

PRONGHORN MIGRATION AND RESOURCE SELECTION
IN SOUTHWESTERN NORTH DAKOTA

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by

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IN SOUTHWESTERN NORTH DAKOTA

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PRONGHORN MIGRATION AND RESOURCE SELECTION IN SOUTHWESTERN NORTH DAKOTA

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ABSTRACT

Wildlife managers need pronghorn (*Antilocapra americana*) movement data in North Dakota because harvest quotas are based on a summer survey, which might not represent the distribution of pronghorn during the fall hunting season. Using data from 121 radio-collared pronghorn, we quantified migration dates, distance, direction and site fidelity for pronghorn in North Dakota, 2004-2008. Nearly half (45%) of the pronghorn were migratory, moving > 15 km between winter and summer ranges. Of the migratory pronghorn, 89% moved northeast in the spring, and 97% moved southwest in the fall. Pronghorn showed higher fidelity to summer ranges than winter ranges. Few fall migrations occurred between the survey and the hunting season; therefore, during our years of study, the survey accurately reflected unit occupancy of pronghorn for the hunting season. It is also important to identify pronghorn seasonal habitat use to guide land management decisions, inform mitigation processes and identify limited resources. We modeled summer and winter resource selection for 50 GPS-collared, female adult pronghorn in North Dakota, 2005–2008. We used vegetation type, ruggedness and distance to nearest roads as predictors. During both seasons, pronghorn selected open vegetation types in non-rugged habitat. Primary roads were avoided in the summer and secondary roads were avoided during both seasons. Reduction of open vegetation, or

increased road developments, in non-rugged areas where habitat is limited, might decrease the suitability of available pronghorn habitat.

CHAPTER 1
MIGRATION PATTERNS OF PRONGHORN
IN SOUTHWESTERN NORTH DAKOTA

ABSTRACT

Current understanding of large-scale movements of pronghorn (*Antilocapra americana*) in North Dakota has been based on anecdotal information. Wildlife managers need empirical data about pronghorn movements in North Dakota because harvest quotas are based on results of a mid-summer survey, which might not represent the distribution of pronghorn during the fall hunting season. Using data from 121 radio-collared pronghorn that survived two or more seasons, we measured pronghorn movements in southwestern North Dakota from 2004-2007 and quantified distance and direction of seasonal migration, timing of migration, and seasonal site fidelity.

Pronghorn exhibited two primary movement patterns between summer and winter ranges: 1) migrations > 15 km (45%); and 2) movement < 15 km (55%). Of the migratory pronghorn (those that moved > 15 km) 89% moved northeast and/or east (between 22.5° and 112.5°) in the spring and 97% moved southwest and/or west (between 202.5° and 292.5°) in the fall. The average distance moved for migratory pronghorn was 70.59 km (range = 17.4 – 253 km). The mean date that pronghorn began migrating in spring was 20 March (SD = 20 days), and in the fall was 22 October (SD = 17 days). Nearly all migratory pronghorn (97%) returned to within 15 km of their previous summer range, whereas only 61% of the pronghorn returned to within 15 km of their previous winter range. Failure to establish well-defined winter ranges might have been due to mild winter weather. We did not identify any migration bottlenecks for pronghorn in

southwestern North Dakota, and pronghorn migrations did not appear to be restricted by movement barriers. Most pronghorn moved across hunting unit boundaries (70%) and survey unit boundaries (75%), and several (31%) moved into South Dakota and Montana (up to 60 km into MT). However, only 7 (10%) fall migrations occurred between the aerial survey and the hunting season, and none of our collared pronghorn moved to Wyoming, as was speculated. About half of the pronghorn in our study site migrate in the spring, which is more than previously understood; however, most movements take place before the aerial survey and at the end of, or after, the hunting season. Therefore, during our years of study, the mid-summer survey accurately reflected unit occupancy of radio-collared pronghorn for the fall hunting season.

INTRODUCTION

Pronghorn (*Antilocapra americana*) are highly valued in North Dakota for hunting and wildlife viewing. In recent years, the demand for hunting licenses in North Dakota greatly exceeds the supply (North Dakota Game and Fish Department [NDGF] Strategic Plan 2005), and in 2007, roughly 6,069 resident rifle hunters and 1,957 resident and nonresident bow hunters spent approximately \$185,000 for pronghorn hunting licenses (Bruce Stillings, NDGF, personal communication), and more approximately 5,000 hunter days are spent in the field annually (Baltezare and Leitch 1992). Furthermore, yearly hunting expenditures for an average resident hunter are around \$995 (Baltezare and Leitch 1992). Additionally, travelers value pronghorn for wildlife viewing in the Theodore Roosevelt National Park (TRNP) and the Little Missouri National Grasslands. Consequently, pronghorn are among the most valued large ungulates in the state.

The NDGF is the primary agency responsible for pronghorn management in North Dakota. Biologists estimate pronghorn population trends from an annual aerial survey, hunter success surveys from previous years, landowner complaints, and general field observations. They manage the harvest by regulating hunting permits for specific hunting units. Currently, the state legislature requires a proposed proclamation with suggested license numbers before the middle of July, approximately 3 months prior to the rifle hunting season. This requires biologists to use a mid-summer survey to make inferences about the spatial distribution and abundance of pronghorn, which directly impact hunting quotas by unit. Use of the mid-summer survey assumes that minimal movement occurs across management boundaries between the survey and hunting seasons. If a large proportion of the pronghorn population makes long movements outside unit boundaries, the aerial census could prove inadequate as a guide for issuing hunting licenses. Consequently, biologists need empirical data about the timing and distances of pronghorn movements occurring between the mid-summer survey and the start of the hunting season. Additionally, movement data would prove useful to managers in alleviating damage issues, understanding whether pronghorn move great distances to meet resource needs, and if so, understanding whether migration corridors exist.

Although sedentary pronghorn populations can be managed within hunting units, many studies throughout their range suggest that pronghorn make regular movements larger than the size of the current NDGF hunting units. Several North American pronghorn populations are relatively sedentary, moving less than 50 km between summer and winter ranges (Ockenfels et al. 1997, Boyle et al. 1998, Boccadori and Garrott 2002,

Sievers 2004, White et al. 2007). Additionally, 13 radio-collared pronghorn in South Dakota moved an average of only 23.1 km between summer and winter ranges (Jacques 2006). Other pronghorn populations move long distances (50 km or more) between winter and summer ranges (Lowe 1945, Bruns 1977, Hoskinson and Tester 1980, Barrett 1984, Berger 2004, Sawyer et al. 2005). Marked pronghorn have reportedly moved further than 300 km in Wyoming (Riddle 1990) and further than 400 km in Alberta (Suitor et al. 2008). These regional differences in pronghorn migration patterns necessitate the need for site-specific information.

We studied pronghorn movements, including the timing of migrations, distances and directions moved during migrations, proportion of the population that migrates, and fidelity to seasonal ranges. In turn, we used this information to assess the utility of the mid-summer survey for prescribing autumn, unit-specific hunting permits, and to provide quantitative data about pronghorn movements for this region.

STUDY AREA

We captured pronghorn in primary areas where pronghorn congregated during winter in southwest North Dakota (Figure 1). Movement of these pronghorn into the Slope region of North Dakota broadened the study area to include the entire corner of North Dakota south and west of the Missouri River. The study area is divided east and west by both the Little Missouri River, which flows north into the Missouri River, and Highway 85, which runs roughly along the eastern edge of the Badlands. Interstate 94 runs east to west across our study area and establishes a prominent north-south division. The area was comprised primarily of private land (85%); the rest was Little Missouri National Grasslands (8.3%), State School land (2.6%), Bureau of Land Management

(0.5%), and National Park Service land (0.5%) including the north and south units of TRNP. More than 10% of the SW corner of North Dakota was public land open to public hunting.

The two major vegetation types were northern wheatgrass plains and needlegrass plains. Dominant grass species included western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Hesperostipa comatai*), green needlegrass (*Nassella viridula*), blue grama (*Bouteloua gracilis*), threadleaf sedge (*Carex filifolia*), sideoats grama (*Bouteloua curtipendula*) and little bluestem (*Schizochyrium scoparium*). Other species included big sagebrush (*Artemisia tridentata*), silver sagebrush (*Artemisia cana*), winterfat (*Krascheninnikovia lanata*), Rocky Mountain juniper (*Juniperus scopulorum*), rubber rabbitbrush (*Chrysothamnus nauseosus*), broom snakeweed (*Gutierrezia sarothrae*) and saltbushes (*Atriplex spp.*; Johnson and Larson 1999). Much of the land was managed as rangeland, cultivated for row crops (wheat [*triticum spp.*], canola, flax [*Linum spp.*], sunflowers [*Helianthus spp.*], oats [*Avena spp.*], barley [*Hordeum spp.*], corn [*Crucita spp.*]), or planted for hayland (alfalfa [*Medicago spp.*], crested wheatgrass [*Agropyron cristatum*], and smooth brome [*Bromus inermis*]).

METHODS

Capture

We searched for pronghorn herds each January, 2004-2007, within 2 weeks prior to captures. We used a fixed wing aircraft to survey North Dakota pronghorn wintering areas and recorded herd locations on a handheld GPS unit. We used the collected waypoints to guide capture crews to pronghorn. The Leading Edge helicopter crew (Cody, WY) captured adult (> 1.5 years old) pronghorn via net-gunning from a

helicopter. A NDGF biologist and pilot observed the capture operations from an overhead plane, led the helicopter to previously located herds, and monitored for potential obstacles. The helicopter crew mounted pronghorn with VHF transmitters (Advanced Telemetry Systems, Isanti, MN) and recorded capture location, sex, and an age estimate (1, 2, 3, or 3+ based on incisor eruption, Jensen 1998b, O’Gara and Yoakum 2004:785). We scheduled pronghorn captures in mid-January when cooler temperatures and snow coverage were most likely.

In January 2004 we captured and radio-collared 60 adult pronghorn (20 males, 40 females). In 2005-2007 we captured and collared additional pronghorn to replace those lost due to mortality to ensure we had 20 males and 40 females collared at the beginning of each winter. We distributed collars as evenly as logistically possible across the original study area on each side of the Little Missouri River with a maximum of 2 collars per herd. We flew a check-up flight within one week of capture to monitor for capture-related mortalities.

Radio Telemetry

We attempted to collect locations on all radio-collared pronghorn by aerial tracking once every 10 days with the NDGF Scout airplane (American Champion Aircraft Corporation, Rochester, WI). We assumed that 2-3 monthly locations would be sufficient for analyzing broad-scale seasonal movements (Sawyer et al. 2005, White et al. 2007). We were restricted to flying during daylight hours, but by rotating starting points, we collected locations from individual pronghorn at different times of the day. We located collared pronghorn using 2 wing-mounted H-antennas. We initiated searches near the last known location for each animal, and then used aerial telemetry techniques

(Gilmer et al. 1981) to obtain a visual location for each collared pronghorn. We saved locations either with the GPS unit onboard the receiver or with a handheld Garmin™ GPS unit and recorded other information such as group size, habitat type, and additional comments.

Movement Analysis

We mapped all locations in ArcGIS, and determined whether or not they had 2 distinct seasonal ranges. Summer and winter ranges were considered distinct if 2, non-overlapping, 100% minimum convex polygons (MCPs) could be drawn around seasonal clusters of locations. For pronghorn that had a distinct summer and winter range, we determined start and end dates for spring and fall migration. We defined a start date as the first location that deviated by 5 km or more from a seasonal range, and the end date as the first location within the next occupied range. We defined seasons by approximately one month after the average migration end date through one month prior to the average migration start date.

We used these seasons to develop winter (15 December–15 March) and summer (15 May 15–15 September) 100% MCPs for each pronghorn. Though MCPs are commonly criticized in the literature for home range size estimates (Laundre and Keller 1984, Seaman et al. 1999), we used them to delineate the full extent of known use areas, merely for deriving centroids. Further, using data from 35 GPS collars, we subsampled locations ($n = 5, 15, 30, 45, 60, 75$ and 100 locations), and found relatively small differences in centroid locations due to sample size (for the subsamples of 5 locations, centroids were only an average of 0.60 km [SE = 0.38, range = 0.17–1.80 km] from the centroids developed using 100 locations). We added centroids to each MCP using the

centroid geometry calculator in ArcGIS, and we measured distances and direction between centroids of winter and summer ranges for all pronghorn. We did not include non-migratory pronghorn in the direction analyses. We measured distance as (Kernohan et al. 2001):

$$D_i = \sqrt{[(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2]}$$

and direction as (Kernohan et al. 2001):

$$a_i = \text{Arc tan}(Y_i / X_i)(180^\circ / \pi) \text{ if } X_i > 0$$

$$a_i = 180^\circ + \arctan(Y_i / X_i)(180^\circ / \pi) \text{ if } X_i < 0$$

Where the distances of the X and Y vectors were calculated as:

$$X_i = x_{i+1} - x_i \text{ and } Y_i = y_{i+1} - y_i$$

We then categorized direction results into 8 directions (N = 337.5–22.5°, NE = 22.5–67.5°, E = 67.5–112.5°, SE = 112.5–157.5°, S = 157.5–202.5°, SW = 202.5–247.5°, W = 247.5–292.5°, and NW = 292.5–337.5°). Because we had pronghorn collared for multiple years, we also estimated seasonal site fidelity by summarizing distances between consecutive winter and consecutive summer centroids.

