

Variability in the Selection Patterns of Pronghorn: Are they Really Native Prairie Obligates?

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ABSTRACT In Canada, pronghorn (*Antilocapra americana*) are primarily considered a native prairie obligate because of their reliance on open grassland vegetation communities, although an assessment of local ecological knowledge suggests that pronghorn in Alberta select a variety of habitat from native prairie to cultivated lands. The primary objective of our study was to assess whether pronghorn in Alberta and Saskatchewan are native prairie obligates. Specifically, we addressed the following questions: 1) do individual pronghorn show similar selection patterns for native prairie and, therefore, support the notion that they are prairie obligates; 2) do pronghorn show consistent resource selection patterns at multiple scales (landscape and within-seasonal range); and 3) to what extent are selection patterns of pronghorn influenced by highways and roads. Within Alberta, we captured, collared, and monitored for one year individual female pronghorn in December 2003 ($n = 24$), March 2005 ($n = 25$), and March 2006 ($n = 25$). A detrended correspondence analysis of patterns of habitat selection revealed three distinct groups of pronghorn ($r^2 = 0.96$, $n = 55$) that we labeled native, cultivated, and mixed, referring to the dominant land cover in their parturition ranges. We used logistic regression to model resource selection patterns of the three groups of pronghorn during the parturition and winter periods at the landscape and within-seasonal range scales. At the landscape scale, each group of pronghorn had top models consisting of the variables land cover, landform, distance to express highways, distance to arterial roads, and distance to collector roads for both periods. The native and mixed groups were less likely to use annual and perennial cropland than native prairie habitats, whereas the cultivated group was more likely to use annual and perennial cropland. At the within-seasonal range scale, the top models for each group in both seasons consisted of one or more road variables, but the top models exhibited poor model fit. Our results do not show a clear association for native prairie, which we would have expected if pronghorn were native prairie obligates, suggestive of plasticity in behavior. We acknowledge that patterns of habitat selection do not indicate habitat quality or fitness; therefore, to understand the individual- and population-level consequences of selecting sub-optimal habitats, such as agricultural landscapes, further research is needed.

KEY WORDS Alberta, *Antilocapra americana*, Canada, pronghorn, resource selection function, Saskatchewan, scale.

Pronghorn (*Antilocapra americana*) are generally considered a prairie species because of their association to grassland, savanna, and shrubsteppe (hereafter collectively referred to as prairies) biomes of North America (Laliberte and Ripple 2004, Yoakum 2004, Gates et al. 2012). Despite the loss and fragmentation of habitat within these biomes, pronghorn are one of the few prairie species of wildlife whose numbers have increased in recent years. According to Yoakum (2004), pronghorn now occupy much of the same range as they did when Europeans first settled North America. Pronghorn use of cultivated areas (tilled native vegetation communities) is variable. Barrett (1982) indicated pronghorn in Alberta, Canada used cultivated lands less than 15% of the time in all months except October and November when it increased to approximately 25%. Both Hepworth (1970) in Nebraska and Torbit et al. (1993) in Colorado indicated pronghorn used winter wheat fields during winter and moved to native range

in the spring once green-up began. Others reported grain was of minor importance in the diets of pronghorn (Dirschl 1963, Mitchell and Smoliak 1971). Anthropogenic features such as highways, fences, energy development, and residential development can alter habitat use, cause fragmentation, and block or restrict movement by pronghorn (Berger 2004, Yoakum 2004, Gavin and Komers 2006, Beckmann et al. 2012).

In Alberta and Saskatchewan, Canada, pronghorn are restricted primarily to the grasslands biome (Yoakum 2004), typically occupying the remaining unaltered habitat and are considered native prairie obligates (Sheriff 2006, Gates et al. 2012). Only about 40% in Alberta and 20% in Saskatchewan of the native prairie, composing the grasslands biome, remains intact (Samson and Knopf 1994). Barrett and Vriend (1980) indicated increased cultivation reduced pronghorn population densities in Alberta, and proposed that cultivation should be considered the most severe limiting factor for

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pronghorn. Anecdotal reports from Alberta sportsmen, however, suggest that the use of cultivated areas by pronghorn has increased and that some pronghorn utilize these areas on a year-round basis. An assessment of local ecological knowledge from the ranching and farming community supported these reports (Jones et al. 2008a). There have been no published studies to confirm whether these anecdotal reports of pronghorn expansion into cultivated areas are accurate, but if these reports are true, then the commonly held perception that pronghorn are native prairie obligates is challenged. The primary objective of our study was to examine patterns of pronghorn occurrence and habitat selection in Alberta and Saskatchewan, at both the individual and population level, to assess whether the species is appropriately characterized as a native prairie obligate. Specifically, we addressed the following questions: 1) are pronghorn a native prairie obligate (i.e., do individual pronghorn show consistent selection patterns for native prairie), 2) do pronghorn show consistent resource selection patterns at multiple scales (second-order and third-order), and 3) do highways and roads influence the selection patterns of pronghorn. If pronghorn are native prairie obligates because of their reliance on open grassland vegetation communities (Barrett 1982, Gates et al. 2012), we predict that the species should exhibit consistent selection patterns for intact native prairie and show evidence of avoidance or limited use of cultivated areas among individual pronghorn. Departures from this expected pattern of selection would suggest that characterizing the species as a native prairie obligate may not be appropriate.

Resource selection can be categorized into a logical sequence of hierarchically nested orders (Johnson 1980, DeCesare et al. 2012). Johnson (1980) defined 4 orders or scales of selection: (1) selection of a physical or geographical range (first-order), (2) selection of a home range within the geographical area (second-order), (3) selection of attributes or components within the home range (third-order), and (4) micro-site selection relating to the location of food items at a feeding site (fourth-order). Yoakum (2004) demonstrated that pronghorn occupy three major biomes (grasslands, shrubsteppe, and desert) across their range. This scale of selection can be identified as first-order of selection, according to Johnson (1980). Therefore, given their strong selection at the first-order (represented essentially by grasslands) and the hierarchical nature of selection, we predicted that pronghorn also would exhibit strong selection for intact native prairie at the landscape scale (i.e., second-order selection; Johnson 1980) if they are to be appropriately characterized as native prairie obligates. Alternatively, if there was no evidence of selection for intact native prairie at the landscape scale then it suggests pronghorn do not behave as native prairie obligates. Finally, if as native prairie obligates exhibiting selection for grasslands at the geographical (first-order) and intact native prairie at the landscape (second-order) scales, we predicted less pronounced selection or neutral response to native prairie

at the within-seasonal range scale (i.e., third-order selection; Johnson 1980), where habitat use would largely reflect the availability of resources at this scale. Additionally, features that impede the movement of pronghorn also could be important, particularly human-made features like highways and roads. We predicted a negative relationship between pronghorn occupancy and distance to highways and roads. Based on these predictions we used a resource selection function approach to test support for three hypotheses; resource selection is best explained by 1) vegetation and topography, 2) roads, or 3) a combination of vegetation, topography, and roads.

