Across scales, pronghorn select sagebrush, avoid fences, and show negative responses to anthropogenic features in winter

ADELE K. REINKING,[1,4,†] KURT T. SMITH,[1] TONY W. MONG,[2,5] MARY J. READ,[3] AND JEFFREY L. BECK [1]

[1]*Department of Ecosystem Science and Management, University of Wyoming, 1000 E University Avenue, Laramie, Wyoming 82071 USA*
[2]*Wyoming Game and Fish Department, Green River Regional Office, 351 W Astle Avenue, Green River, Wyoming 82935 USA*
[3]*Bureau of Land Management, Rawlins Field Office, 1300 3rd Street, Rawlins, Wyoming 82301 USA*

Abstract. Pronghorn (*Antilocapra americana*) are endemic to western North America where they occupy expanses of grassland and sagebrush (*Artemisia* spp.) habitats. The Red Desert region in south-central Wyoming, USA, has historically served as a stronghold for pronghorn populations, but many herds there have experienced declining population trends over the last two decades, concurrent with oil and natural gas development. These demographic changes and the potential for such energy development, its associated infrastructure, and other anthropogenic features including roads and fences to influence pronghorn habitat selection were the impetuses for our study. We sought to evaluate the potential effect of human-induced disturbance on multi-scale seasonal resource selection of 142 adult female pronghorn from 2013 to 2016 using 442 unique animal-season-year datasets. We utilized a traditional resource selection function to evaluate seasonal home-range selection and a step-selection function to assess fine-scale, patch-level seasonal selection. We also compared resource selection during daytime and nighttime hours with step-selection analyses. At the seasonal home-range scale, pronghorn selected for areas with more sagebrush during both seasons and areas farther from fences during summer. This trend was also apparent at the patch-scale level, where pronghorn selected sagebrush-dominant habitats and avoided crossing fences in all seasons during both day and night. Additionally at this scale, pronghorn selected areas farther from fences during daytime in summer. At the broader, home-range scale, pronghorn selected areas with greater road density during summer, but with lower road densities and farther from wells during winter. Avoidance of anthropogenic features during winter was also observed at the finer, patch-scale, with pronghorn selecting for increased density of roads and oil and natural gas wells during daytime in summer, but selecting areas farther from these features during daytime in winter. We recommend minimizing fencing and other forms of anthropogenic disturbance in high-quality seasonal pronghorn habitats with high proportions of sagebrush, particularly during winter when risk-avoidance responses may be amplified.

Key words: *Antilocapra americana;* energy development; fence; oil and gas; pronghorn; resource selection function; roads; sagebrush; step-selection function; summer and winter resource selection; Wyoming.

[4] Present address: Cooperative Institute for Research in the Atmosphere, Colorado State University, 1375 Campus Delivery, Fort Collins, Colorado 80523 USA.
[5] Present address: Wyoming Game and Fish Department, Cody Regional Office, 2820 State Highway 120, Cody, Wyoming 82414 USA.
† **E-mail:** adele.reinking@gmail.com

INTRODUCTION

The distribution of wildlife populations reflects ecological processes of resource selection and avoidance of areas with greater risk and competition (Johnson 1980). The risk-allocation hypothesis suggests that through behavioral decisions, animals balance energetic trade-offs associated with acquiring resources and avoiding potential threats to their survival (Lima and Dill 1990). One of the greatest sources of mortality risk for large mammalian herbivores is predation (Gaillard et al. 2000). In one example, female boreal caribou (*Rangifer tarandus*) avoided open areas and increased their movement speed and path directness when wolves (*Canis lupus*) were within 2.5 km (Basille et al. 2015), exemplifying the rapid behavioral responses central to minimizing risk and maximizing reward (Lima and Bednekoff 1999). In addition to predation as a traditional source of risk, it is conceivable that animals may perceive landscape disturbance as a threat akin to that posed by predators. The risk-disturbance hypothesis of Frid and Dill (2002) proposes that avoidance behaviors resulting from predation risk are similar to behaviors resulting from human-induced disturbances. In support, Sawyer et al. (2006) observed an immediate avoidance of natural gas development by mule deer (*Odocoileus hemionus*) in western Wyoming, USA, and perpetual avoidance of infrastructure remained through 15 yr of continued development (Sawyer et al. 2017). Anthropogenic features associated with energy development including roads, fences, and oil and gas wells may indirectly cause habitat loss for ungulates by inhibiting daily movements and seasonal migrations necessitated by varying climatic conditions and changes in plant phenology (Beckmann et al. 2012, Lendrum et al. 2012, Sawyer et al. 2013, Seidler et al. 2015). Not only can such features serve as physical barriers to ungulate movement, but they may also invoke a stress response that can consequently illicit risk-avoidance behaviors (Frid and Dill 2002, Wasser et al. 2011, Northrup and Wittemyer 2013, Buchanan et al. 2014). As a result of increased vehicular traffic, for example, pronghorn (*Antilocapra americana*) in Alberta, Canada, reduced the amount of time spent foraging and increased the amount of time spent in a vigilant state (Gavin and Komers