Statistical Analysis

We compared migration distances between male and females, among four age classes (yearling, 2-year-old, 3-year-old, and mature), and among years using PROC MIXED in SAS (SAS Institute 2004). We used the REPEATED statement to account for correlation among collared pronghorn that survived multiple years. We used the uncorrelated covariance structure because this structure makes no assumptions regarding equal variances or about correlation between age, sex and year (Littell et al. 1998). We considered $P < 0.05$ as significant.

RESULTS

Between January 2004 and March 2008, we collected 4,764 locations from 121 VHF collared pronghorn. We lost track of one collared animal; the animal was observed several times but we were unable to detect a signal. We collected an average of 23 ± 3 (SD) locations per pronghorn per year.

In the four years of our study, 55 of 121 pronghorn (45%) made seasonal migrations (movements greater than 15 km, Figure 2). The other 55% exhibited non-migratory movements less than 15 km between summer and winter ranges. The longest migration was a male that migrated 224 km in the spring of 2004 and 253 km in the fall of 2004. Of those pronghorn migrating in spring ($n = 77$), 49% migrated NE, 40% E, and 8% NW. Less than 2% of our collared pronghorn migrated N or W, and there were no SE, S, or SW spring migrations. Of 38 fall migrations, 58% of the pronghorn migrated SW and 39% migrated W. The remaining 3% migrated SE, and there were no NW, N NE, E or S fall migrations.

The mean date for pronghorn migration in the spring was 20 March \pm 20 (SD) days and the mean date for arrival on summer range was 10 April \pm 25 (SD) days. The earliest date that a pronghorn began migration in the spring was 1 February and the latest date to settle into a summer range was 2 June. The mean distance moved during the spring was 74.6 km (SD = 48.0 km, range = 17.4–224.2 km) for migratory pronghorn ($n = 77$); 4.9 km (SD = 3.6 km, range = 0.1–14.8 km) for sedentary pronghorn ($n = 116$); and 32.7 km (SD = 45.7 km, range = 0.1–224.2 km) for all spring movements ($n = 193$). There were no differences in migration distances among age ($P = 0.3941$, $d.f. = 3$, $F = 1.00$) or sex categories ($P = 0.6534$, $d.f. = 1$, $F = 0.20$), but there was a year effect ($P =$

0.0161, *d.f.* = 3, *F* = 3.36). The mean migration distance declined from 85.9 km in 2004 to 69.9 km in 2007, and the proportion of pronghorn that migrated decreased from 62.3% in 2004 to 15.7% in 2007.

The mean date for pronghorn migration in the fall was 22 October \pm 17 (SD) days and the mean date pronghorn settled into a winter range was 9 November \pm 21 (SD) days. The earliest date a pronghorn began migrating in the fall was 20 September and the latest date to settle into a winter range was 19 January. The mean distance moved during the fall was 63.1 km (SD = 50.7 km, range = 17.4–252.7 km) for migratory pronghorn (*n* = 41); 4.5 km (SD = 3.4 km, range = 0.2–14.3 km) for sedentary pronghorn (*n* = 91); and 22.7 km (SD = 39.2 km, range = 0.2–252.7 km) for all fall movements (*n* = 132). We observed fewer fall migrations due to harvest of radio-collared pronghorn during the fall hunting seasons, which reduced our sample size. There were no differences in migration distances among age categories (*P* = 0.2901, *d.f.* = 9, *F* = 1.27) or males and females (*P* = 0.4072, *d.f.* = 9, *F* = 0.68), but there was a negative year effect (*P* = 0.0078, *d.f.* = 9, *F* = 4.29). Mean fall migration distance declined from 70.2 km in 2004 to 40.5 km in 2007, and as with the spring migration pattern, the proportion of animals to migrate in the fall decreased from 34.2% in 2004 to 13.8% in 2007.

We analyzed winter fidelity using 132 winter ranges from 75 pronghorn (17 males, 58 females) that survived 2 consecutive winter seasons. The mean distance between consecutive winter ranges was 23.28 km (SD = 32.96 km, range = 0.17–186.03 km, *n* = 132). Although 61% (81 of 132) of the subsequent winter range centroids were < 15 km (\bar{x} = 4.23 km, SD = 3.30 km, range = 0.17–14.14 km, *n* = 132) from the previous winter range centroid, 51% (26 of 51) of the winter ranges that were > 15 km apart were

not within 50 km of their previous winter range (\bar{x} = 53.54 km, SD = 36.14, range = 15.19–186.03 km).

We analyzed summer fidelity using 91 summer ranges from 59 pronghorn (13 males, 46 females) that survived 2 consecutive summer seasons (we removed one outlier, a female that moved to a summer range 88 km away). Pronghorn showed strong site fidelity to summer ranges, returning to within 2.14 km, on average, of the previous summer range (SD = 2.43 km, range = 0.80–10.95 km, n = 91).

DISCUSSION

Our research demonstrated that pronghorn make long distance migrations in North Dakota, occasionally beyond 200 km; however, 55% of the collared pronghorn moved less than 15 km between a winter and summer range. Long distance pronghorn migrations (50 km or more between winter and summer ranges) have been previously documented in southern Alberta (Barrett 1984, Sutor et al. 2008), Montana (Bruns 1977), Idaho (Hoskinson and Tester 1980), and Wyoming (Riddle 1990, Berger 2004, Sawyer 2005). The migrations we observed in North Dakota were somewhat unique in that migrations were not restricted to narrow corridors; even where migration paths appear congregated, just north of Bowman, ND, migrations span a 12 km corridor (Figure 2). In Arizona, woody encroachment forced pronghorn to migrate through a bottleneck (Ockenfels 1994), and topographic features apparently restrict pronghorn to narrow corridors in Idaho (Hoskinson and Tester 1980) and through a bottleneck in Wyoming (Berger 2004). In North Dakota there are only localized areas of woody encroachment, and outside the badlands there are few topographical barriers to movements. Pronghorn in our study migrated around significant buttes (e.g. White Butte which rises 90 meters

from the plains south of Amidon). It is possible that migration bottlenecks exist along the interstate or within localized areas in the badlands, but we did not identify any places where migrations were largely restricted. The migratory portion of the collared pronghorn we studied in North Dakota seemed relatively uninfluenced by traditional movement barriers (fences, primary roads, etc...).

Disregarding elevation-related migrations, pronghorn typically move north in the spring and south in the fall toward warmer winter ranges (Sawyer et al. 2005, Sheldon 2005). However, terrain, water and vegetation might also affect migration direction (Ockenfels et al. 1994, White et al. 2007). White et al. (2007) found pronghorn moved southeast in the spring to lower elevations; however, there is little elevation difference across our study area. North Dakota is on the northeastern edge of the pronghorn distribution in North America, so moving north and east might result in less competition with other pronghorn during the fawning season. Another hypothesis is that migrations are directed by snow cover (Hoskinson and Tester 1980). Generally, annual snow depths increase as one moves northeast across ND, and sage, rabbitbrush, and other shrub species associated with pronghorn winter habitat (Bruns 1977) are more abundant to the west. Furthermore, we observed a correlation between decreasing migration distances and increasingly mild winters during the four years of our study. The winter of 2003-2004 was colder and had significant snow cover over much of the season (NOAA 2009). Recorded snow depths on the eastern portion of our study area were > 3 cm (maximum = 25 cm) from 1 November 2003 to 30 February 2004. The winters between 2005–2008 were mild despite a major snowstorm in October 2005, but this storm was followed by warm weather and did not appear to trigger pronghorn migrations.

Pronghorn in southwestern North Dakota exhibited irregular migration patterns that included a nearly equal combination of migratory and non-migratory behaviors. It was previously believed that pronghorn in North Dakota might make drastic annual movements (> 50 km) in some years (Lowe 1945, Knue 1991). Although researchers have reported individual pronghorn migrate consistently within a population (Deblinger 1988, Sawyer et al. 2005), others have reported that pronghorn exhibit multiple migratory behaviors within a single geography (Bruns 1977, Amstrup 1978, Autenrieth 1978, Rosendale et al. 1980, Barrett 1984, Sheldon 2005, Jacques 2006, Sutor et al. 2008, Jacques 2009). We found that not all pronghorn migrated similarly with respect to other pronghorn from the same winter or summer ranges or even with respect to their own previous migrations. Similar to Matrinka (1967), Bruns (1977), Hoskinson and Tester (1980), and Barrett (1984), the migration patterns we observed fit conditional migration patterns, meaning pronghorn migration sometimes differed across years, perhaps to avoid adverse conditions. The proportion of pronghorn that migrated in our study ranged from 15% in 2007 to 62% in 2004. This is much higher than the 3-6% reported by Jacques et al. (2009) for pronghorn in Harding County, SD, which is immediately adjacent to the southwest corner of our study area. This discrepancy in migration patterns is somewhat surprising because Jacques' (2009) and our capture areas were both on the eastern fringe of sage-steppe communities, and were both near the eastern extent of the pronghorn distribution. There were no notable differences in apparent barriers to movement in either South Dakota or North Dakota, and both studies were conducted over relatively mild winters. This result further justifies the need for region-specific migration information for pronghorn.

The movement dates observed in this study coincide with movement dates in other areas at the same latitude. Hoskinson and Tester (1980) reported varying migration dates between years and individuals in Idaho, but spring dispersal dates were around mid-February to mid-March and fall dispersals were typically in mid-October and as late as January. In central Wyoming, pronghorn migrated during the first half of April, and again in mid-October (Sheldon 2005). In South Dakota, pronghorn dispersed to summer ranges between mid-March and early May, and returned to winter ranges in mid-October to mid-November (Jacques 2006). White et al. (2007) reported Yellowstone pronghorn migrations to occur in late March to early April, and again in September to October. We found that spring movements, not surprisingly, occur near the end of the North Dakota's winter season (mid-March to mid-April) and fall movements occur before the winter season (mid-October to late November; the mean date for the first snowfall of 1" or more is December 15th, Jensen 1998a).

Pronghorn showed strong fidelity to their summer ranges and a weak fidelity to winter ranges. Similarly, Deblinger and Alldredge (1984) reported pronghorn in the Red Desert of Wyoming used the same summer ranges, but showed little or no fidelity to winter range. In contrast, Amstrup (1978) concluded that pronghorn in Montana and Wyoming were opportunistic migrants and did not return to the same summer or winter ranges; however, the difference he noted between the centers of activity was only 3.3 km between consecutive summer ranges and 6.8 km for consecutive winter ranges. Strong fidelity to a summer range and low fidelity to a winter range is indicative of a fall dispersal response due to some factor (e.g., weather, decreasing vegetation moisture, hunting), and implies that spring movements are merely reciprocated efforts to return to a

primary range. This is a shift in perception from movement studies that capture in winter and assume that spring movements are dispersals. Strong fidelity only to summer ranges suggests that pronghorn migrate in the fall when certain conditions spur migrations toward alternate winter ranges.

Management Implications

Regardless of the cause of migration, we observed pronghorn migratory patterns that might impact current NDGF management plans. The current hunting units used by the NDGF are too small (roughly 30-80 km wide by 20-45 km long) to account for some of the large scale movements of pronghorn in the state. However, because pronghorn did not migrate between the survey season and the hunting season, and because pronghorn showed strong site fidelity to their summer ranges, the current survey sufficiently identified collared pronghorn occupancy during our years of study. However, with a large variance around the mean date for fall movements, some pronghorn moved before or during rifle season. For the summer survey to better represent pronghorn distributions during fall hunting seasons, early October hunting season dates should be maintained. Because pronghorn were not distributed similarly in winter as in summer and fall, distribution of fall hunting licenses to help resolve depredation complaints from the previous winter might prove difficult. Although our data suggest a population shift to the north and east in the spring, further work should address this issue to improve the utility of depredation permits.

Big game managers should recognize that seasonal movements of pronghorn are highly variable across regions and between individuals and seasons (Bruns 1977, Amstrup 1978, Autenrieth 1978, Rosendale et al. 1980, Barrett 1984, Sawyer et al. 2005,

Sheldon 2005, Jacques 2006). Wildlife managers of potentially migratory populations using hunting seasons as a management technique should take into consideration spatiotemporal shifts in wildlife distributions, especially when surveys, depredation complaints and hunting seasons occur at different times of year.

