volume of local

vehicle traffic (Kubas & Vachal 2014; Allred *et al.* 2015). In Wyoming, pronghorn

abandoned areas with large gas-infrastructure footprints over a 5-year period of gas

development (Beckman *et al.* 2012). In North Dakota, where oil development has increased

exponentially over the past decade, there appears to be overlap between oil well placement

and pronghorn habitat use at coarse scales. This is likely due to state and federal

facilitation of permitting on native prairie held in public ownership (i.e., State School land

administered by North Dakota Department of Trust Lands, Little Missouri National

Grasslands administered by US Forest Service, Bureau of Reclamation Lands), and the

desire to avoid cropland and place on rangeland when the surface is held in private

ownership.

In this study, we quantified resource selection by female pronghorn over a period of time

(2006-2014) that corresponded with a decline in the pronghorn population (Christie *et al.*

2015). Total counts of pronghorn (based on aerial surveys) in the study area decreased

from 9239 animals in 2006 to 4886 animals in 2014 (Figure 1). Meanwhile, significant oil

and gas development occurred within the study area, and the number of active wells

increased from 1122 in 2006 to 2688 in 2014 (Figure 1). We used resource selection

functions (RSFs) to model the difference between used and available units, thereby

quantifying habitat selection by female pronghorn at a time in their life cycle when habitat

selection decisions are critical for fawn survival (Boyce & McDonald 1999; Manly *et al.*

2002; O'Gara 2004). We addressed the following questions based on locations of

pronghorn groups detected during aerial surveys in early July: 1) What environmental

variables distinguish areas selected by pronghorn from available units? 2) Did pronghorn

avoid oil and gas wells or roads at the time of surveys? 3) Did patterns of resource selection

change from 2006 to 2014? 4) Did habitat types selected by pronghorn also confer fitness

benefits in the form of high fawn:doe ratios, or were different environmental variables

linked with high fawn production? And lastly, 5) in what habitat types were oil wells

typically built, and did these overlap with habitats selected by pronghorn? Based on our knowledge of pronghorn habitat associations, we predicted that pronghorn would select sagebrush and grassland-dominated landscapes as well as alfalfa and wheat fields, and female pronghorn occupying these habitats would produce more fawns. Based on previous studies of pronghorn response to development, we predicted that they would avoid both well pads and roads. Lastly, we expected pronghorn selection coefficients to be stronger when density was low (2014) compared to when pronghorn density was high (2006).

Materials and methods

Study area

This study took place in the Missouri Plateau, Sagebrush Steppe, and Little Missouri Badlands ecoregions of western North Dakota (Omernik 1995). The native vegetation is predominantly grasses, forbs, and sagebrush (*Artemisia* spp.)(Seabloom 2011; Johnson *et al.* 2012), but much of the region is privately owned and cultivated for crops or cattle ranching. Main crops grown in the region include spring and durum wheat, canola, sunflowers, hay, and corn. Sagebrush is dominant in the south-western portion of the study area, with grasslands dominating the rest of the region. Trees and shrubs grow in proximity to the Missouri River and its tributaries, as well as lakes, reservoirs, and stock ponds throughout the study area. The rugged Little Missouri Badlands run through the western part of the state, and consist of sparsely vegetated cliffs and buttes interrupted by wooded arroyos and slopes with a northern and easterly aspect with a canopy predominantly of green ash (*Fraxinus pennsylvanica)* Rocky Mountain juniper (*Juniperus scopulorum)* (Bluemle 1977, Seabloom 2011).

Pronghorn surveys

Aerial surveys for pronghorn were conducted annually using standardized protocols and intensive training of observers. Surveys were conducted from small fixed-wing aircraft such as Piper Supercub (Piper Aircraft, Vero Beach, FL) or Scout (American Champion Aircraft Corporation, Rochester, WI). Each tier of 1 square mile sections (1.6 km^2) was flown, following the center line of the tier (½ mile line of each tier between section lines within a survey unit) at 1.6 km intervals. A pilot and observer team recorded all pronghorn observed within a 0.8 km strip on either side of the plane. Surveys were flown at an altitude of 76 - 106 m and an average speed of 129 kph. In rougher badlands terrain, the aircraft followed terrain contours to ensure full visual coverage of the survey unit. When pronghorn were detected, a GPS waypoint was taken to mark their location, and information on age (fawn vs. adult), and sex of each individual was recorded. Detection probability was assumed to be less than 100%, but constant across years and locations. We believe this to be a safe assumption because the terrain was fairly open and homogeneous, and standardized protocols were followed by trained personnel.