STUDY AREA

The study area was within the dry mixed-grass and mixed-grass natural subregions of the grassland biome (Coupland 1961, Ecological Stratification Working Group 1995) in Alberta and parts of southeastern Saskatchewan, covering an area of approximately 99,158 km². The dominant vegetation consisted of western wheatgrass (*Pascopyrum smithii*), northern wheatgrass (*Elymus lanceolatus*), blue grama (*Bouteloua gracilis*), porcupine grass (*Hesperostipa spartea*), and spear grass (*H. comata*). The dominant shrubs and forbs were silver sagebrush (*Artemisia cana*), winter fat (*Krascheninikovia lanata*), pasture sagewort (*A. frigida*), moss phlox (*Phlox hoodia*), and common broomweed (*Gutierrezia sarothrae*). Urban centers included Lethbridge on the west side and Medicine Hat in the center of the study area. Conversion of mixed grasslands to crop agriculture of approximately 60% in Alberta and 80% in Saskatchewan has occurred (Samson and Knopf 1994). Commercial livestock grazing was the predominant land use activity in the area, with additional activities including energy development, conversion for agricultural crop production, wind energy development, transportation network, rural acreage development, and urban expansion (Alberta Environmental Protection 1997).

METHODS

Capture Methods

We partitioned our study area into three geographic units: south, central, and north. We further divided each geographical unit into three subunits based on blocks of contiguous land cover types; native land cover ($\geq 68\%$ native grass prairie [NGP]), cultivation ($\leq 33\%$ NGP), and areas that were of a mixed land cover (34–67% NGP; Alberta Prairie Conservation Forum 2000). We captured and collared female pronghorn in each subunit within a geographical area in successive years, beginning in the southern unit during the first year, moving northwards each subsequent year (Fig. 1). This sequence allowed us to recover, refurbish, and redeploy the limited number of collars available for the study and en-

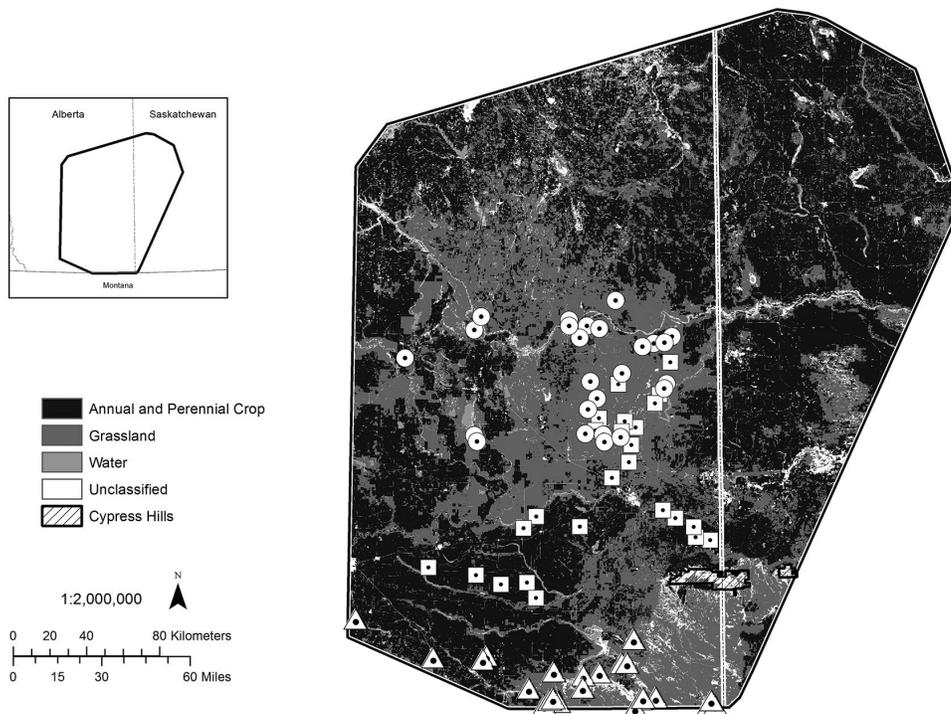


Figure 1. Pronghorn study area within Alberta and Saskatchewan depicting grassland (native prairie), and annual and perennial cropland, 2003–2007. Triangles represent pronghorn capture sites in December 2003, squares represent capture sites in March 2005, and circles represent capture sites in March 2006.

sured that pronghorn were marked throughout most of their distributional range in Alberta. We conducted pre-capture pronghorn surveys from the air and ground to identify groups of animals for potential capture within each subunit. Where possible, we tried to deploy collars evenly among the three subunits within a geographic unit (i.e., eight collars in native, eight collars in cultivation, and eight collars in mixed subunits). Due to the distribution of pronghorn in March 2006, there was some overlap in the general capture locations with those from 2005 (Fig. 1).

We captured and radio collared pronghorn females in December 2003 (south unit), March 2005 (central unit), and March 2006 (north unit; Fig. 1), using a net fired from a helicopter (Jones and Grue 2006, Jacques et al. 2009a, Yoakum et al. 2014). We fitted each captured female with a Lotek GPS3300 collar (Lotek Wireless Inc., Newmarket, Ontario, Canada) and Allflex ear tag (Allflex Canada, St-Hyacinthe, Quebec, Canada). Collars recorded a location every 4 hrs and dropped-off after 46 to 52 weeks. We completed an additional round of capturing in March 2007 (north unit) to remove collars that failed to drop off due to faulty mechanisms. The Alberta Wildlife Animal Care Committee reviewed and approved the capture and handling protocol prior to issuance of agency wildlife capture and handling permits (Alberta Sus-

tainable Resource Development, Fish and Wildlife Research Permits 11861, 16707, and 20394).

Seasonal Date Determination

We determined the start and end dates of the seasons based on the analysis of movement rates (Jones and Grue 2006, Sutor 2011). We examined graphs of weekly mean four-hour displacements and looked for inflections (Jones et al. 2007) that were consistent with seasonal behaviors and dates previously reported in the literature (Bruns 1977, Mitchell 1980, Barrett 1982). The seasonal periods occupied during parturition extended from 22 May–11 June 2004, 20 May–16 June 2005, and 19 May–15 June 2006 in the three years of our study. The periods occupied during the winter extended from 13 December 2003–19 March 2004, 2 December 2005–16 February 2006, and 8 December 2006–28 February 2007.