2006). To compensate for such losses in daytime resource acquisition, animals may alter nighttime selection behaviors to utilize habitats that would otherwise be avoided because of anthropogenic activity (Lendrum et al. 2012). For example, Buchanan (2015) found that elk in a coalbed methane natural gas field selected areas closer to roads and with decreased escape cover during nighttime compared with daytime, potentially to mitigate the impacts of daytime human disturbance associated with this development. Furthermore, when environmental conditions are particularly harsh, such as during winters with heavy snowfall, lost access to crucial resources due to anthropogenic infrastructure and activity can have a combined effect that exacerbates the challenges environmental conditions may present on their own (Bruns 1977, Gates et al. 2012, Yoakum et al. 2014). Knowledge of behavioral changes such as increased vigilance or altered resource use is critical, as these changes may have severe impacts on individual and population-level fitness (Creel and Christianson 2008, Sawyer et al. 2017).

The Red Desert region in south-central Wyoming, USA, has experienced a dramatic increase in intensive energy extraction efforts. Of all active and producing oil, and traditional and coalbed methane natural gas wells in the area, roughly 80% were drilled since 2000 (WOGCC 2017). Sagebrush (*Artemisia* spp.)-steppe habitats similar to those in the Red Desert are expected to experience increasing disturbance as a result of continued energy development (Copeland et al. 2009). This region has historically served as a stronghold for Wyoming pronghorn populations. Whereas some Red Desert herds have experienced population increases over the last two decades, others have declined more than 20% (WGFD 1996–2016), concurrent with expanding energy development in the area. Pronghorn behavior is altered by anthropogenic features including roads (Gavin and Komers 2006, Seidler et al. 2015), fences (Sheldon 2005), and natural gas wells (Beckmann et al. 2012), often resulting in the loss of high-quality resources. Given declining trends in pronghorn populations and coinciding anthropogenic change in the region, we sought to evaluate the potential influence of natural gas extraction, its associated infrastructure, and other anthropogenic features on

resource selection of adult female pronghorn in the Red Desert.

We quantified pronghorn resource selection within the home-range (third-order resource selection; Johnson 1980) at both the seasonal home-range scale and the seasonal patch-scale from 2013 to 2016 with traditional resource selection (resource selection function [RSF]) and step-selection (step-selection function [SSF]; Fortin et al. 2005) approaches. Step-selection functions are unique in that they allow the characterization of selection as the animal moves through the landscape by linking consecutive locations (Thurfjell et al. 2014), which is not captured with more coarse-scale RSF approaches. An RSF at the seasonal home-range level may fail to identify fine-scale, temporally linked behavioral responses, while the seasonal patch-level SSF does not wholly characterize the selection process occurring at the seasonal home-range scale (Johnson 1980, Fortin et al. 2005). Therefore, we used multi-scale methods to identify third-order pronghorn resource use in response to anthropogenic activity within the Red Desert.