Environmental covariates

We restricted this analysis to groups of pronghorn containing at least one fawn; therefore, our inference was for fawn:doe groups only. We created a 500-m buffer around each observed pronghorn group, and considered the resulting 0.785-km^2 resource units to be "used" by pronghorn. We generated a dataset of "available" 500-m resource units randomly located throughout the survey area for comparison with used resource units. The

number of randomly generated available units was five times the number of used units. We

chose the 500-m scale to represent fine-scale habitat selection by pronghorn, with the goal

of differentiating between used and available resource units. We summarized

environmental data within this buffer. We used the USGS GAP land cover data set (USGS

2011) based on Landsat TM satellite imagery to quantify the proportionate cover of the

following land cover types in each 500-m (radius) resource unit: sagebrush steppe,

grassland, development (including urban centers, industrial areas, and roads), woodland,

shrubland (shrubs and young trees often in close proximity to woodland and wetlands),

badlands (including sparsely vegetated clay and rocky slopes, cliffs, and arroyos), wetlands

(including stock ponds and vegetated wetlands), and pastureland intended for cattle

grazing. We obtained year-specific spatial data on alfalfa, corn, and wheat production from

the Cropland Data Layer (Cropscape) provided by the National Agricultural Statistics

Service (National Agricultural Statistics Service 2015). We calculated an index of

ruggedness in ArcGIS using a Vector Ruggedness Measure script based on digital elevation

models. The ruggedness index differentiates between even and broken terrain (0 = flat and

even terrain, 1 = highly heterogeneous, broken terrain), and provides a representation of

escape terrain for mammals (Sappington, Longshore & Thompson 2007). Normalized

Difference Vegetation Index (NDVI) data were used to indicate vegetation biomass, and is

strongly correlated with aboveground net primary productivity (Tucker & Sellers 1986;

Box, Holben & Kalb 1989). Composite images from the month of July were obtained from

USGS's archived Web-Enabled Landsat Data (WELD) for 2006 and from USGS's

EarthExplorer for 2014. For each unit, we calculated the distance to the nearest active oil

well in 2006 and 2014, and well locations were obtained from the North Dakota

Department of Mineral Resources (DMR). We included oil and gas, salt water disposal, water supply, and injection wells, all of which were considered high or moderate use according to DMR. We used two variables related to roads in our analysis: 1) the density of all roads (any type) in each unit, and 2) the distance to the nearest state or federal highway. Data layers depicting roads and highways were obtained from the North Dakota Department of Game and Fish.

RSF analysis

We analyzed data from 2006 and 2014 separately because we were interested in whether the importance and relative strength of the different covariates varied between years. Prior to conducting the analysis, we tested for correlations between covariates using the Pearson's correlation using a threshold of $r = 0.7$ (Dormann *et al.* 2013). We used AIC to determine which of the correlated variables was a better predictor of habitat selection by pronghorn, and included it in subsequent models (Burnham & Anderson 2002). We divided the environmental variables into five categories: 1) land cover (sagebrush steppe, shrub, woodland, wetland, hay/pasture, development, badlands, grassland, ruggedness), 2) agriculture (alfalfa, corn, wheat, total crops), 3) roads (road density, highway distance), 4) distance to the nearest active well, and 5) NDVI (NDVI and $NDVI^2$). $NDV1^2$ was included in models to test for non-linear relationships with biomass (i.e., pronghorn might select habitats with intermediate vegetation biomass). We tested all possible combinations of these five categories, in addition to the null model with only a constant term. We fit a total of 32 models using logistic regression in Program R (R Development Core Team 2010). We evaluated the relative support for each model of habitat use using AIC (Burnham and

Anderson 2002). Covariates were scaled to the mean prior to analysis. To create maps of pronghorn selection in the study area, we used the highest-ranked model to predict pronghorn selection in 500×500 m grid cells, each of which was associated with a suite of environmental variables.

K-fold cross-validation

We evaluated models using k-fold cross-validation (Boyce *et al.* 2002). We randomly divided the pronghorn location data into five equal datasets to be used in the cross-validation process. In each step, 20% of the pronghorn data would be withheld from the analysis to be subsequently used for validation (Huberty 1994). RSF models were constructed based on the remaining training data (80%). After models were run, the random "available" locations were ranked according to the RSF scores calculated from RSF models, and these were binned into 10 equally sized groups. Then, using the model parameters obtained from the training data, we predicted the probability of occurrence of pronghorn for each withheld resource unit, with the expectation that if the model had high predictive power, most pronghorn observations should fall within the highest RSF bins. We tallied the number of predicted observations in each of the 10 bins, and used a Spearman-rank correlation to test the correlation between the frequency of withheld locations in each bin and the ranking of each bin based on the original data. The analysis was repeated five times, with different sets of the training and validation data, and correlations were averaged.