Pronghorn Grouping

We used detrended correspondence analysis (DCA) to assess whether there was variability in selection patterns during the parturition period between individual pronghorn and whether it was appropriate to pool our animals for further

analysis. We used DCA as a tool to reduce the multivariate data (see below) by extracting a small number of composite variables that explains as much of the information or variability in the original multidimensional data (McCune and Grace 2002). Pronghorn can show strong fidelity to ranges used for parturition and varying levels of fidelity to ranges used for wintering (Hoskinson and Tester 1980, Deblinger et al. 1984, Jacques et al. 2009b, Kolar et al. 2011). We calculated ranges occupied during the parturition period for each individual pronghorn using the fixed kernel method (Worton 1987) at the 95% level, using the h method for smoothing in Home Range Tools for ArcGIS (Rodgers et al. 2005, Sutor 2011).

We used the biophysical variables (McGarigal et al. 2000, McCune and Grace 2002) associated with pronghorn ranges during the parturition period in our DCA analysis. We calculated the density of biophysical variables contained within the range occupied during the parturition period of each collared female deemed important for habitat selection by pronghorn as part of a larger study (see Sutor 2011): express highway density, arterial road density, collector road density, local road density, percent water, percent exposed land, percent developed land, percent shrub, percent wetland, percent grassland (for clarity we refer to it as native prairie hereafter), percent annual cropland, percent perennial cropland, percent coniferous trees, percent deciduous trees, percent mixed tree cover, oil and gas well density, average terrain ruggedness index, average enhanced vegetation index, and distance to identified critical winter range in the DCA analysis. Details on the variables not used in the resource selection function (RSF) analysis described below can be found in Sutor (2011). We used a stepwise approach to evaluate a suite of models composed of the above variables to determine if individuals showed variability in selection of fawning ranges and if it was appropriate to pool all individuals. The first model we evaluated contained all the variables listed above. We then removed a single variable from the subsequent model and compared its performance to the previous using the r^2 value calculated using the Euclidean distance method (McGarigal et al. 2000, McCune and Grace 2002). We continued to remove single variables from the previous model until we arrived at the top model. We determined the top model as the one that explained the greatest variability in the data using the r^2 value. We then placed individual pronghorn into a group based on our interpretation of two-dimensional graphs of the top model and patterns within the data where natural breaks between groups occurred. We used the program PC-ORD version 5.01 (MjM Software Design, Gleneden Beach, Oregon, USA) to complete the DCA analysis.

Habitat Selection

Habitat Availability and Variables.— We examined habitat selection patterns by comparing used habitat (GPS locations) to available habitat at two spatial scales (Johnson

1980): the landscape scale and within-seasonal range scale. We examined habitat selection patterns during the parturition and winter periods for each grouping of pronghorn separately. To assess habitat availability, we generated one set of random points per season (parturition and winter) at each of the landscape and within-seasonal range scales. We used a similar approach to Beckmann et al. (2012) and used a ratio of one random point for every pronghorn location ($n_{\text{total}} = 30,746$ across both seasons). One set of random points was used to model habitat selection at the landscape scale with the random points being distributed throughout the study area. The study area boundary was chosen to be the 100% minimum convex polygon (MCP) of all the pronghorn GPS locations from within Alberta and Saskatchewan. We did, however, exclude Cypress Hills Provincial Park (Fig. 1) from the study area, because this area is part of the montane sub-region, not the grasslands, and is not typically used by pronghorn. A second set of random points was used to model habitat selection at the within-seasonal range scale and consisted of an equivalent number of random points per animal observation per season, distributed within the seasonal 100% MCP (parturition and winter) range of each individual. We conducted all spatial analysis using ArcMap 10.0 (Esri, Inc., Redlands, California, USA).

To address our three hypothesized effects (influence of vegetation/topography, influence of roads or a combination of both) we identified seven variables that potentially could influence the selection patterns of pronghorn during the parturition and winter periods at the two spatial scales. The selection of the seven variables, as opposed to the 19 used in the DCA analysis, was based on a review of the literature to limit the number of variables assessed to our specific hypotheses. The variables land cover, landform, aspect, and slope were used to evaluate the vegetation/topography hypothesis. We used the variable land cover as a surrogate for broad scale cover types as pronghorn have shown selection or avoidance of certain types (Yoakum 2004, Kolar 2009). Land cover was classified as native prairie, annual crop, perennial crop, shrub, wetland, and other (deciduous tree cover, coniferous tree cover, mixed tree cover, exposed land, developed land, and water). Land cover variables were derived from the land cover for agricultural regions of Canada (Agriculture and Agri-Food Canada 2008). In all models tested we used native prairie as the reference category for land cover. We expect pronghorn to use annual crop, perennial crop, and other less and the remaining land cover types in proportion to the reference category native prairie. We used landform to represent the variability in topography across the study area as pronghorn have shown a preference for flat to low rolling expansive terrain (Yoakum 2004, Yoakum et al. 2014). Landform types reflect terrain features and were classified as plains, constrained valleys, gentle incline, large hilltops, open basins, shallow drainages, and small hills. We determined the landform types by extracting local mean terrain properties

from digital elevation models at a 20-m resolution using the approach described by Tagil and Jenness (2008). Further details on the landform types and classification can be found in Suitor (2011). In all models tested we used plains as the reference category for landform. We expected pronghorn to use the constrained valleys and shallow drainages less than and the remaining landform categories in proportion to the reference category plains. Beckmann et al. (2012) demonstrated that pronghorn selected southeast, southwest, and northeast aspects during the winter in Wyoming. We used a similar approach to Beckmann et al. (2012), where we classified points with slope $\geq 2^\circ$ into one of four categories: northeast, northwest, southeast, or southwest. Points with slope $< 2^\circ$ were classified as flat and were used as the reference category in the analysis. We expect pronghorn to use all categories of aspect in proportion to the reference category flat during the parturition period and to use southeast, southwest and northeast aspects greater than the reference category during the winter period (Beckmann et al. 2012). We included slope as a variable as pronghorn have shown preference to use slopes less than 10% and to generally avoid slopes greater than 20% (Yoakum et al. 2014). We expect pronghorn distribution to be in areas with slopes less than 10%.

To test our hypothesis related to the influence of roads on pronghorn selection patterns we used three variables: distance to express highways, distance to arterial roads, and distance to collector roads. Previous research has demonstrated a general pattern of avoidance of roads by pronghorn (Yoakum 2004, Sheldon 2005, Gavin and Komers 2006). We used three categories of roads based on surface type and traffic volume (GeoBase 2003). Express highways were major, often divided, numbered highways, arterials were other numbered highways that may be either paved or gravel, and collectors are all other roads that were not highways, arterials or local roads, and were dedicated to providing access to properties (GeoBase 2003). Collector roads had the highest density in our study area (0.52 km/km^2), followed by arterial roads (0.05 km/km^2), and then express highways (0.03 km/km^2). We considered a linear relationship for distance to express highways and quadratic terms for distance to arterial and collector roads, as previous studies have indicated that the influence of distance to roads may not be linear (Gavin and Komers 2006, Kolar 2009). We expected pronghorn to show avoidance of all three types of roads. We determined all variables for each GPS and random location using ArcMap 10.0.