METHODS

Study area

The Red Desert region in south-central Wyoming, USA (42.03° N, −108.31° W), roughly extends north to south from the southern end of the Wind River Mountain Range south to the Colorado state border; and east to west from Rawlins to Rock Springs, Wyoming, USA (Fig. 1). We designated a single study area within the Red Desert encompassing 19,558 km^2. The study area boundary was defined using a 100% minimum convex polygon around locations of 142 female pronghorn captured primarily within five Wyoming Game and Fish Department (WGFD) Antelope Hunt Areas (53, 55, 57, 60, and 61; Fig. 1).

The Red Desert region provided the unique opportunity to assess pronghorn habitat use in response to a wide range of conditions, as environmental characteristics, land ownership, and levels of anthropogenic development were highly varied throughout. Average elevation was 2141 m (range: 1850–3287 m). Across the study area, the 30-yr normal annual precipitation (1981–2010; Prism Climate Group 2017) averaged

29.3 cm (range: 16.0–124.5 cm), with higher elevation areas usually receiving greater amounts of precipitation. Between 2013 and 2016, annual precipitation averaged 30.6 cm (range: 21.0–118.8 cm; Prism Climate Group 2017). Our study area was primarily federal land (66.3%), followed by private property (29.4%), and lands under state ownership (4.3%). At the initiation of our study in November 2013, density of active and producing oil and gas wells in the area averaged 0.2 wells/km^2 (range: 0.0–12.4 wells/km^2; WOGCC 2017). Fence density averaged 0.1 km/km^2 (range: 0.0–2.5 km/km^2), and road density averaged 0.3 km/km^2 (range: 0.0–14.2 km/km^2; O'Donnell et al. 2014).

Vegetation in our study area mostly consisted of Wyoming big sagebrush (*A. tridentata wyomingensis*) communities with perennial grasses and forbs forming the understory. In low-lying areas, greasewood (*Sarcobatus vermiculatus*) and Gardner's saltbush (*Atriplex gardneri*) were the dominant species. At higher elevations, mountain big sagebrush (*A. t. vaseyana*), mixed shrub communities, and aspen (*Populus tremuloides*) stands were common. Major land uses included oil and natural gas extraction, livestock production, and big game hunting.

Capture, processing, and monitoring

We used helicopter net-gunning (Native Range Capture Services, Ventura, California, USA) to capture adult (≥1.5 yr) female pronghorn in November 2013, February 2014, and November 2014. To minimize capture-related mortality, we limited chase time to 2 minutes or less and the distance between capture and processing locations to 2 km or less, and administered a cold-water enema to animals whose rectal temperature approached or exceeded 40°C (Jacques et al. 2009). We weighed each female to the nearest 0.1 kg, collected biological samples, and estimated age of individuals based on tooth eruption and wear (Lubinski 2001). We fitted individuals with store-on-board GPS necklace transmitters (model G2110D; Advanced Telemetry Systems, Isanti, Minnesota USA).