Fawn:doe analysis

We were interested in quantifying patterns of fawn production within sites selected by female pronghorn, and wanted to test whether the environmental conditions that were selected by females also resulted in high fawn: doe ratios. To test this, we divided the study area into 500×500 m grid cells, and calculated mean fawn:doe ratios for each grid cell containing at least one group of pronghorn. A separate analysis was conducted for 2006 and 2014 data. We summarized environmental data for each grid cell in ArcGIS. Fawn:doe ratios were log-transformed to achieve normality, and correlations among environmental variables were tested using Pearson's correlations. The same 32 models combining land cover variables, agricultural data, NDVI, roads, and wells were fitted using linear regression, and models were compared using AIC.

Analysis of well occurrence

To determine correlations between well site placement and environmental variables, we conducted a similar analysis to the one we used to estimate resource selection by pronghorn. To describe the results of this analysis, we use the term "occurrence," which for our purposes is synonymous with selection. We created a 500-m buffer around each well location in 2014, and generated a set of random locations in the study area. For each "used" and "available" location, we summarized environmental variables, and used logistic regression to fit 16 models of all combinations of four environmental categories: land cover variables, agricultural data, roads, and NDVI. The most parsimonious model describing sites selected for well locations was selected using AIC. Again, K-fold cross-validation was used to evaluate alternative models (Boyce et al. 2002).

Results

Adult Female Pronghorn resource selection

For the analysis of adult female pronghorn habitat selection in 2006, total crop cover, wheat cover, and grassland cover were highly correlated ($r > 0.7$) and could not all be included in the same model. The model of grassland cover fit the data better than the other two covariates according to AIC, and was therefore used in subsequent models of land cover. Additional correlations were found between our ruggedness index and shrub cover, forest cover, and badlands cover. The ruggedness index did not fit the data as well as the other covariates and was therefore dropped from models. The most parsimonious model of pronghorn habitat selection in 2006, with an AIC weight of 0.81, included the terms land cover, NDVI, wells, distance to roads, and road density (Table S1). Selection by pronghorn was positively correlated with sagebrush, and negatively correlated with badlands, wetlands, woodland, hay/pasture, shrubs, development, and NDVI (Figure 2). Female pronghorn selected units close to wells, but far from roads. Selection was negatively correlated with densities of roads (Figure 2). Estimates for the effects of grassland cover and $NDVI^2$ had large standard errors, indicating uncertainty as to whether the effect of these parameters overlapped zero. K-fold cross-validation of the pronghorn RSF model indicated that strong correlations existed between predicted and actual occurrence of pronghorn (mean $r_s = 0.92$, $p < 0.001$).

For the 2014 analysis, grassland cover and ruggedness were dropped from models due to stronger correlations with other variables. Four models received equal support, as indicated by their model weights, which ranged from 0.20 to 0.30 (Table S1). We chose to

interpret parameter estimates from the simplest model (land cover + wells + roads, AIC

weight = 0.30) because the other models in the top model set included parameters (for

NDVI and agriculture) that were estimated with very high uncertainty (95% confidence

intervals overlapped zero). Similar to the 2006 analysis, pronghorn RSFs had positive

coefficients for sagebrush cover, and negative coefficients for badlands, wetlands,

woodland, hay/pasture, shrubs, and development (Figure 2). Pronghorn selected units far

from roads, but close to wells (Figure 2). Selection coefficients for 8 of the 10 parameters

estimated in both years were greater in magnitude in 2014 compared to 2006, and the

reverse was true for only 2 out of 10 parameters (Figure 2). Stronger avoidance of roads

and development was observed in 2014 compared to 2006, but the negative correlation

with well distance was also more pronounced in 2014 compared to 2006 (Figure 2).

Results of the k-fold cross validation showed strong correlations between predicted

selection and actual occurrence (mean r_s = 0.95, p<0.001). Maps of predicted selection by

pronghorn over the study area in 2006 and 2014 were similar, and indicated that

environmental conditions were most conducive to high pronghorn occurrence in the

southwest corner of the study area. Low occurrence of pronghorn was predicted near the

rugged badlands, rivers and wetlands, and developed areas including roads and cities in

both years (Figure 3).