RSF Models.—We used binomial generalized linear models to identify important variables influencing the selection patterns of pronghorn during the parturition and winter periods at the two spatial scales of interest. We tested a suite of a priori models that consisted of combinations of the seven predictor habitat variables that we felt were biologically and behaviorally relevant (Burnham and Anderson 2002) to pronghorn, with careful attention to exclude any combination

of variables that did not seem plausible, such as redundant variables (Appendix A). We tested for colinearity between the predictor variables using Pearson's product-moment correlation matrix, with $r > |0.6|$ as the threshold cut-off value. If two predictor variables exceeded the threshold value, we did not include both in the same model (Beckmann et al. 2012). We used Akaike's Information Criteria (AIC) to assess model fit and identify the best model (Burnham and Anderson 2002). We used k-fold cross validation to test the performance of our top models by withholding 20% of the data for validation (Boyce et al. 2002, Koper and Manseau 2012). Resource selection function values were placed into 10 equal bins, and the mean Spearman's rank correlation calculated (Boyce et al. 2002). If the data appeared clumped, we introduced a fuzzy factor of 0.001 into the k-fold cross validation procedure (R Core Team, Vienna, Austria). All RSF analysis and model validation was completed using R version 3.0.1 (R Core Team, Vienna, Austria).

RESULTS

We captured female pronghorn and outfitted them with GPS collars in Alberta in December 2003 ($n = 24$), March 2005 ($n = 25$), and March 2006 ($n = 25$). Though captured in Alberta, we monitored females who moved seasonally out of Alberta and into Saskatchewan and/or Montana. For the purpose of our analysis, we used only pronghorn with seasonal ranges contained completely within our study area, with two exceptions discussed in the paragraph below, because of availability of contiguous spatial data for these areas.

Pronghorn Grouping

We used 55 pronghorn fawning ranges in the DCA analysis including pronghorn P1 and P20 whose fawning range extended into Montana. For pronghorn P1 and P20 we used their fawning range portion that was in Alberta in the DCA analysis so that they could be placed in a group, which then allowed the use of their preceding winter range in the RSF analysis. We felt this was acceptable as only a very small portion of their fawning range extended into Montana and using just their Alberta portion, and not their complete fawning range, did not affect their placement into a group. There were three distinct groups of pronghorn based on the results of the DCA performed on the composition data of the ranges occupied during the parturition period. Our selection as the top model was the one with just eight variables and a cumulative r^2 value of 0.96 ($n = 55$). The top model contained the variables percent water, percent exposed land, percent developed land, percent shrub, percent wetland, percent native prairie, percent annual cropland, and percent perennial cropland (Table 1). There was wide variation in the percent native prairie, percent annual cropland, and percent perennial cropland composing the ranges occupied during the parturi-

Table 1. Mean percent composition for the variables comprising the top model in the detrended correspondence analysis of parturition ranges for three groups of pronghorn in Alberta and Saskatchewan, Canada, 2003–2007.

Group	Number	Water	Exposed Land	Developed Land	Shrub	Wetland	Grass (Native Prairie)	Annual Cropland	Perennial Cropland
Native	26	0.64 (SE 0.37)	1.18 (SE 0.85)	0.16 (SE 0.09)	0.58 (SE 0.40)	2.73 (SE 2.01)	91.85 (SE 2.71)	1.27 (SE 0.59)	1.53 (SE 0.61)
Cultivated	16	0.44 (SE 0.16)	0.21 (SE 0.11)	0.46 (SE 0.15)	0.09 (SE 0.04)	1.87 (SE 1.07)	9.70 (SE 1.96)	64.52 (SE 8.36)	22.61 (SE 7.47)
Mixed	13	0.72 (SE 0.38)	0.99 (SE 0.62)	0.21 (SE 0.07)	0.33 (SE 0.22)	2.22 (SE 1.02)	54.23 (SE 3.34)	31.29 (SE 3.58)	9.91 (SE 2.89)

tion period for individuals assigned to the three groups (Table 1). We therefore labeled the groups as native, cultivated, and mixed.

Habitat Selection at the Landscape Scale

We used 53 animals in the RSF analysis during the parturition period. Sample sizes to construct the RSF models for the different groupings were (1) native group: 25 pronghorn for a total of 3,867 GPS locations, (2) cultivated group: 16 pronghorn for a total of 2,577 GPS locations, and (3) mixed group: 12 pronghorn for a total of 1,869 GPS locations. At the landscape scale, none of the seven variables were correlated, and we tested 16 biologically plausible a priori models (Burnham and Anderson 2002), plus the null model, for each of the parturition and winter periods. During the parturition period, for each of the three pronghorn groups at the landscape scale, the top model consisted of five variables: land cover, landform, distance to express highways, and quadratic terms for distance to arterial roads and distance to collector roads. All other competing models resulted in $>2 \Delta AIC$ from the highest-ranked model. The k-fold cross validation results indicated good model performance for each group (Table 2). Of significance is the fact that although each top model included the same variables, there was variation among the coefficients for each predictor variable when comparing models among the three groups (Table 3) which we found interesting. The native and mixed groups were less likely to select annual cropland and perennial cropland than native prairie, whereas the cultivated group was more likely to select annual cropland and perennial cropland. The native and mixed groups were less likely to select areas proximate to express highways than the animals in the cultivated group (Fig. 2). All three groups showed a quadratic relationship for the distance to arterial and collector roads (Fig. 2).

We used data from 50 pronghorn to complete the RSF analysis at the landscape scale during winter. Sample sizes used were (1) native group: 23 pronghorn for a total of 10,458

GPS locations, (2) cultivated group: 14 pronghorn for a total of 5,607 GPS locations, and (3) mixed group: 13 pronghorn for a total of 6,368 GPS locations. Similar to the parturition period at the landscape scale, the top model for the winter period for all three groups consisted of five variables; land cover, landform, distance to express highways, and quadratic terms for distance to arterial roads and distance to collector roads. All other competing models resulted in $>2 \Delta AIC$ from the highest-ranked model. The k-fold cross validation of the top model indicated good model performance for each group (Table 2). The native and mixed groups selected annual and perennial crops less than native prairie, while the cultivated group selected annual crops more (Table 4). All three groups showed avoidance of express highways and had a quadratic relationship for both arterial and collector roads (Fig. 2).

Habitat Selection at the Within-Seasonal Range Scale

At the within-seasonal range scale, there were correlations between the road variables, therefore we expanded the suite of a priori models evaluated at the within-seasonal range scale to use only one of the pair of correlated variables in any one model (Appendix A). During the parturition period, the highest-ranked model for the native group consisted of the quadratic term for arterial roads, whereas the top model for the cultivated and mixed groups consisted of the variables distance to express highways and the quadratic term for distance to collector roads (Table 2). All other competing models resulted in $>2 \Delta AIC$ from the highest-ranked models. Model performance was not strong for any of the groups for the parturition period (Table 2) indicative of the data being clumped, and none of the parameter estimates differed from zero for the top model for any group during the parturition period (Table 5).