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Figure 1. Pronghorn capture locations in southwestern, North Dakota, 2004-2007 in relation to hunting unit boundaries, the Little Missouri River, and U.S. Interstate 94.

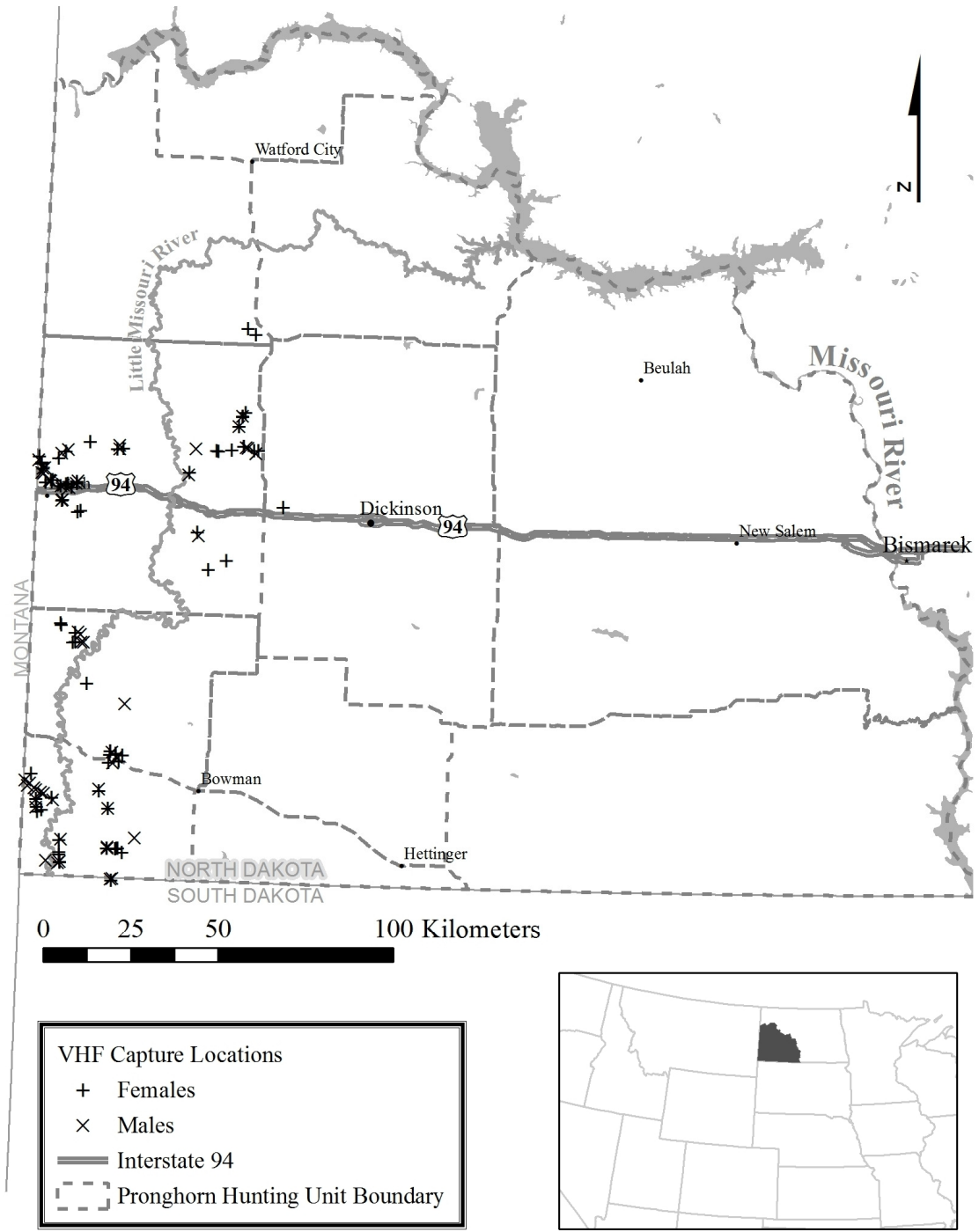
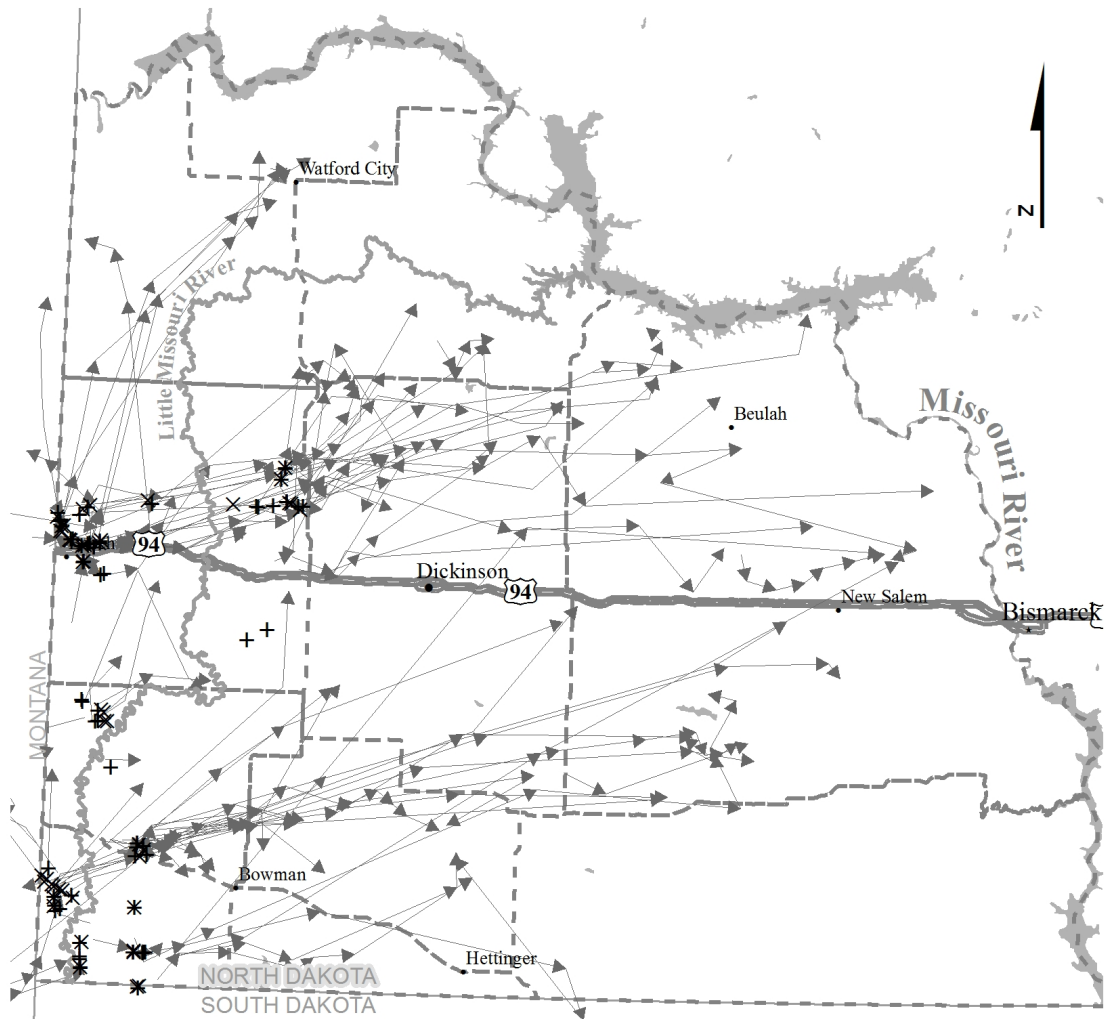
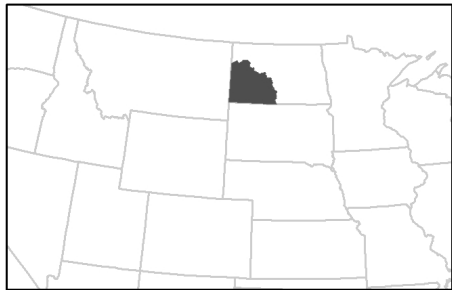


Figure 2. Migration routes during spring 2004-2007, for pronghorn in southwestern North Dakota that moved further than 15 km. We used locations collected just before, during, and after migrations to estimate lines of travel between winter and summer ranges.



0 25 50 100 Kilometers

VHF Capture Locations	
+	Females
×	Males
—	Interstate 94
- - -	Pronghorn Hunting Unit Boundary
→	Migrations



CHAPTER 2
RESOURCE SELECTION BY PRONGHORN
IN SOUTHWESTERN NORTH DAKOTA

ABSTRACT

Pronghorn (*Antilocapra americana*) populations in North Dakota are primarily driven by summer reproduction, hunter harvest, disease outbreaks, and severe winter die-offs. Better information about seasonal resource selection might allow biologists to improve summer habitats to promote successful production of offspring and improve habitat conditions on winter ranges to minimize the severity of winter die-offs. Also, knowledge of pronghorn resource selection could help mitigate problems with depredation of agriculture fields or oil and agricultural development. We used discrete choice analysis to model summer and winter resource selection of 50 female adult pronghorn, equipped with GPS collars in southwestern North Dakota, from January 2005 to March 2008. Within an information theory framework, we examined vegetation type, ruggedness and distance to primary, secondary and tertiary roads as predictors of pronghorn habitat selection within home ranges. Our top summer model contained vegetation type, ruggedness, and distance to primary and secondary roads. Pronghorn selected alfalfa, Conservation Reserve Program tracts (CRP), grassland, uncultivated and cultivated vegetation types in the summer, and avoided woodland and riparian vegetation types and primary and secondary roads. Rugged terrain was avoided during both seasons, but avoidance was more prominent in winter. Our top winter model contained vegetation type, ruggedness and distance to primary, secondary and tertiary roads. Pronghorn selected for stubble uncultivated, grassland and barren vegetation types in the winter, and

avoided woodlands and secondary roads. During both seasons, pronghorn selected open, planted and native vegetation types in non-rugged habitat, and generally avoided roads, specifically secondary roads. Given pronghorn selection of open, planted and native vegetation types, reduction of these resources in areas where they are limited might increase depredation complaints. Further, development of secondary roads in flat areas, where flat areas are limited, might increase the severity of winter die-offs by decreasing the use of locally available resources.

INTRODUCTION

To effectively manage pronghorn (*Antilocapra americana*) and make recommendations for land managers, biologists need region-specific resource selection information. Pronghorn in southwestern North Dakota occupy the eastern edge of traditional pronghorn range (O’Gara and Yoakum 2004:80), which is characterized by a unique diversity of rugged terrain and energy development to the west, and row crop agriculture dissected by road and fence networks to the east. However, pronghorn typically avoid areas with human development (Deblinger and Alldredge 1984, Ockenfels 1997, Gavin and Komers 2006) and prefer less rugged areas with slopes < 20% in other parts of their range (Canon 1993, Amstrup 1978, O’Gara and Yoakum 2004:416). Pronghorn select resources differently throughout their range. In Arizona, pronghorn selected home ranges primarily by proximity to water sources (Ockenfels 1997), whereas, in northern states, habitat selection seems to be influenced by topography, winter weather, and vegetation type (Amstrup 1978, Barrett 1982, Stastny 2004, White et al. 2007). Existing knowledge about pronghorn resource use in North Dakota is derived from anecdotal observations, including data from unmarked animals,

during small temporal windows (e.g. a summer survey); however, pronghorn do not utilize similar vegetation types across all seasons (Barrett 1980, Barrett 1984, Stastny 2004, Hervert et al. 2005). Pronghorn in North Dakota exhibited long distance seasonal migration (up to 284 km, Chapter 1), so seasonal variation in resource availability may also exist. These factors hamper the applicability of habitat use and resource selection of other pronghorn populations to the management of North Dakota pronghorn. Due to the checkerboard pattern of land use in western North Dakota, pronghorn home ranges are likely to span lands with various land management practices, and land managers would benefit from local resource selection information.

Current land issues in southwestern North Dakota highlight the need for detailed knowledge of pronghorn habitat use. Due to recent political and economic factors, southwestern North Dakota is subject to significant land alterations from oil and natural gas development and cultivation (Stubbs 2007), much of which is occurring in the state's primary pronghorn range in the Big Gumbo oil field (in the far southwestern corner of our study area) and in the Little Missouri National Grasslands along the Little Missouri River. Information on pronghorn habitat selection should be incorporated into land management plans. In addition, pronghorn depredation complaints are common in North Dakota during severe winters when pronghorn resort to grain piles and haystacks for forage (Bruce Stillings, personal communication, North Dakota Game and Fish Department [NDGF]). Pronghorn depredation complaints also occur in the summer due to their high visibility when standing in mature crops, although mature crops are not typical habitat (O'Gara and Yoakum 2004:420-423). The NDGF is the state's leading provider for information concerning pronghorn management, and biologists have need of

resource use data to monitor and make recommendations concerning habitat conditions, target population levels, and harvest regulations.