Fawn:doe ratios

For the analysis of fawn:doe ratios in 2006 and 2014, the variables wheat, grassland, and

shrubs were excluded from analysis due to correlations with other variables. The highest-

ranked model had an AIC weight of 0.69 and included only NDVI and NDVI[2] (Table S2).

Fawn: doe ratios were positively correlated with NDVI (Figure 4), which contrasts with the negative correlation between NDVI and pronghorn habitat selection in 2006 (Figure 2). This indicates that although female pronghorn selected areas with relatively low NDVI or greenness in 2006, fawn:doe ratios were higher in areas of high NDVI within those areas selected by pronghorn. In 2014, the highest-ranked fawn:doe model, with an AIC weight of 0.28, included NDVI and distance to the nearest well. The next-best model, with an AIC weight of 0.18, included wells and agriculture, but 95% confidence intervals for the effect of agricultural variables overlapped zero; therefore, estimates were interpreted from the model that received the most support. Fawn:doe ratios in 2014 were positively correlated with NDVI, and negatively correlated with distance to the nearest well (Figure 4).

Well occurrence

Because female pronghorn selected units close to wells (Figure 2), and fawn production was relatively high near active wells in 2014 (Figure 4), we conducted an analysis of well occurrence to determine whether wells were placed in areas of high habitat value to pronghorn. Total crop cover and ruggedness were dropped from models due to strong correlations with other variables. The highest-ranked model of well-site selection (AIC weight = 1.0) included land cover, agriculture, NDVI, and roads (Table S3). Similar to pronghorn RSF, occurrence of wells was positively associated with sagebrush, and negatively associated with badlands, wetlands, hay/pasture, development, and NDVI (Figure 5). Wells sites were positively correlated with grasslands, wheat, and alfalfa, and were situated in areas with high road density, and in close proximity with major highways.

Results of the k-fold cross validation showed strong correlations between predicted site selection and actual occurrence of wells (mean r_s = 0.98, p<0.001).

Discussion

Our results show that pronghorn consistently selected sagebrush steppe habitats, and avoided wetlands, woodlands, shrubland, hay fields, pastures, and the rough terrain of the Little Missouri badlands. These findings are largely consistent with other studies of pronghorn throughout their range (Griffin 1991; Yoakum 2004; Kolar 2009). In 2006, adult female pronghorn selected sites with low NDVI, indicating an avoidance for areas with high vegetation biomass, such as corn fields, tall warm season grasses, and woodlands (Paruelo and& Lauenroth 1995; Wang, Zhong & Yang 2014). This is not surprising, because pronghorn typically avoid habitats with vegetation taller than 76 cm (Yoakum 2004).

Adult female pronghorn avoided areas with high densities of roads and highways, as well as developed areas, which agrees with other research on pronghorn habitat selection in North Dakota (Kolar 2009). Pronghorn have difficulty crossing roads, many of which are lined with livestock fencing, and typically avoid fenced roads and right-of-ways (Sheldon 2005). Roads pose an impediment to migration of pronghorn within and between seasonal ranges and are a major concern for pronghorn conservation (Ockenfels, Carrel & VanRiper 1997; Gates *et al.* 2012). In addition to roads, pronghorn in our study avoided the "developed" land class in our USGS GAP vegetation layer, which corresponds to roads, low and high intensity residential areas, and industrial areas.

Despite this avoidance of human-impacted areas, adult female pronghorn did not show an obvious avoidance of well pads in our study, or at least not at the scale measured (within a 500-m radius of the pronghorn location). The selection for habitats near wells was likely due to the fact that wells were placed in areas of high value to pronghorn, such as sagebrush steppe and grassland habitats away from the rugged badlands, wetlands, and developed areas. The placement of well sites is dependent on a complex suite of factors such as the location of sub-surface oil reservoirs, topography, land ownership, and existing infrastructure. Due to constraints with obtaining access to the mineral rights of privately owned lands, it is probable that in areas with sub-surface oil, producers preferentially built on publically owned lands dominated by native sagebrush and grassland vegetation. In a follow-up analysis, we found that adult female pronghorn selected habitats near older wells (established prior to 2008) but avoided new wells (established after March 2010). The majority of old wells were located in the southwestern part of the study area where pronghorn density remained high in 2014 (Figure 1, Christie *et al.* 2015), whereas new wells were located further north, where both pronghorn density and habitat quality were lower. This lends support to the idea that pronghorn selection of well sites was context-dependent and likely a function of habitat quality. Although they were not avoided by pronghorn, well pads replaced otherwise high-value habitats for pronghorn, and the doubling of wells during the course of our study is part of an overall trend of declining net primary productivity of Great Plains ecosystems due to oil and gas activities (Allred *et al.* 2015).