During the winter period, the top model for the native and cultivated groups consisted of one variable, distance to express highways, while the top model for the mixed group consisted of the quadratic term for distance to arterial roads

Table 2. K-fold cross-validated^a Spearman rank correlations of the top models at the landscape and within-seasonal range scales during the parturition and winter periods by pronghorn placed into native, cultivated, and mixed groups as a function of their parturition range composition of native prairie in Alberta and Saskatchewan, Canada, 2003–2007.

Scale	Season	Group	Model Description ^b	Mean_r.rho ^c	P-value
Landscape	Parturition	Native	Land_Cover + Land_Form + Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)	0.81	0.008
		Cultivated	Land_Cover + Land_Form + Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)	0.95	<0.001
		Mixed	Land_Cover + Land_Form + Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)	0.98	<0.001
Landscape	Winter	Native	Land_Cover + Land_Form + Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)	0.90	0.001
		Cultivated	Land_Cover + Land_Form + Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)	1.00	<0.001
		Mixed	Land_Cover + Land_Form + Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)	0.99	<0.001
Within-Seasonal Range	Parturition	Native	Art_Km + I(Art_Km ²)	0.08	0.83
		Cultivated	Express_Km + Coll_Km + I(Coll_Km ²)	0.66	0.04
		Mixed	Express_Km + Coll_Km + I(Coll_Km ²)	0.04	0.91
Within-Season Range	Winter	Native	Express_Km	0.52	0.12
		Cultivated	Express_Km	0.52	0.12
		Mixed	Art_Km + I(Art_Km ²)	0.52	0.12

^a All evaluations involved k-fold cross validation with 5 partitions and 10 bins. At the within-seasonal range scale, a fuzzy factor of 0.001 was included in the k-fold cross validation procedure because the data were clumped; ^bLand_Cover = land cover type (native prairie (reference category), annual crop, perennial crop, shrub, wetland and other), Land_Form = landform type (plains (reference category), constrained valleys, gentle incline, large hill tops, open basins, shallow drainages and small hills), Express_Km = distance (km) to express highways, Art_Km + I(Art_Km²) = the quadratic term for distance (km) to arterial roads, Coll_Km + I(Coll_Km²) = the quadratic term for distance (km) to collector roads; ^c Mean_r.rho = mean Spearman's rank correlation coefficient values.

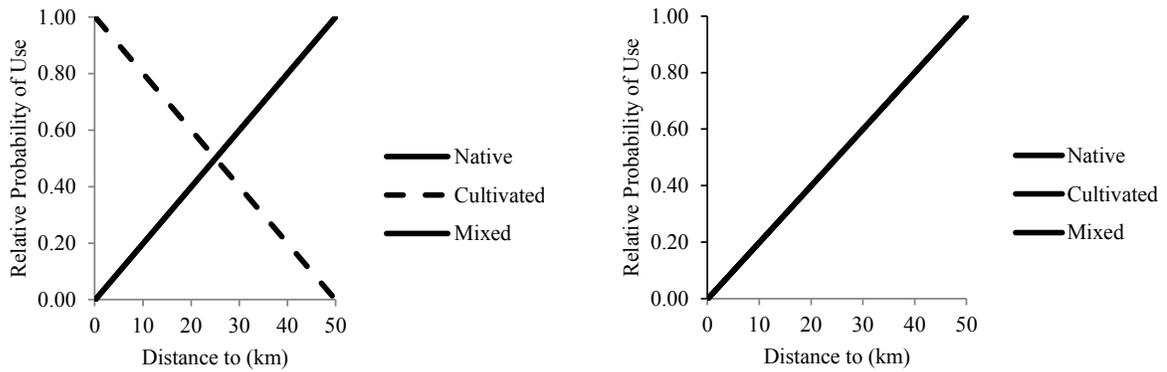
(Table 2). All other competing models resulted in >2 Δ AIC from the highest-ranked model. The highest-ranked models for all three groups did not perform well (Table 2), indicative of the data being clumped. None of the parameter estimates differed from zero for the top models for any group during the winter period (Table 6).

DISCUSSION

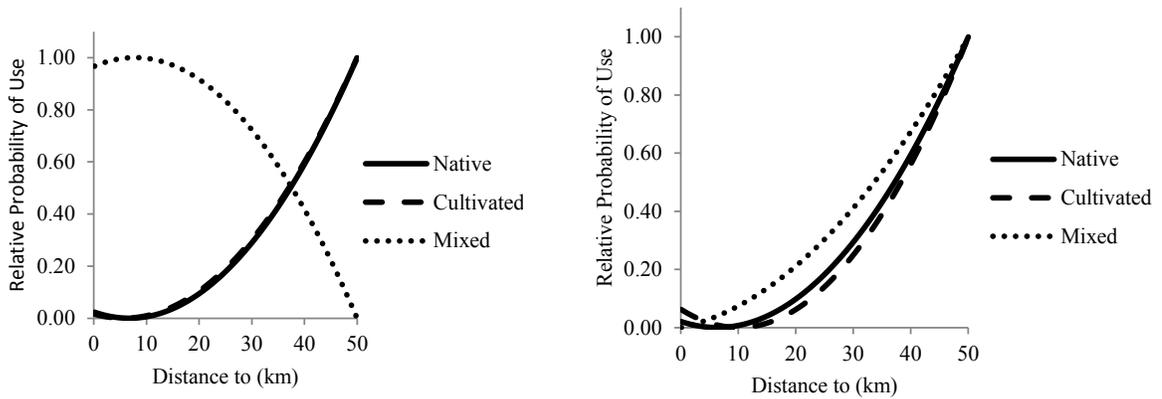
The pronghorn is a specialized and free-roaming ungulate in the grasslands biome of Canada and commonly assumed to be a native prairie obligate. Therefore, logic suggests that all pronghorn should select for native prairie within the grasslands biome, and avoid or show limited use of cul-

tivated areas (annual or perennial cropland). Our results at both the individual and population level do not support the notion that pronghorn are native prairie obligates. At the individual level, our prediction that all pronghorn would show consistent patterns of selection for native prairie habitats and therefore could be placed into a single group was not supported. The DCA results indicated that individual pronghorn did not show a consistent pattern of selection; composition of parturition habitat ranged from 100% native prairie to almost no native prairie. We therefore did not pool our study animals into a single group but instead completed subsequent analysis using three groups. Whether this wide range in selection at the individual level is a behavioral syndrome and whether these traits represent an adaptive or maladaptive strategy, and