Biologists can indirectly manage pronghorn populations by maintaining adequate summer and winter habitats. Summer habitat is crucial for pronghorn populations because fawning and fawn rearing occur on summer ranges. In other regions, pronghorn select grassland habitats in the summer (Buechner 1950, Barrett 1980) with slopes less than 10% (Canon 1993, O’Gara and Yoakum 2004:416). Pronghorn in North Dakota show fidelity to summer ranges (Chapter 1), but biologists have yet to model the resources pronghorn select within these ranges. Along with successful fawning, pronghorn populations require adequate winter habitat to minimize the effects of severe winter weather. Winter die-offs have been documented in northern pronghorn populations where insufficient winter habitat is available (Matrinka 1967, Amstrup 1978, Barrett 1978, Knue 1991:211). In addition to winter mortality, severe winters are also correlated with lower reproduction in subsequent summer seasons (McKenzie 1970, West 1970). In other regions, ideal winter habitat consists of diverse shrub species for browse (Matrinka 1967, Bruns 1977, Amstrup 1978, Barrett 1984, Stastny 2004) and a diversity of slopes (9-25%) to provide shelter from wind and snow and windswept ridges for access to forage (Allen et al. 1984, Ryder and Irwin 1987, Canon 1993). However, winter habitat selection has not been modeled on the eastern fringes of pronghorn distributions, where sage (*Artemisia spp.*), greasewood (*Sarcobatus spp.*), rabbitbrush (*Chrysothamnus spp.*) and other winter browse species are not abundant.

We used discrete choice models to evaluate seasonal resource selection within home ranges (i.e. third-order habitat selection, Johnson 1980) for 50 GPS-collared female

adult pronghorn in southwestern North Dakota, 2005-2008. We used this information to develop predictive maps of relative pronghorn use in southwestern North Dakota to identify the influence of roads, vegetation type and ruggedness on pronghorn habitat selection in this region.

STUDY AREA

We captured pronghorn in areas identified by the NDGF as the primary pronghorn winter range (see Figure 1). Dispersal of these pronghorn into the Slope region of North Dakota broadened the study area to include the entire corner of North Dakota south and west of the Missouri River (Chapter 1). Much of North Dakota's pronghorn range includes the Little Missouri Badlands characterized by steep slopes and rugged topography (Figure 1) and the Missouri Choteau Slope characterized by intensive agricultural development and grids of highways, country roads, and trails (Figure 2). The area is comprised primarily of private land (85%); the rest is Little Missouri National Grasslands (8.3%), State School land (2.6%), Bureau of Land Management (0.5%), and National Park Service land (0.5%) including the north and south unit of the Theodore Roosevelt National Park (TRNP).

The two major vegetation types are northern wheatgrass plains and needlegrass plains. Dominant grass species include: western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Hesperostipa comatai*), green needlegrass (*Nassella viridula*), blue grama (*Bouteloua gracilis*), threadleaf sedge (*Carex filifolia*), sideoats grama (*Bouteloua curtipendula*) and little bluestem (*Schizochyrium scoparium*). Other species included big sagebrush (*Artemisia tridentata*), silver sagebrush (*Artemisia cana*), winterfat (*Krascheninnikovia lanata*), Rocky Mountain juniper (*Juniperus scopulorum*), rubber

rabbitbrush (*Chrysothamnus nauseosus*), broom snakeweed (*Gutierrezia sarothrae*) and saltbushes (*Atriplex spp.*; Johnson and Larson 1999). Much of the land was managed as rangeland, cultivated for row crops (wheat [*Triticum spp.*], canola, flax [*Linum spp.*], sunflowers [*Helianthus spp.*], oats [*Avena spp.*], barley [*Hordeum spp.*], corn [*Crucita spp.*]), or planted for hayland (alfalfa [*Medicago spp.*], crested wheatgrass [*Agropyron cristatum*], and smooth brome [*Bromus inermis*]).

METHODS

Capture

We searched for pronghorn herds each January, 2005-2007, within 2 weeks prior to captures. We used a fixed wing aircraft to survey North Dakota pronghorn wintering areas and recorded herd locations on a handheld GPS unit. We used the collected waypoints to guide capture crews to pronghorn. The Leading Edge helicopter crew (Cody, WY) captured female adult (> 1.5 years old) pronghorn via net-gunning from a helicopter. We used female adult pronghorn because they are the reproductive drivers in a pronghorn population and because territoriality is not as influential on resource selection as it would be for males. A NDGF biologist and pilot observed the capture operations from an overhead plane, led the helicopter to previously located herds, and monitored for potential obstacles. The helicopter crew mounted pronghorn with onboard GPS collars (Advanced Telemetry Systems, Isanti, MN) and recorded capture location, body condition, and an age estimate (1, 2, 3, or 3+ based on incisor eruption, Jensen 1998, O’Gara and Yoakum 2004:785). We scheduled pronghorn captures in mid-January when cooler temperatures and snow coverage were most likely.

We captured and radio-collared 29, 35, and 33 female adult pronghorn in 2005, 2006, and 2007, respectively. We distributed collars as evenly as logistically possible across the original study area on each side of the Little Missouri River with a maximum of one collar per herd (Figure 1). We flew a check-up flight within one week of capture to monitor for capture-related mortalities.

Radio Telemetry

To avoid losing collars, we attempted to monitor all individuals by aerial tracking (Gilmer et al. 1981) once every 10 days with the NDGF Scout airplane (American Champion Aircraft Corporation, Rochester, WI). We recorded the collar status based on signal patterns (e.g., 5 single beeps at 60 beats per minute followed by one double beep at 120 beats per minute indicated that the collar was functioning properly).

The programmed sampling regime for the GPS collars consisted of two schedules: 1) the main schedule where locations acquired every 23 hours, and 2) the auxiliary schedule where locations acquired every 5 hours during migratory seasons (16 February through 31 May and 1 October through 31 December). Locations were recorded at varying times of day to assure that we detected use for all regular activities. Collars released from pronghorn after 390 days via timed release mechanisms.

We located collars aerially after the collar release date to assure that collars dropped from the pronghorn and to attain approximate (\pm 0.25 mile) locations. If dropped collars had strong batteries (determined by pulse rate), we let them lay for up to two weeks in order to collect locations for estimating GPS precision. On the ground, we used a handheld receiver (Icom America, Inc. Bellevue, WA) and a Rubber "H" type

antenna (Telonics, Inc., Mesa, AZ) to retrieve collars. We extracted data from collars using program WinCollar (Advanced Telemetry Systems, Isanti, MN).

Prior to developing home ranges, we subsampled locations, from the end of our winter season (15 December – 31 December), that were collected during the auxiliary GPS schedule. We systematically subsampled (morning, afternoon, evening, night) one location from the 4-5 daily locations collected to achieve a consistent, daily sampling regime for the entire winter seasons. By subsampling during these times, we removed the unequal weighting that occurred within a season given our GPS collection schedule. We pooled data across the three years of our study with the assumptions that habitat selection was similar during three years with mild winters and relatively dry summers. Pooling was appropriate because we were not interested in year-specific models (i.e., we wanted to examine resource selection over the period of our study), and because we had a small sample size during winter seasons.

Habitat Data

We used three main variables to model winter (15 December – 15 March) and summer (1 June – 15 September) pronghorn resource selection: nearest road by type, terrain ruggedness and vegetation type. We included terrain ruggedness and vegetation type because tall vegetation and rugged terrain decrease predator detection and evasion (Byers 1997, O’Gara and Yoakum 2004:110, 139, Stastny 2004). Vegetation types also provide different qualities and quantities of forage between seasons (Bruns 1977, Tucker and Garner 1983, Canon 1990, Stastny 2004). We examined distances to roads because roads affect pronghorn behavior (Gavin and Komers 2006) and might be a source of disturbance to pronghorn.

Roads and Ruggedness-We obtained road layers and 30 m national elevation data (NED) from the North Dakota GIS hub (<<http://www.nd.gov/gis/>>, accessed August 2008). We used the Euclidean distance tool in the Spatial Analyst extension of ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA 92373) to create continuous raster files representing the distances (km) to nearest primary roads (paved), secondary roads (high grade gravel and maintained county roads) and tertiary roads (dirt roads and prominent trails). We computed a ruggedness raster from the elevation dataset using a Vector Ruggedness Measure script (Sappington et al. 2005). This script computes ruggedness using a moving-window routine to analyze x, y, and z values of vectors orthogonal to grid cells from our NED, resulting in a raster of values between 0 (flat) and 1 (rugged). These values are not necessarily correlated with slope, so steeper but smooth hillsides, which do not limit visibility for pronghorn, were not considered rugged. We used a 3 × 3 moving window as suggested by Sappington et al. (2005) and scaled these values on a scale of 0–100.

Vegetation type-For vegetation data we used Land Use Land Class data from the National Agricultural Statistics Service (NASS) and the Gap Analysis Project (GAP), both acquired from the North Dakota GIS hub (<<http://www.nd.gov/gis/>>, accessed August 2008). These datasets were developed from 2006 (NASS) and 1992-1998 (GAP) Landsat imagery, with 56 m (NASS) and 30 m (GAP) resolution. NASS uses broad land use categories to define uncultivated land including: non-agricultural, rangeland, waste, woods, and farmstead, so we supplemented non-agricultural areas with information from the GAP analysis. The GAP data were developed from images taken several years prior to our study, so we only used the GAP dataset for vegetation classes that were unlikely to

change (e.g. riparian vegetation in proximity to hydrological features, woodlands, and sparsely vegetated badlands). We used 11 vegetation types: alfalfa, riparian, grassland, barren, CRP (planted perennials), woodland, fallow, cultivated, developed, pastures (included agricultural land that was not cultivated), and shrubland. We consolidated alfalfa, cultivated and fallow for the winter season because they were similar after harvest.

Statistical Analysis

We used discrete choice modeling (Proc MDC; SAS Institute 2003) to assess resource selection of pronghorn during winter and summer. In the discrete choice modeling framework, used resources (as defined by the relocation point) are compared to available points within a defined choice set (Cooper and Millspaugh 1999). We used this method to evaluate the habitats selected within home ranges (i.e., third-order habitat selection [Johnson 1980]).

Because most pronghorn could move across entire home ranges in one day, we defined each choice set as the 100% utilization distribution (UD) boundary for an individual pronghorn. We chose 100% boundaries because they represented the area where we had 100% probability of finding the pronghorn. The 100% UD boundaries (hereafter, home ranges) also assured that all used locations would be included in the choice set. To minimize potential bias in home range estimation due to small sample sizes, we calculated UD only for pronghorn with ≥ 30 locations per season (Seaman et al. 1999, Kernohan et al. 2001). We computed UD grids using KernelHR (National Biological Service, Port Angeles, WA; Seaman 1997) with least square cross validation to select bandwidth. We converted UD grids to shapefiles in ArcGIS 9.2, and we used

Hawth's Analysis Tools (Beyer 2004) to generate 5 random available points for each used location within the respective home range (McFadden 1974). We did not allow available locations to be generated in open water parcels, which we deemed unavailable.

We used a two-stage model fitting approach. In the first stage, we evaluated which form (linear or pseudothreshold) best represented the relationship between distance to nearest road (by type) and use. Previous studies suggested that the effects of distance to nearest roads may be non-linear. For example, Gavin and Komers (2006) found that pronghorn in Alberta spent a higher proportion of time foraging at sites >400 m from roads. We modeled both forms for each class of roads (primary, secondary and tertiary) using Proc MDC (SAS Institute 2003) (Table 1). We identified the best model using an Akaike Information Criterion (AIC, Burnham and Anderson 2002), and we used the form with the lowest AIC score for all subsequent models where roads were included.

In the second stage, we developed 12 *a priori* models for summer and winter resource selection (Table 2). We developed models around a combination of the 3 main variables: vegetation type, distance to nearest roads (by type), and terrain ruggedness, and we also included models of the 3 main variable alone. For each model with roads we also included a model where distance to nearest tertiary road was removed because tertiary roads have very little traffic, are commonly unfenced and not raised, and might not affect habitat use for pronghorn. We examined the fit of each model with Proc MDC (SAS Institute 2003) using mixed logit estimation, which assumes normal distribution of errors for repeated locations from individuals (SAS Institute 2006:639). We used AIC (Burnham and Anderson 2002) to assess the relative support among candidate models.

We created summer and winter maps of predicted probabilities of pronghorn resource selection in our study area. We used the top models and the associated parameter estimates to calculate relative probability raster files using the raster calculator in ArcGIS 9.2.