Models of pronghorn occurrence contained similar parameters in 2006 and 2014, indicating consistency in resource selection between years, with the exception of NDVI and grassland cover, which were not present in 2014 models. We predicted that resource selection coefficients would be stronger when pronghorn density was low (2014) compared to when pronghorn were near their population peak in 2006, and found that this was the case for 8 out of 10 parameters that were estimated in both years. The reverse was true for only 2 out of 10 parameters. When animals are at high densities, individuals are forced to use marginal habitats; therefore resource selection is expected to be weaker (Rosenzweig 1991; Morris 2003; van Beest *et al.* 2014). This appears to be the case with adult female pronghorn, whose avoidance of roads, developed areas, woodlands and wetlands was weaker when they were at low densities. However, additional years of data would be required to more rigorously test this hypothesis.

Regional variation in fawn:doe ratios depends on multiple factors including variation in pregnancy and birth rates, fawn survival, and habitat selection by females with young. We would expect fawn: doe ratios to be highest in areas where females are in good nutritional condition and where fawn predation rates are low, presumably habitats that are strongly selected by females. In contrast to patterns of resource selection where females selected areas with low vegetation biomass (measured by NDVI), fawn:doe ratios were positively correlated with NDVI, suggesting that reproductive success may have been highest in areas with dense vegetation. As previously discussed, female pronghorn selected fairly low-biomass habitats away from woodlands and other tall vegetation. However, *within* these selected habitats, fawn:doe ratios were highest in relatively high-biomass vegetation. Aerial

surveys were timed so that the majority of fawns were old enough to associate with groups

of females, and only a small proportion were still concealed in the vegetation. Nevertheless,

predation of fawns at this age is high, and selection of habitats with dense cover by

fawn:doe groups helps to minimize predation by coyotes, bobcats, and other predators

(Barrett 1984). We believe that this finding does not indicate that adult female pronghorn

select areas that result in low reproductive success, or "ecological traps" (McCollin 1998),

but that a delicate balance exists between selecting areas that maximize visibility of

approaching predators to pronghorn (O'Gara 2004) and adequately concealing fawns so

that they avoid detection (Barrett 1984).

In this study, we found several important results pertaining specifically to pronghorn

conservation and more broadly, to resource selection in animal populations. Our finding

that pronghorn were associated with sagebrush steppe habitat and avoided developed

areas, densely-roaded regions, and major highways underscores the importance of

preserving contiguous sagebrush steppe habitat in southwestern North Dakota. Our

analysis of oil well locations indicates that oil development in North Dakota is non-random

with respect to habitat type, and significant overlap exists between high-value habitat for

pronghorn and well pad locations. Differences in strength of selection among years lends

support to the idea that at low densities, animals show stronger patterns of resource

selection than at high densities. Lastly, our analysis of fawn:doe ratios suggests that

although pronghorn females select relatively open habitats, higher reproductive success

occurs in more heavily vegetated areas within selected habitats. This reflects tradeoffs

between early detection of predators and concealment of young at time of high fawn

vulnerability to predators.