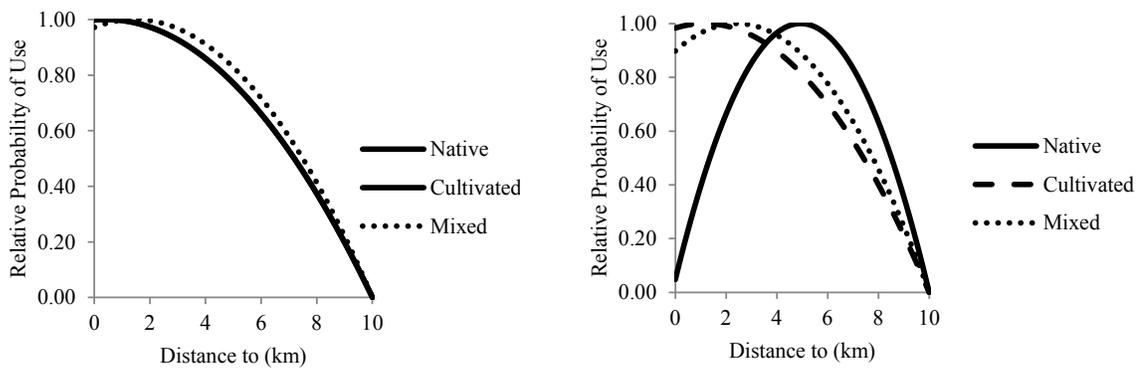
Express Highway



Arterial Roads



Collector Roads



Fawn

Winter

Figure 2. Probability of use curves for distance to express highways (top), arterial roads (middle), and collector roads (bottom) during the parturition (left column) and winter periods (right column) at the landscape scale for pronghorn grouped into native, mixed, and cultivated groups as a function of their parturition range composition of native prairie in Alberta and Saskatchewan, Canada, 2003–2007. Graphs depict the functional response to the road variables for each group of pronghorn because we rescaled the values to range from zero to one; therefore, they do not represent relative probabilities of use.

Table 3. Parameter estimates and p-values from the top-ranked logistic regression models at the landscape scale for the parturition period for pronghorn placed into native, cultivated, and mixed groups as a function of their parturition range composition of native prairie in Alberta and Saskatchewan, Canada, 2003–2007.

Parameter	Native		Cultivated		Mixed	
	β	<i>P</i> -value	β	<i>P</i> -value	β	<i>P</i> -value
Intercept	0.07	0.499	-0.19	0.155	-0.33	0.007
Annual Cropland ^a	-5.07	<0.001	1.16	<0.001	-1.14	<0.001
Perennial Crop ^a	-3.65	<0.001	1.26	<0.001	-1.18	<0.001
Shrub ^a	-3.09	<0.001	-1.61	0.031	-15.89	0.950
Wetland ^a	-0.53	0.001	0.83	0.005	-0.28	0.251
Other ^a	-0.47	0.033	1.68	<0.001	-0.59	0.049
Constrained Valleys ^b	0.02	0.898	-2.80	<0.001	0.05	0.830
Gentle Incline ^b	0.16	0.396	-0.03	0.912	-0.05	0.824
Large Hill Tops ^b	-0.40	0.015	-1.94	<0.001	0.85	<0.001
Open Basins ^b	-0.04	0.826	-3.43	<0.001	-0.35	0.094
Shallow Drainages ^b	-0.01	0.937	0.36	0.081	0.31	0.114
Small Hills ^b	-0.18	0.190	0.19	0.296	0.18	0.332
Upper Slope ^b	0.54	<0.001	-1.28	<0.001	0.98	<0.001
Express_Km ^c	0.05	<0.001	-0.06	<0.001	0.02	<0.001
Art_Km ^d	-0.01	0.392	-0.01	0.576	0.05	0.002
I(Art_Km ²) ^d	0.001	0.089	0.001	0.327	-0.003	<0.001
Coll_Km ^e	0.07	0.386	0.47	0.016	0.98	<0.001
I(Coll_Km ²) ^e	-0.09	<0.001	-0.57	<0.001	-0.34	<0.001

^a Land cover types compared to the reference category native prairie, ^b Landform types compared to the reference category plains, ^c Express_Km = distance (km) to express highways, ^d Art_Km = distance (km) to arterial roads, I(Art_Km²) = the quadratic term for distance (km) to arterial roads, ^e Coll_Km = distance (km) to collector roads, I(Coll_Km²) = the quadratic term for distance (km) to collector roads.

therefore create trade-offs for each group (Sih et al. 2004), is unknown at this time. Our results, however, do highlight the ecological flexibility of pronghorn to occupy native prairie habitats that have been highly altered by humans.

Given that pronghorn select grasslands at the geographical scale and the hierarchical nested nature of resource selection (Johnson 1980, DeCesare et al. 2012), we predicted pronghorn selection for native prairie would occur at the landscape scale rather than at the within-seasonal range scale. Although similar predictor variables influenced the selection patterns of all three groups at the landscape scale, the patterns of selection varied in relative magnitude and direction among groups. The native and the mixed groups used annual and perennial crops less than grasslands, and showed a tendency to select native prairie the most. This selection pattern is consistent with the literature, where strong selection for native rangelands has been observed (e.g., Bruns 1977, Barrett 1982, Bright and Van Riper III 2000, Yoakum 2004). The

cultivated group tended to show the opposite pattern, with annual and perennial crop (except winter) being used more than native prairie, a pattern similar to the findings of Kolar (2009). Indeed, 11% of our study animals remained in areas dominated by cultivation on a year-round basis, a situation not previously documented in the literature. Acknowledging our sample size, the fact we were able to detect selection for non-native land cover types by the cultivated group at the landscape scale casts doubt as to whether pronghorn are native prairie obligates. Future studies with increased sample sizes should confirm the pattern of selection we detected for the cultivated group and provide further evidence as to whether pronghorn are a native prairie obligate.

Previous studies have indicated that resource selection can occur at multiple scales (Rettie and Messier 2000, Jones and Hudson 2002, Boyce et al. 2003, Ciarniello et al. 2007, DeCesare et al. 2012). While patterns of selection by pronghorn was significantly influenced by intact native prairie hab-

Table 4. Parameter estimates and p-values from the top-ranked logistic regression model at the landscape scale for the winter period for pronghorn placed into native, cultivated, and mixed groups as a function of their parturition range composition of native prairie in Alberta and Saskatchewan, Canada, 2003–2007.