We validated the predictive accuracy of our top model using k-fold cross validation (Boyce et al. 2002, Johnson et al. 2006). For this validation, we randomly assigned choice sets into 5 folds, each containing 20% of our original data. We then used Proc MDC (SAS Institute 2003) to compute new coefficients for 4 of the 5 folds of data (training data), and tested these coefficients using the used points from the remaining fold (test data). We repeated this process so that each fold was used as test data. To test the training coefficients, we calculated probabilities of use for all points that were not used as training data, sorted probabilities from the available points into 20 equal-interval bins, and counted the number of used locations with probabilities corresponding to a particular bin. We then compared predicted bin rankings to the ranking of number of used points within each bin using Spearman rank coefficients (Boyce et al. 2002).

RESULTS

Between January 2005 and March 2008, we retrieved 53 GPS collars from pronghorn that survived through at least the summer season and 33 of those survived through the winter season. We used an experimental GPS collar design, and several collars malfunctioned in 2005 (17/29) and 2006 (7/35) prior to recovery. In 2007, nearly all (31/33) redesigned collars functioned properly until mortality or the drop date. We removed 3 summer home ranges and 1 winter home range from analysis due to migrations outside of our study area, so 50 and 32 home ranges were used for each

season respectively. Hunters harvested 7, 4, and 5 collared pronghorn in the falls of 2005, 2006 and 2007 respectively, so much of the disparity between the summer and winter sample size relates to low survival during the fall hunting season. Approximately 88% (53/60) of the collared pronghorn survived through the summer season, but only 55% (33/60) survived through the end of the fall hunting season. For each pronghorn, we collected an average of 106.89 (SD = 8.04, range = 52–115) locations per summer season and 62.29 (SD = 22.83, range = 45–137) locations per winter season. We used 5,486 and 2,028 locations for the summer and winter seasons, respectively. Locations collected from stationary locations (post collar drop) deviated from the mean drop location by an average of 3.26 m ($n = 41$ collars, SD = 2.68 m, range = 0.07–453.19 m). The mean size of 100% fixed kernel choice sets was 8.91 km² (SD = 6.00 km², range = 0.80–22.11 km²) for summer and 23.98 km² (SD = 24.26 km², range = 1.82–122.42 km²) for winter.

The forms for the relationship between use and distance to nearest road varied among road classes and between seasons (Table 1). For summer models, we used a pseudothreshold relationship for primary and secondary roads, and a linear relationship for tertiary roads. For winter models we used a linear relationship for primary roads, and a pseudothreshold relationship for secondary and tertiary roads.

During summer the top model included all variables in the global model with distance to tertiary roads removed (Table 3), and during winter the top model was the global model (Table 4). All models predicted pronghorn use greater than the null model, providing evidence that third-order habitat selection was selective. Further, the proportions of used and available locations per vegetation types were not similar across vegetation type (Figure 3).

Summer coefficients.—During the summer season, we found that pronghorn selected alfalfa, CRP, grassland, non-agricultural, and cultivated vegetation types; and avoided woodland and riparian vegetation types (Table 5). Pronghorn used areas further from primary and secondary roads within their home ranges. Pronghorn were twice as likely to use areas that were > 1 km from primary roads, and were 2 times more likely to use areas > 3 km from secondary roads than areas <1 km of secondary roads (Figure 4). Pronghorn also used areas that were in the lowest quantile of the ruggedness index (there were no used locations in areas with ruggedness values > 28, Figure 4). Our predictive map for pronghorn relative use during the summer depicts the strong influence of major roads, especially in the Slope region, and the negative influence of rugged terrain, primarily in the badlands (Figure 5). For our top model, we found a significant positive correlation between expected and observed frequencies across all folds of the data (Table 6), suggesting our model predicted resource selection well.

Winter coefficients.—During winter, pronghorn selected stubble, non-agricultural, grassland, and barren vegetation types, and avoided the woodland vegetation type (Table 7). Pronghorn used areas randomly with respect to primary roads (Table 7), but avoided secondary roads and selected for areas nearer to tertiary roads. Pronghorn were 7.5 times less likely to select areas within 1 km from secondary roads than they were to select areas beyond 1 km; however, use was actually slightly higher (1.6 times more likely) in areas < 1 km from tertiary roads than beyond 1 km (Figure 6). Pronghorn avoided rugged areas in the winter season and were 4.5 times more likely to use areas in the lowest quarter of used ruggedness values (Figure 6). Our predictive map for pronghorn relative use during the winter depicts the negative influence of rugged terrain and secondary roads and the

positive influences of open vegetation types (Figure 7). For our winter global model, we found a significant positive correlation between expected and observed frequencies across all folds of the data (Table 6), suggesting our model predicted resource selection well.

DISCUSSION

During both seasons, pronghorn selected open vegetation types in non-rugged terrain, and roads played an important role on pronghorn resource selection, particularly secondary roads. We found that pronghorn avoided primary and secondary roads in the summer and avoided secondary roads in the winter. Researchers have previously found that pronghorn avoid areas of human disturbance (Ockenfels 1997), and pronghorn in Alberta spent a higher proportion of time foraging at sites >400 m from roads, suggesting that pronghorn perceived roads as sources of increased predation risk (Gavin and Komers 2006). Other ungulate species avoided roads or traffic, during at least some periods, including: elk (*Cervus elaphus*, Millspaugh 1999, Rowland et al. 2000, Sawyer et al. 2007, Naylor et al. 2009), caribou (*Rangifer tarandus*, Dyer et al. 2001, Joly et al. 2006), bighorn sheep (*Ovis canadensis*, Keller and Bender 2007), and moose (*Alces alces*, Laurien et al. 2008). Frid and Dill (2002) hypothesized that animals perceive human-caused disturbance as a predation risk, and will shift distributions after long term disturbances (such as perceived risk), unless the cost of shifting habitat outweighs the benefit. Woodland caribou (Dyer et al. 2001), elk (Millspaugh et al. 2000), bighorn sheep (*Ovis canadensis*; Keller and Bender 2007), and pronghorn (Berger et al. 1983, Gavin and Komers 2006) avoided roads during times of increased traffic and during autumn hunting seasons. However, in the winter we did not observe avoidance for

primary roads. This may be a result of some pronghorn congregating in areas adjacent to movement barriers; raised highways and bordering fences truncated pronghorn movements in other areas (O’Gara and Yoakum 2004:621, Sheldon 2005, Harrington and Conover 2006). Another possibility for why we did not discern a stronger avoidance, and to explain the selection for areas nearer to tertiary roads in the winter, might be due to an inverse relationship between roads and ruggedness (in rough terrain roads are generally constructed on the smoothest route, following drainages, plateaus, and valleys). Predictive maps make it apparent that ruggedness was more influential than distance to roads in the winter season (Figure 7).

Although land conversion to row crops and increased road densities may negatively affect habitat suitability for pronghorn, results from our study reveal positive associations between pronghorn selection and certain human-altered vegetation types. Pronghorn are adapted for short-grass prairies (Buechner 1950) and do not prefer tall structured vegetation types (O’Gara and Yoakum 2004:420-423), so pronghorn should select pastures and grasslands for summer ranges. We found that pronghorn selected grassland vegetation and uncultivated agricultural vegetation. In contrast, we might hypothesize that mature agricultural fields, CRP plots and large riparian areas should not be suitable habitat because they lack the heterogeneity to meet both high visibility and diverse forb availability (Bruns 1977, Tucker and Garner 1983, Stastny 2004), adequate hiding cover for fawns (Bruns 1977, Tucker and Garner 1983, Canon 1993, Sievers 2004, Stastny 2004), or tall shrub height for winter forage (Matrinka 1967, Bruns 1977, Amstrup 1978, Stastny 2004). However, researchers found that Sonoran pronghorn used vegetation in proportion to what was available (Krausman et al. 2005), suggesting that

pronghorn are adaptable to different habitats, and 16 of 18 western conservation agencies surveyed noted pronghorn depredation on alfalfa and wheat fields (O'Gara and Yoakum 2004:692). Pronghorn in Colorado also used winter wheat fields during the winter months (Torbitt et al. 1993). Although taller shrubs may be important in severe winters (Bruns 1977, Amstrup 1978, Barrett 1984, Stastny 2004), our findings suggest that pronghorn appear adaptable to human-altered areas, such as stubble fields and planted perennial grasses during the mild winters, when our study was conducted (Figure 7). Also, we found positive relationships for cultivated land, alfalfa and CRP tracts during summer. We suggest that future research on summer vegetative associations, in highly cultivated landscapes, should incorporate temporal changes in available vegetation (i.e. from plowed fields, sprouting fields, mature fields to harvested stubble fields).

Pronghorn in our study area selected less rugged habitats than what were available within their home ranges. Similarly, Amstrup (1978) found 44% of marked pronghorn observations in central Montana and Wyoming had less than 5% slope, and only 7% of all locations had slopes greater than 20%. Canon (1993) hypothesized that during dry years, pronghorn fawns in the Trans-Pecos region of Texas selected bedding sites in hilly areas, which provided higher forb and cacti availability. However, he suggested that ideal pronghorn fawning ranges have between 4-5% slopes. Pronghorn use more rugged terrain (up to 25-35%, Ryder and Irwin 1987) in severe winters when rugged areas provide microhabitats with both relief from wind and windblown hilltops (Barrett 1984, Ryder and Irwin 1987). In contrast, we found a stronger negative association with ruggedness in winter than in summer, which might be representative for pronghorn habitat selection during mild winters. The stronger negative association with rugged

terrain in winter might also be due to a seasonal distribution shift. The North Dakota pronghorn population westward during the winter (Chapter 1) where availability of rugged terrain ($\bar{x} = 2.49$, $SD = 5.99$) was slightly higher than in summer ($\bar{x} = 1.92$, $SD = 4.84$), but use remained similar (summer $\bar{x} = 1.31$, $SD = 3.38$; winter $\bar{x} = 1.35$, $SD = 2.82$). Our predictive maps show overall low probabilities of use in the badlands for summer (Figure 6) and winter (Figure 7), however we observed winter and summer pronghorn home ranges in the badlands. It is likely that pronghorn in the badlands are using limited flat areas in broad drainages and on top of large plateaus.

Although we have modeled pronghorn resource selection in North Dakota using a liberal number of pronghorn locations, digitized road networks, ruggedness and habitat types, a few issues limit the conclusions we can make concerning pronghorn resource selection. To begin with, we only monitored female adult pronghorn. Female pronghorn are less territorial than males (Byers 1997:106-117, 183-186), might not receive as much hunting pressure as males (O’Gara and Yoakum 2004:767), and although highly gregarious, might not associate with males the entire year (Byers 1997:28-32). In addition, nearly every pronghorn (46 of 50) made daily movements of 2 km or more during the summer season and 31 of 32 made movements > 2 km during the winter season. Therefore, it is likely that occasional, used locations were incidental locations recorded while animals traversed between two desired resources (Buskirk and Millsbaugh 2006). Also, although hydrologic streambed data were available in GIS format, we did not have information on locations of the many unmapped, ephemeral water sources (dugouts and stock dams), which we noticed during our study period. We would have greatly underestimated available water sources, so we were unable to examine the

influence of water sources on pronghorn habitat. Fence density might also influence pronghorn distribution and resource selection (Harrington and Conover 2006), but due to our large study area, we were unable to map and investigate the influence of fences on resource selection. And finally, sage brush, rabbitbrush and greasewood are important components of winter habitat (Bruns 1977, Amstrup 1978, Barrett 1984, Stastny 2004), but species specific density and distribution data for shrubs were not available or examined in our study. Biologists should complement this research with conclusions from natural history studies, behavioral studies, movement studies, survival studies and dietary studies to attain a more complete understanding of pronghorn habitat selection.

Management Implications

Habitat management “is the most practical and effective method to ensure that pronghorn remain stable and viable in North America” (Autenrieth et al. 2006:22). We found a negative association between pronghorn habitat and secondary roads so our results support Gavin and Komers’ (2006) suggestion that land management plans should incorporate consequences of increased road density. Neither the U.S. Fish and Wildlife Service habitat suitability model for pronghorn (Allen et al. 1984), the Habitat Management Guide: 2006 (Autenrieth et al. 2006), nor O’Gara and Yoakum’s (2004) review of pronghorn literature mentioned pronghorn distribution in relation to roads unless discussing roads as impediments to movement or replacement of forage. This reflects the current need for additional information on pronghorn habitat use in relation to roads. Our research suggests that pronghorn winter habitat should be available > 1 km from secondary roads; however, because it is more economically feasible to construct roads in relatively smooth terrains, road development for oil exploration might decrease

the quality of available pronghorn winter habitat in North Dakota. Further, O’Gara and Yoakum (2004:688) estimated that 55-62% of pronghorn in North America are on private land, and more than 80% of the pronghorn range in North Dakota is privately owned. When making recommendations concerning pronghorn habitat, it is important that managers do not dismiss the potentially beneficial habitat components provided on private land management practices such as increased forage (alfalfa in the summer) or decreased vegetation height (stubble fields in the winter). However, converting land to row crops might decrease the social carrying capacity for pronghorn because crop depredation complaints are probable, due to pronghorn use of cultivated lands.