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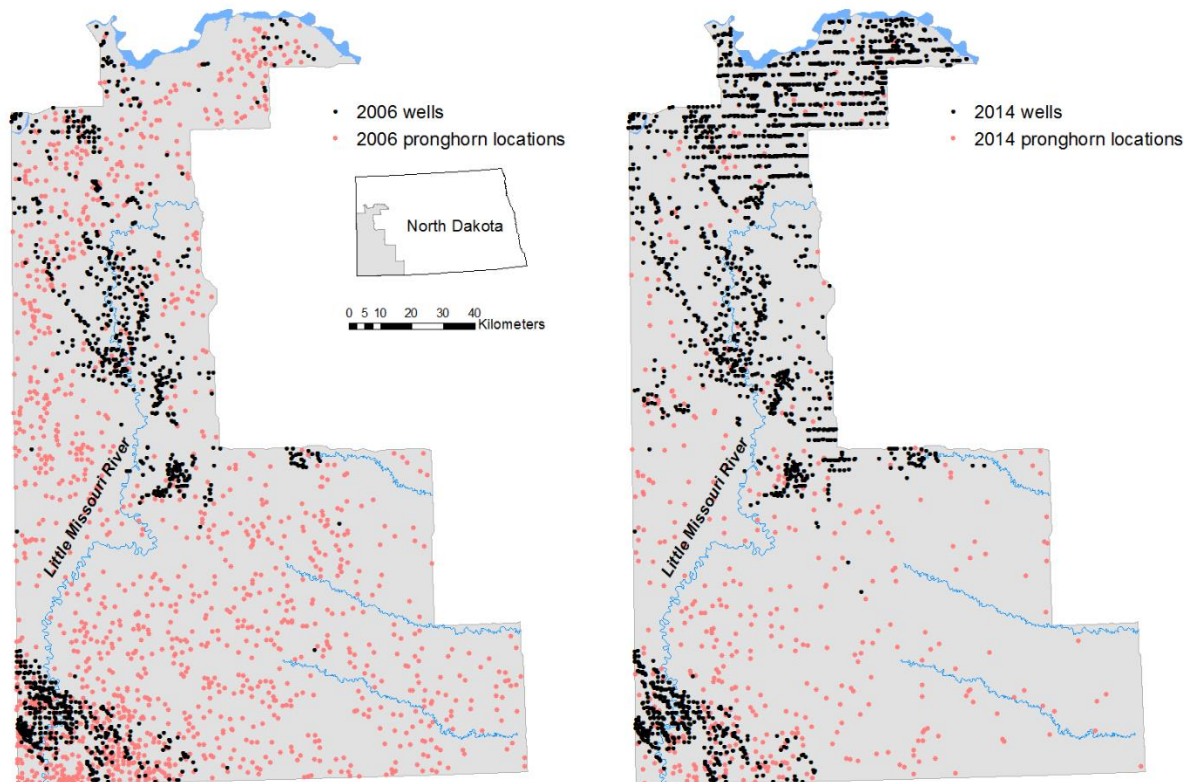
Figures