Parameter ^a	Native		Cultivated		Mixed	
	β	<i>P</i> -value	β	<i>P</i> -value	β	<i>P</i> -value
Intercept	-0.61	<0.001	-1.02	<0.001	-1.39	<0.001
Annual Cropland ^a	-2.42	<0.001	0.51	<0.001	-0.89	<0.001
Perennial Crop ^a	-3.04	<0.001	-1.35	<0.001	-1.26	<0.001
Shrub ^a	-2.06	<0.001	-18.37	0.902	-1.58	<0.001
Wetland ^a	-1.06	<0.001	-1.63	<0.001	-0.72	<0.001
Other ^a	0.28	0.012	-1.40	<0.001	1.32	<0.001
Constrained Valleys ^b	-0.57	<0.001	-0.93	<0.001	-0.93	<0.001
Gentle Incline ^b	-0.23	0.039	0.71	<0.001	-0.79	<0.001
Large Hill Tops ^b	0.21	0.030	-0.21	0.219	-0.28	<0.042
Open Basins ^b	0.20	0.028	-0.93	<0.001	-0.61	<0.001
Shallow Drainages ^b	-0.13	0.184	-0.05	0.718	-1.01	<0.001
Small Hills ^b	-0.03	0.702	0.02	0.869	-0.68	<0.001
Upper Slope ^b	0.44	<0.001	-0.51	<0.001	-0.20	0.040
Express_Km ^c	0.04	<0.001	0.06	<0.001	0.06	<0.001
Art_Km ^d	-0.07	<0.001	-0.21	<0.001	0.02	0.067
I(Art_Km ²) ^d	0.01	<0.001	0.01	<0.001	0.001	<0.001
Coll_Km ^e	0.50	<0.001	1.33	<0.001	0.98	<0.001
I(Coll_Km ²) ^e	-0.06	<0.001	-0.57	<0.001	-0.20	<0.001

^a Land cover types compared to the reference category native prairie, ^b Landform types compared to the reference category plains, ^c Express_Km = distance (km) to express highways, ^d Art_Km = distance (km) to arterial roads, I(Art_Km²) = the quadratic term for distance (km) to arterial roads, ^e Coll_Km = distance (km) to collector roads, I(Coll_Km²) = the quadratic term for distance (km) to collector roads.

Table 5. Parameter estimates and p-values from the top-ranked logistic regression model at the within-seasonal range scale for the parturition period for pronghorn placed into native, cultivated, and mixed groups as a function of their parturition range composition of native prairie in Alberta and Saskatchewan, Canada, 2003–2007.

Parameter ^a	Native		Cultivated		Mixed	
	β	<i>P</i> -value	β	<i>P</i> -value	β	<i>P</i> -value
Intercept	-8.26	<0.001	-22.02	0.976	-21.78	0.977
Express_Km			43.56	0.976	24.10	0.992
Art_Km	883.88	0.792				
I(Art_Km ²)	-26.17	0.792				
Coll_Km			455.25	0.982	231.89	0.988
I(Coll_Km ²)			-231.35	0.976	-69.79	0.986

^a Express_Km = distance (km) to express highways, Art_Km = distance (km) to arterial roads, I(Art_Km²) = the quadratic term for distance (km) to arterial roads, Coll_Km = distance (km) to collector roads, I(Coll_Km²) = the quadratic term for distance (km) to collector roads.

Table 6. Parameter estimates and p-values from the top-ranked logistic regression model at the within-seasonal range scale for the winter period for pronghorn placed into native, cultivated, and mixed groups as a function of their parturition range composition of native prairie in Alberta and Saskatchewan, Canada, 2003–2007.

Parameter ^a	Native		Cultivated		Mixed	
	β	<i>P</i> -value	β	<i>P</i> -value	β	<i>P</i> -value
Intercept	-15.14	0.188	-17.39	0.719	-17.95	0.765
Express_Km	1146.05	0.267	327.57	0.705		
Art_Km					909.41	0.756
I(Art_Km ²)					-24.88	0.756

^a Express_Km = distance (km) to express highways, Art_Km = distance (km) to arterial roads and I(Art_Km²) = the quadratic term for distance (km) to arterial roads.

itats at the landscape scale, we did not find evidence of third-order selection at the within-seasonal range scale. The poor predictive power of the highest-ranked models at the within-seasonal range scale was as we predicted and is indicative of use being in proportion to availability. Kie et al. (2002) found a similar pattern for mule deer (*Odocoileus hemionus*) where unexpected results occurred at the third-order scale because mule deer had already selected favorable attributes within their seasonal range, and avoided others that were present outside their range. They found evidence of scale-dependent selection, and that it appears deer also chose resources at one scale but just used them as they were available at other, finer scales. Our results support the conclusion of Kie et al. (2002) that when looking at selection patterns at the third-order one needs to be aware that selection at higher scales may have already occurred.

We acknowledge a perceived potential source of bias with our results: the influence that our grouping of individuals might have had on the selection patterns observed at the population level, particularly during the parturition period. Grouping individuals based on their composition of parturition range may lend itself to finding a significantly distinct pattern of selection during the parturition period. We believe our approach for grouping pronghorn based on compositional data of their parturition ranges allowed us to capture the variability in selection that would not have been apparent if all animals were pooled (Jones et al. 2008b). Any bias arising from the grouping should be small, because we captured pronghorn in the winter but used the subsequent parturition period to categorize animals (which represents two seasonal periods and locations separated by the spring migration period). Related to the bias associated with grouping our animals is the resulting sample sizes for the different groups. The possibility is real that low power of detection may have occurred as a result of our sample sizes and therefore prevented the detection of some effects; however, a trade-off had to be made, and the alternative (pooling all individuals)

would have precluded looking at the variability in behavior, which was a focus of our paper (i.e., the behavioral plasticity in use of habitat types would not have been detected had all individuals been pooled). The use of DCA proved to be a useful approach for identifying and working with individual variation in our population-level models, and we suggest that this approach could be a suitable alternative for assessing and incorporating individual variation in resource selection models, especially if more intensive procedures, such as random-effects models (Gillies et al. 2006), are impractical or not feasible.

At the landscape and within-seasonal range scales of analysis, habitat selection by pronghorn was influenced by highways and roads for all groups in both seasons, although selection patterns were strongest at the landscape scale. Roads are highly influential in determining patterns of selection and behavior of pronghorn (O'Gara 2004, Gavin and Komers 2006, Gates et al. 2012, Seidler et al. 2014). The typical response from pronghorn relative to roads has been to either avoid them or remain in close proximity when the road (or associated features, such as fence lines) acts as a barrier to movement, resulting in a non-linear response to these features (Gavin and Komers 2006, Kolar 2009). Our results indicate that pronghorn used areas closer to collector roads in the parturition period (all three groups) and avoided roads in the winter (native group), which was opposite to that for pronghorn in North Dakota (Kolar 2009). The use of areas closer to collector roads (and express highways for the cultivated group) during parturition may be an artifact of two factors. Ditches or right-of-ways along roads tend to contain succulent vegetation in the spring/early summer because of accumulation of snow over the winter and delayed green-up, which likely provides a valuable food source. Alternatively, pronghorn may use areas closer to roads as an anti-predator strategy during the parturition period, because coyote (*Canis latrans*) densities are negatively correlated with road density (Randa and Yunker 2006). Berger (2007) reported a similar

use of roads as an antipredator strategy by female moose (*Alces alces*) from brown bears (*Ursus arctos*) during the calving season in the Yellowstone Ecosystem, USA.