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Table 1. Ranking of exploratory models to determine appropriate forms for the relationship between pronghorn habitat use and distance to nearest primary, secondary and tertiary roads, for summer and winter seasons in southwestern North Dakota. K is the number of parameters in the model, -2LogL is -2 times the log-likelihood value, AIC is Akaike's information criterion, and Δ AIC is the difference in AIC value from the top model.

	Model	K	-2LogL	AIC	Δ AIC
Summer	Nearest primary road (primary)	2	19656	19661	11
	*Primary + primary ²	3	19644	19650	0
	Nearest secondary road (secondary)	2	19654	19658	11
	*Secondary + secondary ²	3	19642	19647	0
	*Nearest tertiary road (tertiary)	2	19658	19661	0
	Tertiary + tertiary ²	3	19658	19663	2
	*Nearest primary road (primary)	2	7264	7268	0
Primary + primary ²	3	7268	7270	2	
Winter	Nearest secondary road (secondary)	2	7264	7264	30
	*Secondary + secondary ²	3	7234	7234	0
	Nearest tertiary road (tertiary)	2	7270	7270	6
	*Tertiary + tertiary ²	3	7264	7264	0

*Form used for subsequent models

Table 2. *A priori* models used to examine pronghorn resource selection in southwestern North Dakota, 2005-2007.

Hypothesis	Model	Model Structure with expected signs for β values
1) Vegetation type ^a , ruggedness and distance to 1°, 2°, and 3° roads ^b influence pronghorn habitat selection.	Global	$\beta_1(V_{\text{alf}})^b - \beta_2(V_{\text{rip}}) + \beta_3(V_{\text{grass}}) - \beta_4(V_{\text{bare}}) - \beta_5(V_{\text{CRP}}) - \beta_6(V_{\text{wood}}) +$ $\beta_7(V_{\text{fall}})^b - \beta_8(V_{\text{crop}})^b - \beta_9(V_{\text{stub}})^c - \beta_{10}(V_{\text{dev}}) + \beta_{11}(V_{\text{past}}) + \beta_{12}(V_{\text{shrub}}) -$ $\beta_{13}(\text{Rugged}) - \beta_{14}(R_{\text{prim}}) - \beta_{15}(R_{\text{prim}})^{2b} - \beta_{16}(R_{\text{sec}}) - \beta_{17}(R_{\text{sec}})^2 -$ $\beta_{18}(R_{\text{tert}}) - \beta_{19}(R_{\text{tert}})^{2c}$
2) Vegetation type, ruggedness and distance to 1° and 2° roads influence pronghorn habitat selection, 3° roads do not affect selection.	Global w/o trails	$\beta_1(V_{\text{alf}})^b - \beta_2(V_{\text{rip}}) + \beta_3(V_{\text{grass}}) - \beta_4(V_{\text{bare}}) - \beta_5(V_{\text{CRP}}) - \beta_6(V_{\text{wood}}) +$ $\beta_7(V_{\text{fall}})^b - \beta_8(V_{\text{crop}})^b - \beta_9(V_{\text{stub}})^c - \beta_{10}(V_{\text{dev}}) + \beta_{11}(V_{\text{past}}) + \beta_{12}(V_{\text{shrub}}) -$ $\beta_{13}(\text{Rugged}) - \beta_{14}(R_{\text{prim}}) - \beta_{15}(R_{\text{prim}})^{2b} - \beta_{16}(R_{\text{sec}}) - \beta_{17}(R_{\text{sec}})^2$
3) Vegetation type, ruggedness influence pronghorn habitat selection.	Habitat & rugged	$\beta_1(V_{\text{alf}})^b - \beta_2(V_{\text{rip}}) + \beta_3(V_{\text{grass}}) - \beta_4(V_{\text{bare}}) - \beta_5(V_{\text{CRP}}) - \beta_6(V_{\text{wood}}) +$ $\beta_7(V_{\text{fall}})^b - \beta_8(V_{\text{crop}})^b - \beta_9(V_{\text{stub}})^c - \beta_{10}(V_{\text{dev}}) + \beta_{11}(V_{\text{past}}) + \beta_{12}(V_{\text{shrub}}) -$ $\beta_{13}(\text{Rugged})$
4) Vegetation type and distance to 1°, 2° and 3° roads influence pronghorn habitat selection.	Habitat & roads	$\beta_1(V_{\text{alf}})^b - \beta_2(V_{\text{rip}}) + \beta_3(V_{\text{grass}}) - \beta_4(V_{\text{bare}}) - \beta_5(V_{\text{CRP}}) - \beta_6(V_{\text{wood}}) +$ $\beta_7(V_{\text{fall}})^b - \beta_8(V_{\text{crop}})^b - \beta_9(V_{\text{stub}})^c - \beta_{10}(V_{\text{dev}}) + \beta_{11}(V_{\text{past}}) + \beta_{12}(V_{\text{shrub}}) -$ $\beta_{13}(R_{\text{prim}}) - \beta_{14}(R_{\text{prim}})^{2b} - \beta_{15}(R_{\text{sec}}) - \beta_{16}(R_{\text{sec}})^2 - \beta_{17}(R_{\text{tert}}) - \beta_{18}(R_{\text{tert}})^{2c}$

- 5) Vegetation type and distance to 1° and 2° roads influence pronghorn habitat selection, 3° roads do not affect selection. Habitat w/o trails
- $$\beta_1(V_{\text{alf}})^b - \beta_2(V_{\text{rip}}) + \beta_3(V_{\text{grass}}) - \beta_4(V_{\text{bare}}) - \beta_5(V_{\text{CRP}}) - \beta_6(V_{\text{wood}}) + \beta_7(V_{\text{fall}})^b - \beta_8(V_{\text{crop}})^b - \beta_9(V_{\text{stub}})^c - \beta_{10}(V_{\text{dev}}) + \beta_{11}(V_{\text{past}}) + \beta_{12}(V_{\text{shrub}}) - \beta_{13}(R_{\text{prim}}) - \beta_{14}(R_{\text{prim}})^{2b} - \beta_{15}(R_{\text{sec}}) - \beta_{16}(R_{\text{sec}})^2$$
- 6) Vegetation type influences pronghorn habitat selection. Habitat
- $$\beta_1(V_{\text{alf}})^b - \beta_2(V_{\text{rip}}) + \beta_3(V_{\text{grass}}) - \beta_4(V_{\text{bare}}) - \beta_5(V_{\text{CRP}}) - \beta_6(V_{\text{wood}}) + \beta_7(V_{\text{fall}})^b - \beta_8(V_{\text{crop}})^b - \beta_9(V_{\text{stub}})^c - \beta_{10}(V_{\text{dev}}) + \beta_{11}(V_{\text{past}}) + \beta_{12}(V_{\text{shrub}}) - \beta_1(\text{Rugged}) - \beta_2(R_{\text{prim}}) - \beta_3(R_{\text{prim}})^{2b} - \beta_4(R_{\text{sec}}) - \beta_5(R_{\text{sec}})^2 - \beta_6(R_{\text{tert}}) - \beta_7(R_{\text{tert}})^{2c}$$
- 7) Ruggedness and distance to 1°, 2°, and 3° roads influence pronghorn habitat selection. Rugged & roads
- $$-\beta_1(\text{Rugged}) - \beta_2(R_{\text{prim}}) - \beta_3(R_{\text{prim}})^{2b} - \beta_4(R_{\text{sec}}) - \beta_5(R_{\text{sec}})^2 - \beta_6(R_{\text{tert}}) - \beta_7(R_{\text{tert}})^{2c}$$
- 8) Ruggedness and distance to 1° and 2° roads influence pronghorn habitat selection, 3° roads do not affect selection. Rugged w/o trails
- $$-\beta_1(\text{Rugged}) - \beta_2(R_{\text{prim}}) - \beta_3(R_{\text{prim}})^{2b} - \beta_4(R_{\text{sec}}) - \beta_5(R_{\text{sec}})^2$$
- 9) Ruggedness influences pronghorn habitat selection, pronghorn habitat selection. Rugged
- $$-\beta_1(\text{Rugged})$$
- 10) Distance to 1°, 2°, and 3° roads influence pronghorn habitat selection. Roads
- $$-\beta_1(R_{\text{prim}}) - \beta_2(R_{\text{prim}})^{2b} - \beta_3(R_{\text{sec}}) - \beta_4(R_{\text{sec}})^2 - \beta_5(R_{\text{tert}}) - \beta_6(R_{\text{tert}})^{2c}$$

- 11) Distance to 1° and 2° roads influence
 pronghorn habitat selection, 3° roads do not
 affect selection. Roads w/o trails

$$- \beta_1(R_{\text{prim}}) - \beta_2(R_{\text{prim}})^{2b} - \beta_3(R_{\text{sec}}) - \beta_4(R_{\text{sec}})^2$$
- 12) Vegetation type, ruggedness nor distance to
 1°, 2° and 3° roads influence pronghorn
 habitat selection. Null
-

^a We coded vegetation types (V_{type}) as binary (0/1) responses for: alfalfa (V_{alf}), riparian (V_{rip}), grassland (V_{grass}), barren (V_{bare}), CRP (V_{CRP}), woodland (V_{wood}), fallow (V_{fall}), cultivated (V_{crop}), developed (V_{dev}), pasture (V_{past}), and shrubland (V_{shrub}); we merged alfalfa, fallow and cultivated vegetation types into a single stubble (V_{stubb}) response for the winter season.

^b Included only in summer models.

^c Included only in winter models.

Table 3. Ranking of candidate discrete choice models for pronghorn during the summer seasons, 2005-2007, in southwestern North Dakota. K is the number of parameters in the model, -2LogL is -2 times the log-likelihood value, AIC is Akaike's information criterion, Δ AIC is the difference in AIC value from the top model, and w_i is the Akaike weight.

Model	K	-2LogL	AIC	Δ AIC	w_i
Global w/o trails	17	19372	19407	0	0.6240
Global	18	19372	19408	1	0.3760
Vegetation & ruggedness	13	19414	19440	33	0.0000
Ruggedness w/o trails	6	19482	19494	87	0.0000
Ruggedness & roads	7	19482	19496	89	0.0000
Vegetation & roads	17	19480	19513	106	0.0000
Vegetation w/o trails	16	19482	19514	107	0.0000
Ruggedness	2	19522	19526	119	0.0000
Habitat	12	19522	19546	139	0.0000
Roads	6	19618	19630	223	0.0000
Roads w/o trails	5	19620	19631	224	0.0000
Null	1	19660	19661	254	0.0000

Table 4. Ranking of candidate discrete choice models for pronghorn during winter seasons, 2006-2008, in southwestern North Dakota. K is the number of parameters in the model, -2LogL is -2 times the log-likelihood value, AIC is Akaike's information criterion, Δ AIC is the difference in AIC value from the top model, and w_i is the Akaike weight.

Model	K	-2LogL	AIC	Δ AIC	w_i
Global	16	6918	6951	0	0.6152
Global w/o trails	14	6924	6952	1	0.3848
Vegetation & ruggedness	11	6962	6984	33	0.0000
Vegetation & roads	15	7026	7055	104	0.0000
Vegetation w/o trails	13	7032	7057	106	0.0000
Vegetation	10	7066	7086	135	0.0000
Ruggedness & roads	7	7080	7093	142	0.0000
Ruggedness w/o trails	5	7086	7095	144	0.0000
Ruggedness	2	7134	7137	186	0.0000
Roads	6	7216	7228	277	0.0000
Roads w/o trails	4	7222	7231	280	0.0000
Null	1	7268	7269	318	0.0000

Table 5. Third-order habitat selection parameter coefficients from the top summer discrete choice model (the global model with distance to nearest tertiary road removed) for pronghorn in southwestern North Dakota, 2005-2008.

Parameter	Estimate	95% CI	t-value	P-value
Alfalfa	0.8561	0.4541 – 1.2581	4.17	<.0001
Riparian	-0.6858	-1.0331 – -0.3385	-3.87	0.0001
Grassland*	0.2365	.	.	.
Barren	0.0371	-0.1152 – 0.1894	0.48	0.6330
CRP	0.2528	0.1746 – 0.3310	6.33	<.0001
Woodland	-0.9404	-1.3273 – -0.5535	-4.76	<.0001
Fallow	0.1071	-0.4654 – 0.6796	0.37	0.7138
Cultivated	0.1953	0.0875 – 0.3031	3.55	0.0004
Developed	-0.2355	-0.5369 – 0.0659	-1.53	0.1257
Pasture	0.2294	0.0965 – 0.3622	3.38	0.0007
Shrubland	-0.0527	-0.3318 – 0.2264	-0.37	0.7112
Ruggedness	-0.0531	-0.0625 – -0.0437	-11.04	<.0001
Nearest primary road	0.0520	0.0095 – 0.0945	2.4	0.0165
Nearest primary road ²	-0.0045	-0.0067 – -0.0023	-4.01	<.0001
Nearest secondary road	0.1566	0.0431 – 0.2701	2.71	0.0068
Nearest secondary road ²	-0.0672	-0.0991 – -0.0353	-4.12	<.0001
Pronghorn ID	1	.	.	.