Figure 1. Locations of active oil wells (black circles) and fawn/doe groups (red circles) in 2006 (left) and 2014 (right).
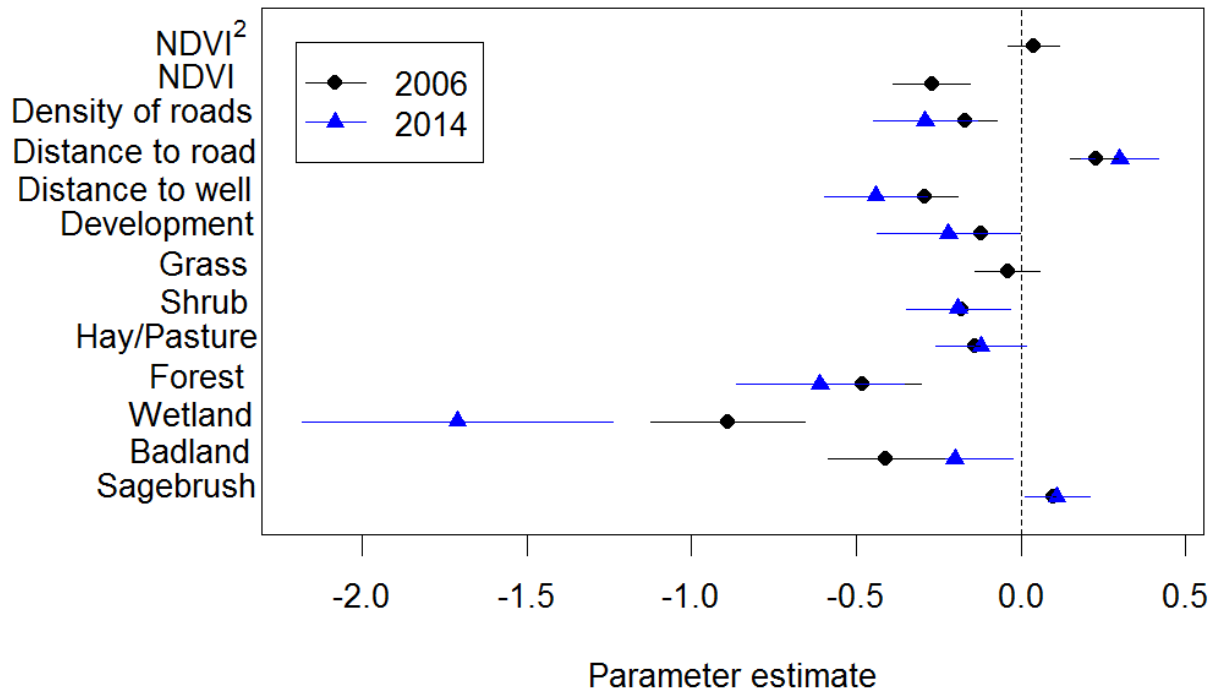
Figure 2. Parameter estimates from models of pronghorn resource selection in 2006 (black circles) and 2014 (blue triangles). Horizontal lines indicate 95% confidence intervals. Estimates to the left of the dotted vertical line indicate selection against a resource; estimates to the right of the line indicate selection for a resource. The most parsimonious model in 2014 did not include Grass, NDVI or NDVI[2]; therefore, these estimates are not shown for 2014.
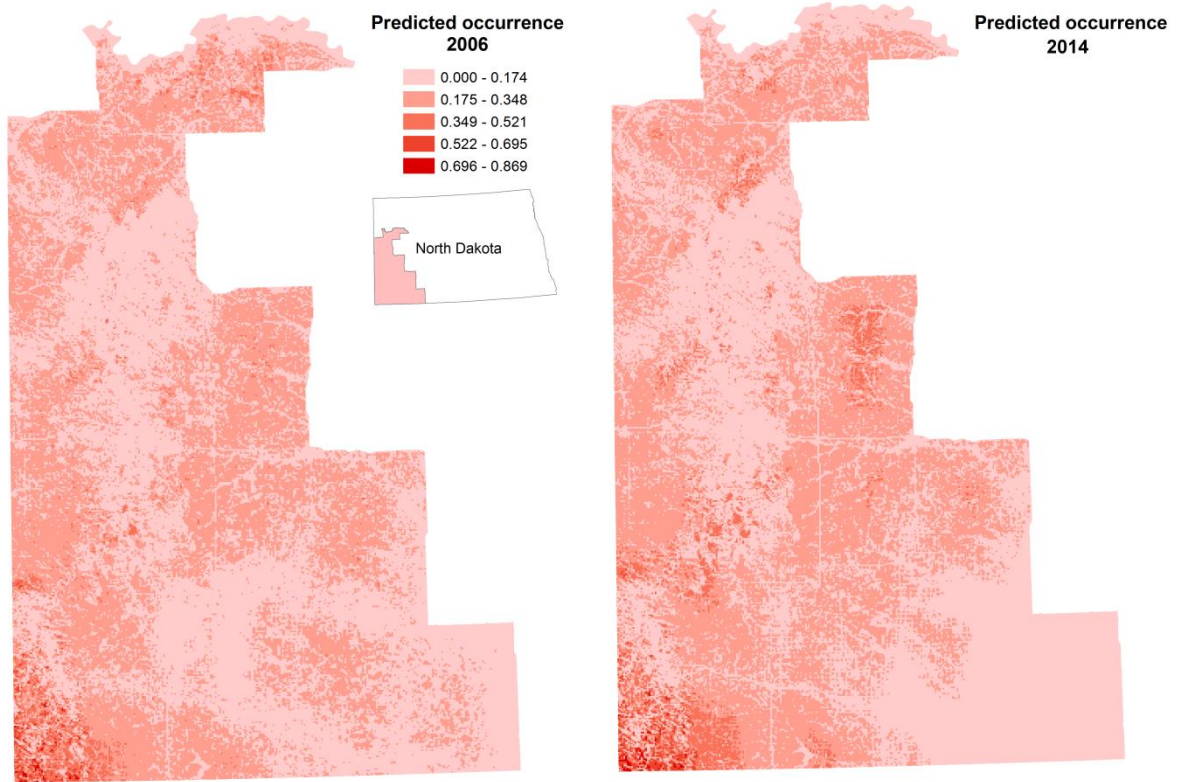
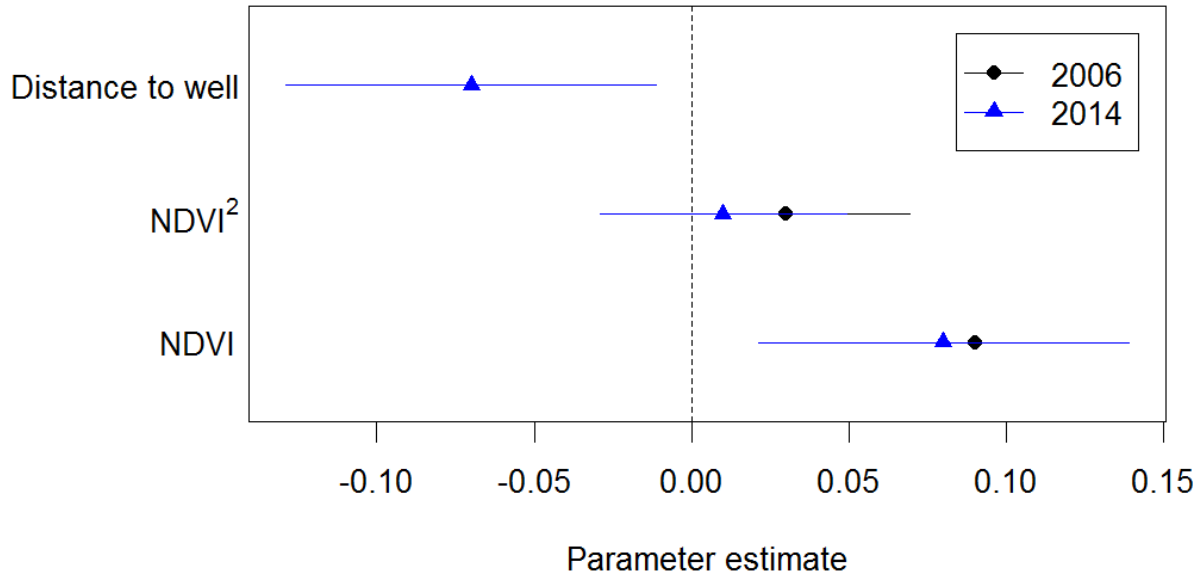Figure 3. Predicted occurrence of pronghorn in southwestern North Dakota in 2006 and
2014.