Our interpretation of the selection patterns exhibited by pronghorn towards roads are based on the presumption that pronghorn are reacting to the road and/or the traffic on the road. This presumption may be only partially supported, because pronghorn are not likely reacting to just the road and associated traffic volume, but also to fences, which often are found in proximity to roads and have been shown to influence pronghorn selection patterns (Sheldon 2005, Yoakum et al. 2014). Seidler et al. (2014) noted that fences associated with highways appeared to contribute to the degree of impermeability, with some fences being a complete barrier while others, consisting of wildlife-friendly fencing, being completely permeable. Unfortunately, we were unable to obtain spatial data for fence lines within our study area and, therefore, unable to discern whether it is roads, fences, or a combination of the two that influences selection patterns by pronghorn.

We recognize that the distribution of the animals among habitat types does not necessarily indicate anything about the quality of those habitats (Van Horne 1983). Heinrichs et al. (2010) state that patterns of occurrence are sometimes used to infer important habitat, even though the habitat may not contribute anything to the long-term viability of that population. Our study was not meant to assess the quality of alternate habitat types used by pronghorn, such as cultivated areas. Although pronghorn occur in cultivated areas, the highest densities in our study region occur in large, open native rangelands where they satisfy life-history requirements, including forage switching and migrating in response to environmental conditions and regional-scale variations of forage availability in winter (Sheriff 2006, Gates et al. 2012). Sheriff (2006) also showed that, based on landscape composition, higher fawn to doe ratios but a generally low rate of population growth (suggesting lower survival rates) existed in areas with a high proportion of cultivation. The selection of human-altered systems by the cultivated group may result in poor fitness, a situation reported by Battin (2004) for other animals. Therefore, despite the apparent adaptability to local conditions, pronghorn still remain sensitive to changes in our native prairie landscapes (Beckmann et al. 2012, Gates et al. 2012) and to environmental conditions (Barrett 1982, Pyrah 1987, Brown and Ockenfels 2007).

MANAGEMENT IMPLICATIONS

In Alberta and Saskatchewan, pronghorn are clearly exhibiting selection patterns at the individual and population level, with certain individuals strongly selecting native prairie, others selecting cultivated areas, and some individuals selecting areas with a mixture of both. Our results do not show a clear association for native prairie, which we would have expected if pronghorn were native prairie obligates,

suggestive of plasticity in behavior. We were able to detect three distinct groups of pronghorn, and acknowledging the sample size for individual groups, were able to demonstrate variability in selection patterns (e.g., used annual crop land more or less than native prairie) by these groups, suggesting that pronghorn are adaptable to a degree to the current landscape in Alberta and Saskatchewan. Understanding the consequences of these habitat choices (e.g., on vital rates) cannot be determined from occurrence data, yet such information is necessary for making informed decisions regarding future management actions of pronghorn and their habitat. Therefore, further research is needed to understand the individual and population-level consequences of selecting sub-optimal habitats, such as cultivated areas.

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Appendix A. Suite of a priori models tested using logistic regression for pronghorn habitat selection during the parturition and winter periods by pronghorn placed into native, cultivated, and mixed groups as a function of their parturition range composition of native prairie at two spatial scales in Alberta and Saskatchewan, Canada, 2003–2007.

Scale	Season	Group	Model ^a
Landscape	Both	All	null model (intercept only)
			Art_Km + I(Art_Km ²)
			Aspect
			Coll_Km + I(Coll_Km ²)
			Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Cover
			Land_Cover + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Cover + Aspect
			Land_Cover + Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Cover + Land_Form
			Land_Cover + Land_Form + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Cover + Land_Form + Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Cover + Slope + Aspect
			Land_Form
			Land_Form + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Form + Express_Km + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
Within Seasonal Range	Parturition	All	null model (intercept only)
			Art_Km + I(Art_Km ²)
			Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Aspect
			Coll_Km + I(Coll_Km ²)
			Express_Km + Coll_Km + I(Coll_Km ²)
			Land_Cover
			Land_Cover + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Cover + Aspect
			Land_Cover + Land_Form
			Land_Cover + Land_Form + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Cover + Land_Form + Express_Km + Coll_Km + I(Coll_Km ²)
			Land_Cover + Slope + Aspect
			Land_Form
			Land_Form + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Form + Express_Km + Coll_Km + I(Coll_Km ²)
LC_Code + Express_Km + Coll_Km + I(Coll_Km ²), Art_Km + I(Art_Km ²)			
Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)			
Aspect			
Coll_Km + I(Coll_Km ²)			
Express_Km + Coll_Km + I(Coll_Km ²)			
Land_Cover			
Land_Cover + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)			

Scale	Season	Group	Model ^a
Within Seasonal Range	Winter	All	Land_Cover + Aspect
			Land_Cover + Land_Form
			Land_Cover + Land_Form + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Cover + Land_Form + Express_Km + Coll_Km + I(Coll_Km ²)
			Land_Cover + Slope + Aspect
			Land_Form
			Land_Form + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Form + Express_Km + Coll_Km + I(Coll_Km ²)
			LC_Code + Express_Km + Coll_Km + I(Coll_Km ²),
			Slope + Aspect
			null model (intercept only)
			Art_Km + I(Art_Km ²)
			Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Aspect
			Coll_Km + I(Coll_Km ²)
Land_Cover			
Land_Cover + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)			
Land_Cover + Aspect			
Land_Cover + Land_Form			
Land_Cover + Land_Form + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)			
Land_Cover + Slope + Aspect			
Land_Form			
Slope + Aspect			
Within Seasonal Range	Winter	Native and Cultivated	Express_Km
			Land_Cover + Express_Km
			Land_Cover + Land_Form + Coll_Km + I(Coll_Km ²)
			Land_Cover + Land_Form + Express_Km
			Land_Cover + Coll_Km + I(Coll_Km ²)
			Land_Form + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Form + Coll_Km + I(Coll_Km ²)
			Land_Form + Express_Km
			Express_Km + Coll_Km + I(Coll_Km ²)
			Land_Cover + Land_Form + Express_Km + Coll_Km + I(Coll_Km ²)
Within Seasonal Range	Winter	Mixed	Land_Form + Art_Km + I(Art_Km ²) + Coll_Km + I(Coll_Km ²)
			Land_Form + Express_Km + Coll_Km + I(Coll_Km ²)
			LC_Code + Express_Km + Coll_Km + I(Coll_Km ²)

^a Land_Cover = land cover type (native prairie (reference category), annual crop, perennial crop, shrub, wetland and other), Land_Form = landform type (plains (reference category), constrained valleys, gentle incline, large hill tops, open basins, shallow drainages and small hills), Express_Km = distance (km) to express highways, Art_Km + I(Art_Km²) = the quadratic term for distance (km) to arterial roads, Coll_Km + I(Coll_Km²) = the quadratic term for distance (km) to collector roads.