*The grassland vegetation type was selected as the reference binary variable, so no SE, 95% CI, or P-values were calculated.

Table 6. Spearman-rank correlation (r_s) of the top summer and winter models for each fold, from k -fold cross-validation of pronghorn discrete choice models in southwestern North Dakota, 2005-2008.

Season	Fold	r_s	P -value
Summer	1	0.9748	< 0.0001
	2	0.9714	< 0.0001
	3	0.9628	< 0.0001
	4	0.9680	< 0.0001
	5	0.9561	< 0.0001
	Combined	0.3206	0.0011
Winter	1	0.9880	< 0.0001
	2	0.9910	< 0.0001
	3	0.9849	< 0.0001
	4	0.9759	< 0.0001
	5	0.9827	< 0.0001
	Combined	0.7309	< 0.0001

Table 7. Third-order habitat selection parameter coefficients from the top winter discrete choice model (Global) for pronghorn in southwestern North Dakota, 2005-2008.

Parameter	Estimate	95% CI	t-value	P-value
Riparian	-0.5315	-1.1309 – 0.0679	-1.74	0.0822
Grassland*	0.4598	.	.	.
Barren	0.3273	0.1050 – 0.5496	2.89	0.0039
CRP	0.0156	-0.1553 – 0.1865	0.18	0.8576
Woodland	-1.5092	-2.5070 – -0.5114	-2.96	0.003
Stubble	1.0037	0.8326 – 1.1748	11.5	<0.0001
Developed	-0.2122	-0.8374 – 0.4130	-0.67	0.506
Pasture	0.7490	0.5350 – 0.9630	6.86	<0.0001
Shrubland	-0.3025	-0.8666 – 0.2616	-1.05	0.2932
Ruggedness	-0.0842	-0.1038 – -0.0646	-8.43	<0.0001
Nearest primary road	-0.0165	-0.0430 – 0.0100	-1.22	0.2213
Nearest secondary road	-0.5041	0.3279 – 0.6803	5.61	<0.0001
Nearest secondary road ²	0.122	-0.1686 – -0.0754	-5.13	<0.0001
Nearest tertiary road	-0.1393	-0.2983 – 0.0197	-1.72	0.0859
Nearest tertiary road ²	0.0395	0.0001 – 0.0789	1.96	0.0497
Pronghorn ID	1	.	.	.

*The grassland vegetation type was selected as the reference binary variable, so no SE, 95% CI, or P-values were calculated.

Figure 1. Pronghorn capture locations in southwestern North Dakota, 2005-2007 in relation to study area and ruggedness values. (The darker grid of ruggedness values to the southeast in our study area originated from a different data source; these values were not used in analysis.)

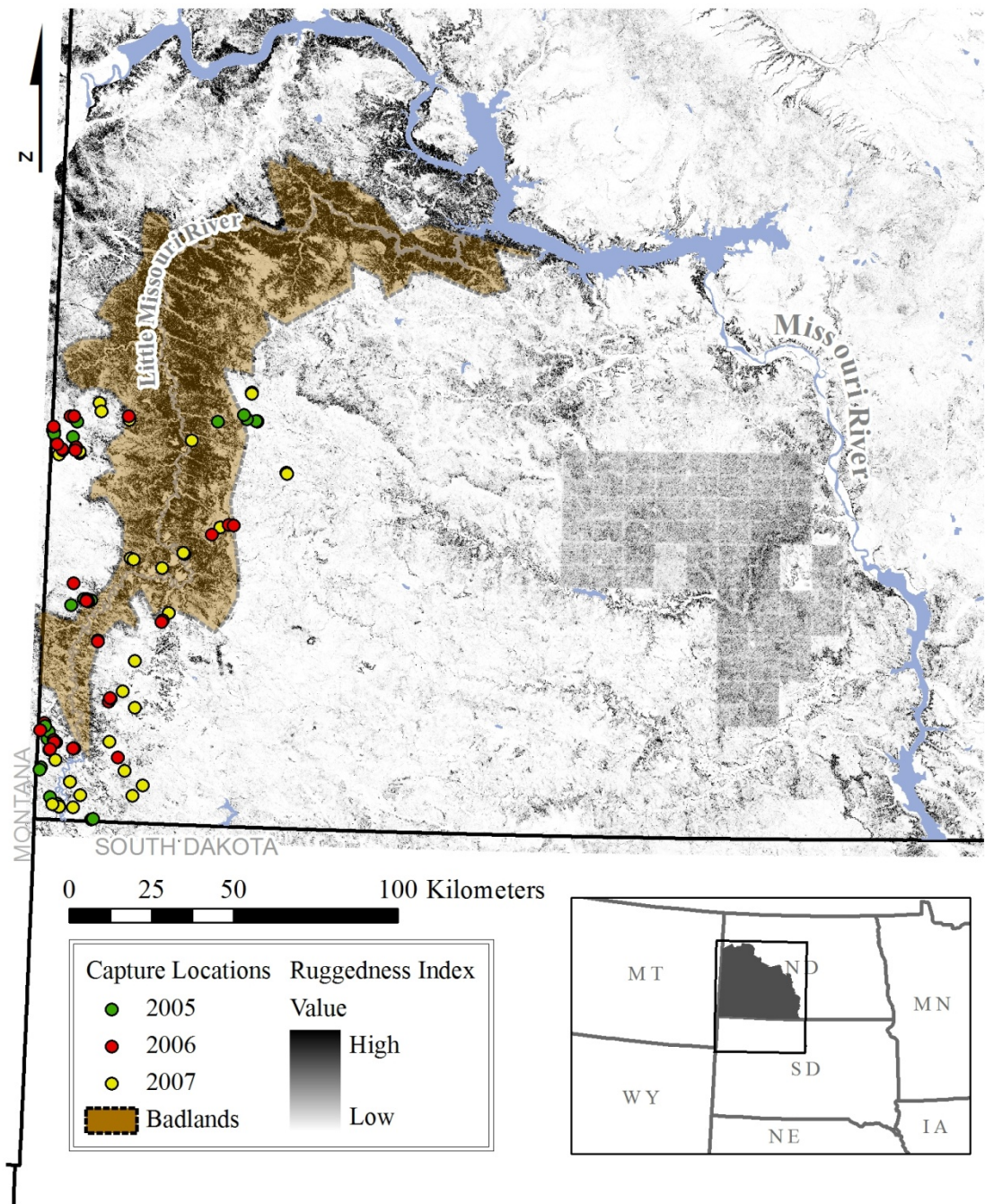
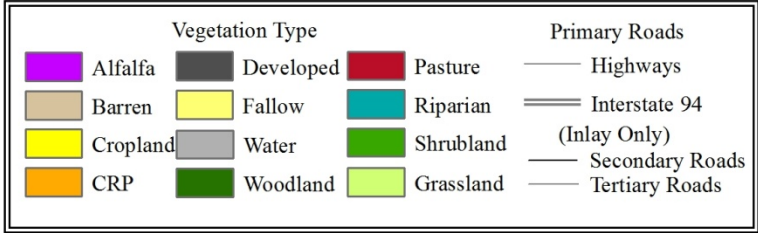
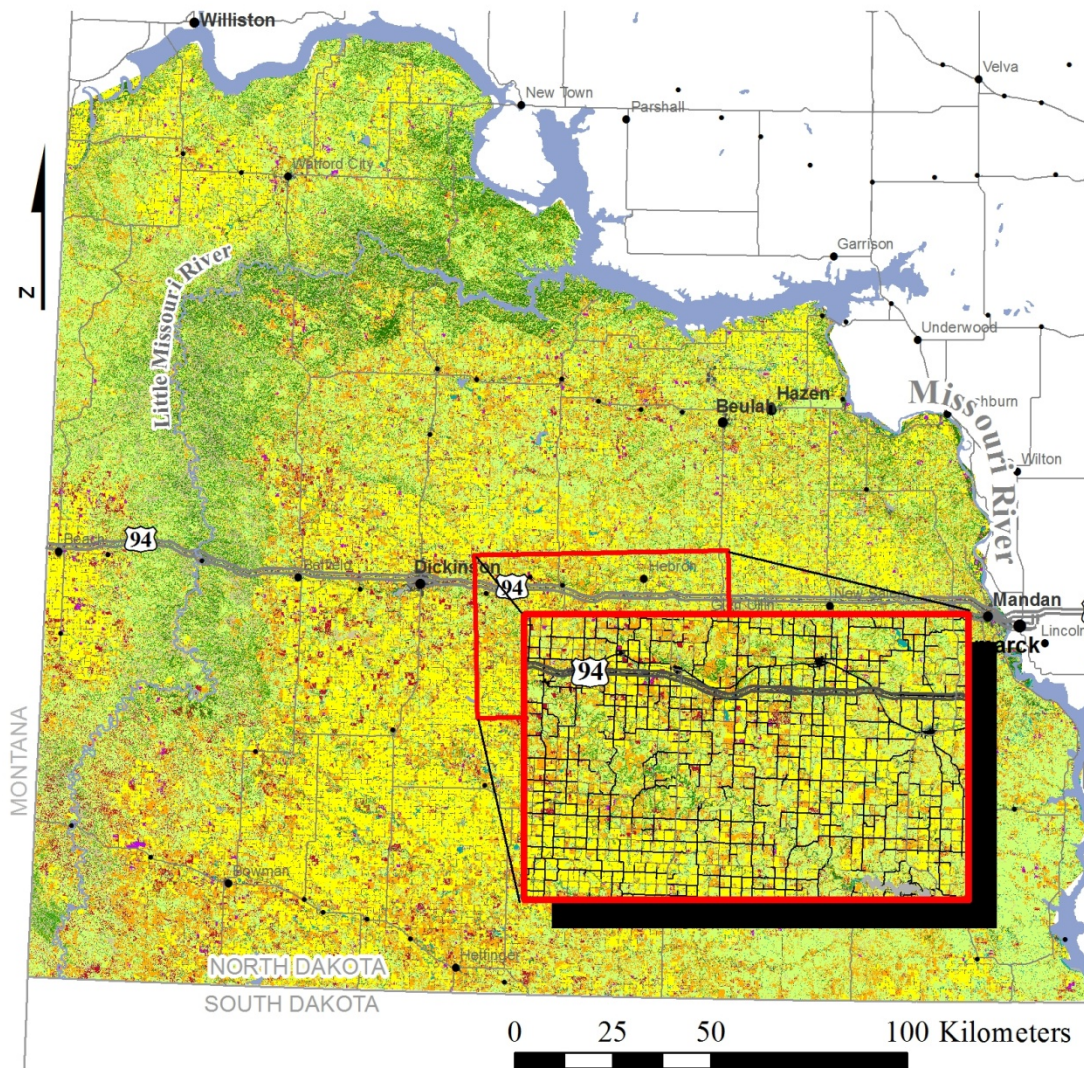


Figure 2. Vegetation type, 2007, with primary road networks for southwestern North Dakota. The inlay depicts the grid of secondary roads in much of the study area.