Figure 4. Parameter estimates from models of fawn: doe ratios in 2006 and 2014. Horizontal lines indicate 95% confidence intervals. Estimates to the left of the dotted vertical line indicate selection against a resource; estimates to the right of the line indicate selection for a resource. The variable "distance to well" was not present in the top model of fawn: doe ratios in 2006 and therefore is not shown in this figure.
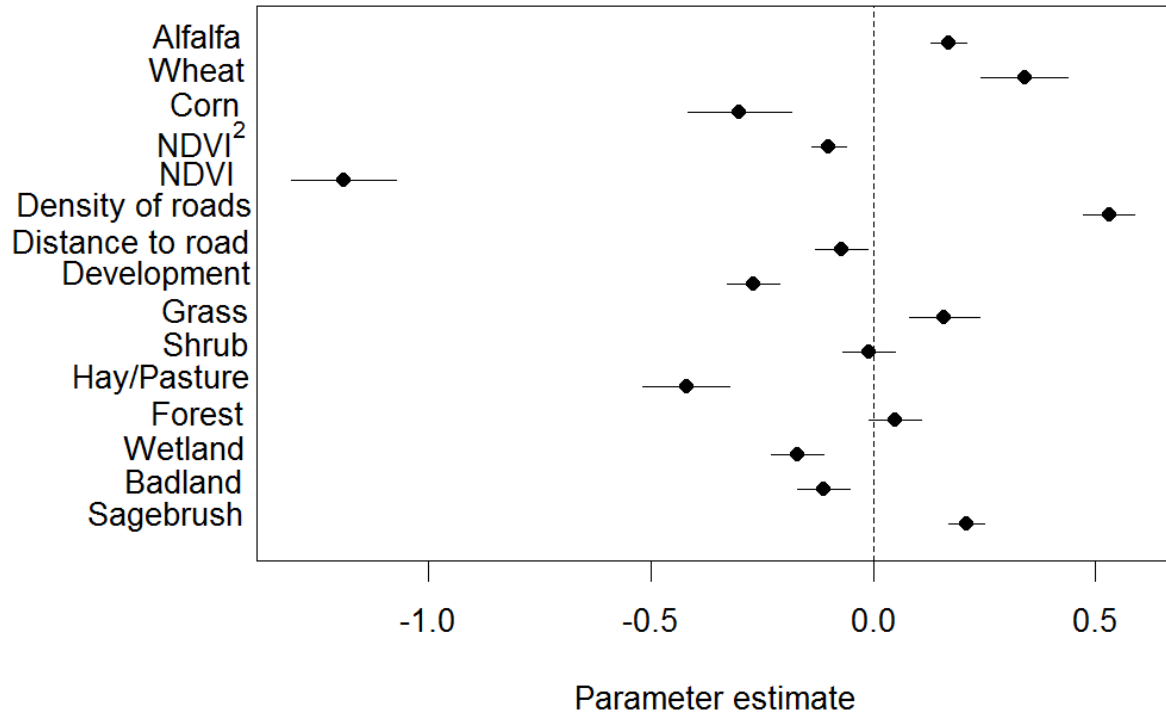
Figure 5. Parameter estimates for the most parsimonious model descring active oil well placement in North Dakota in 2014. Estimates to the left of the dotted vertical line indicate a negative relationship with the resource; estimates to the right of the line indicate a positive relationship.