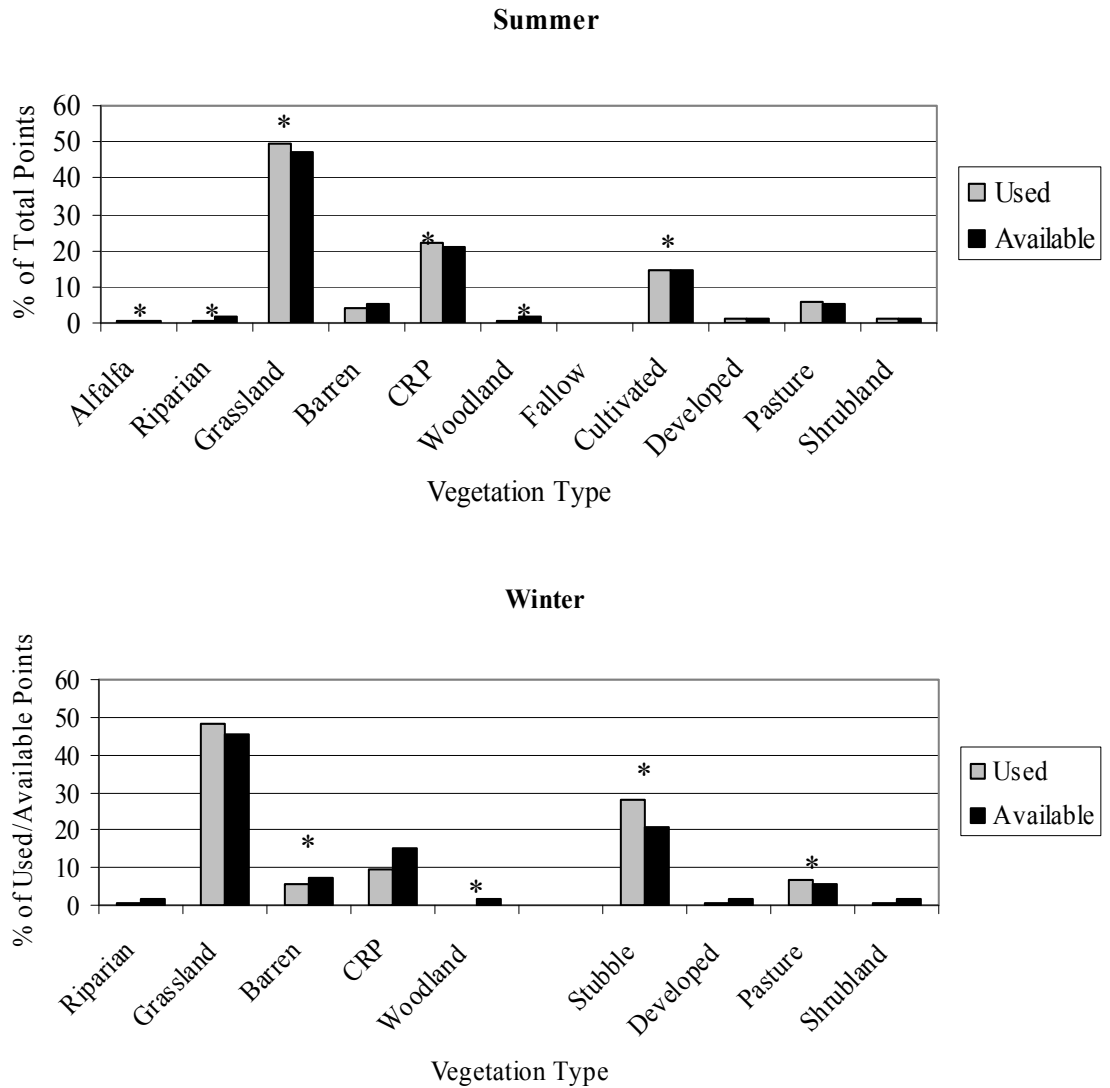


Figure 3. The proportion of points used by pronghorn and available (randomly sampled from pronghorn home ranges) for each vegetation type during the (a) summer and (b) winter in southwestern North Dakota, 2005-2008. Asterisks represent vegetation parameters that had significant coefficients (95% CI did not include 0) in habitat selection models.

Figure 4. Graph of relative probabilities of use for (a) distance to nearest primary road, (b) distance to nearest secondary road, and (c) ruggedness for pronghorn during the summer in southwestern North Dakota, 2005–2007. Probabilities were estimated using the range of used values for the parameter of interest and mean values for all other parameters.

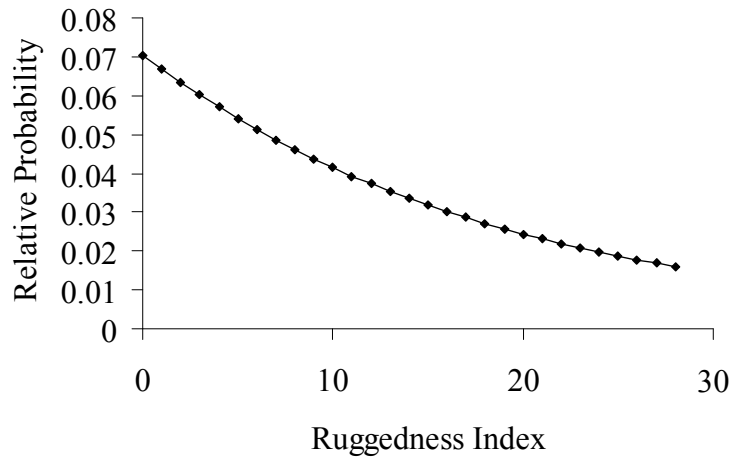
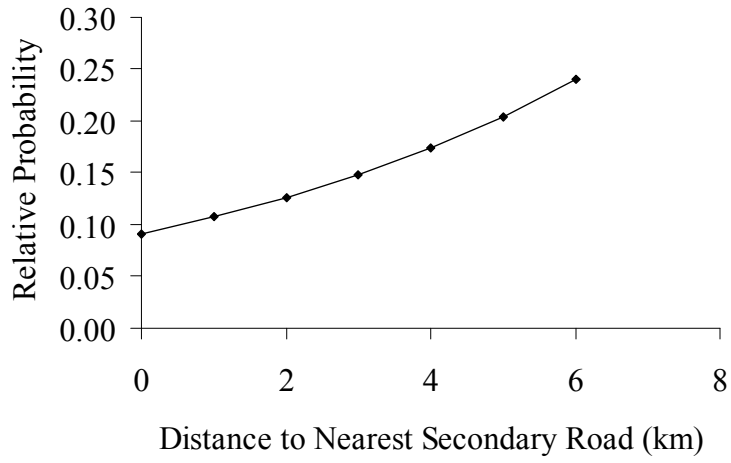
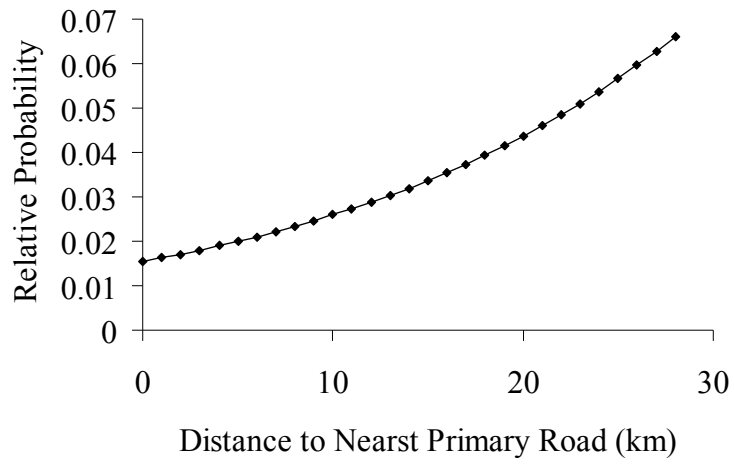
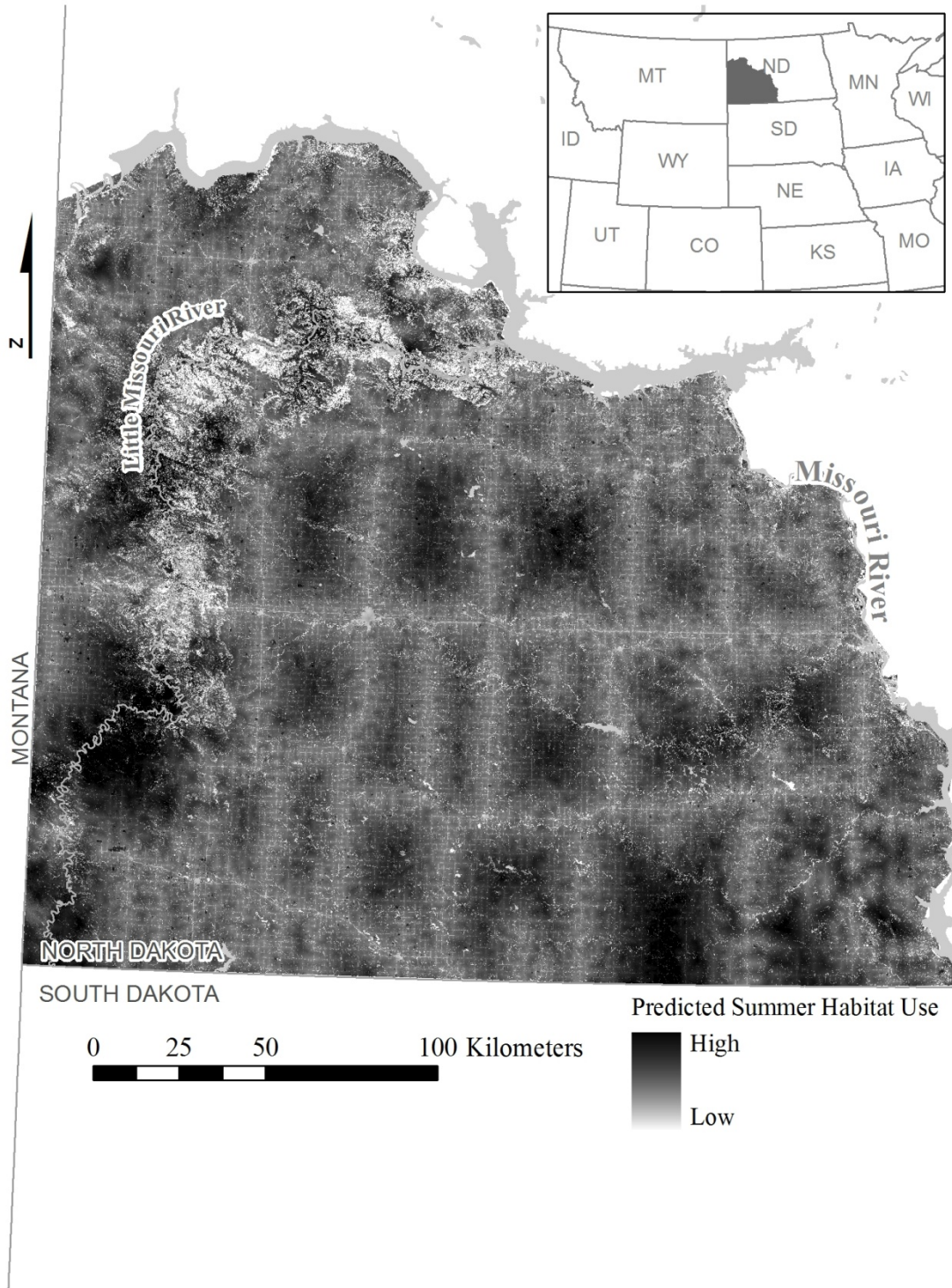


Figure 5. Predicted summer third-order habitat use values for pronghorn in southwestern North Dakota, 2005-2008. The prediction model included vegetation type, terrain ruggedness and distance to nearest primary and secondary roads.



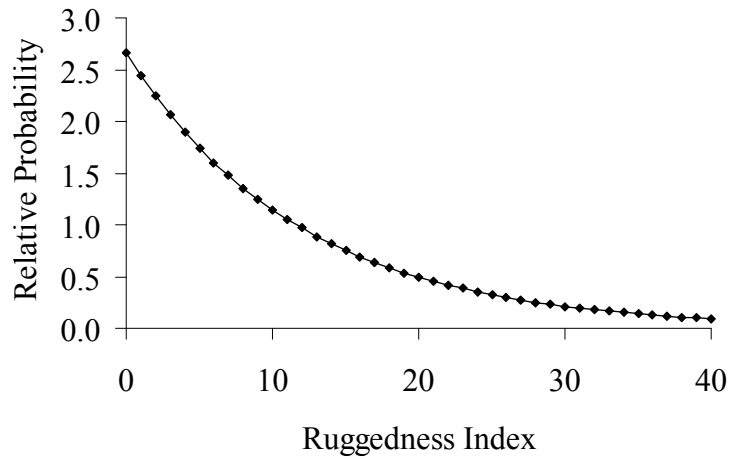
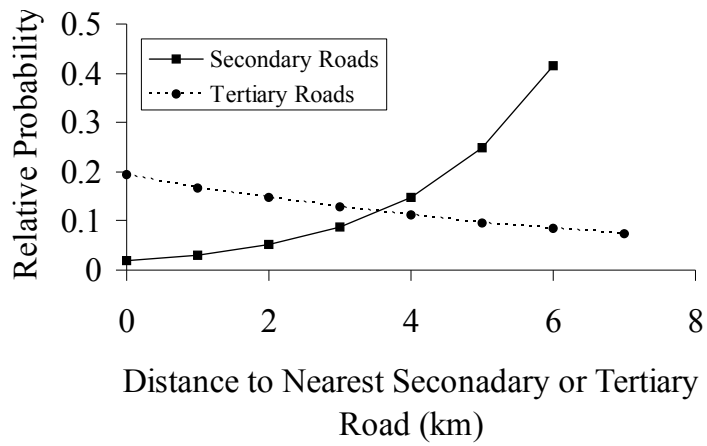


Figure 6. Graph of relative probabilities of use for (a) distance to secondary and tertiary roads, and (b) ruggedness for pronghorn during the winter in southwestern North Dakota, 2005–2008. Probabilities were estimated using the range of used values for the parameter of interest and mean values for all other parameters.

Figure 7. Predicted winter third-order habitat use values for pronghorn in southwestern North Dakota, 2005-2008. The prediction model included vegetation type, terrain ruggedness and distance to nearest primary, secondary and tertiary roads.