Transmitters were set to record locations every two hours over a two-year period. We censored locations recorded within the first week of capture to avoid any influence of capture events on individual movement behavior (Northrup et al.
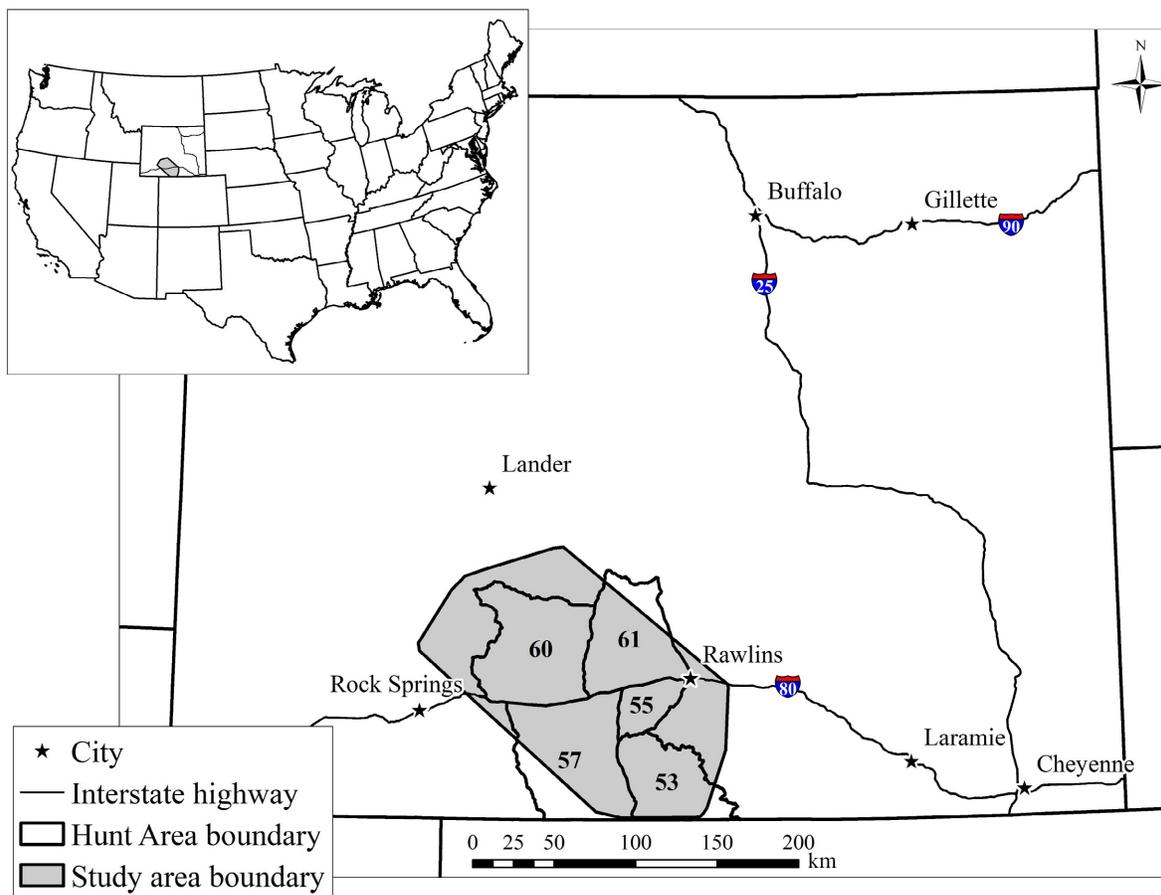
Fig. 1. Map of the Red Desert study area where adult female pronghorn seasonal resource selection was evaluated across multiple scales in south-central Wyoming, USA, 2013–2016. Animals were primarily captured in Wyoming Game and Fish Department Antelope Hunt Areas 53, 55, 57, 60, and 61. The study area boundary was delineated using a 100% minimum convex polygon encompassing locations recorded by 142 pronghorn.

2014, 2015). We defined summer as May through August and winter as December through February of the following year and retained data for animals with 500 or more locations for each individual season to ensure accurate characterization of seasonal ranges (Prokopenko 2016). Other techniques of seasonal designation, such as visual or net squared displacement methods, are not consistently accurate, particularly for animals that make frequent excursions or do not have clear, spatially clustered locations (Peters et al. 2017). Our seasonal definitions also ensured that all pronghorn had roughly the same number of locations and therefore the same weight in seasonal models. All pronghorn were captured, processed, and monitored in accordance with

protocols approved by Wyoming Game and Fish Department (Chapter 33-923 Permit) and University of Wyoming Institutional Animal Care and Use Committee (protocol 20131028JB00037).

Habitat selection covariates

We evaluated resource selection of adult female pronghorn using environmental and anthropogenic covariates (Table 1). Environmental covariates included climate and land cover variables, and different suites of environmental covariates were used to assess selection during summer and winter seasons across multiple scales. Anthropogenic covariates remained the same for summer and winter analyses, and included the distance to and density of roads,

Table 1. Predictor covariates considered in multi-scale pronghorn seasonal resource selection modeling using both traditional resource selection function (RSF) and step-selection function (SSF) methods with data collected in the Red Desert, Wyoming, USA, 2013–2016.

Variable class	Covariate	Description
Environmental		
Climate		
Heat Load Index	HLI†	Heat load index, derived from digital elevation model (USGS 2016)
Temperature	Temp‡	Average daily air temperature (°C)
Snow depth	Snow†'‡	Average daily snow depth (cm)
Land cover		
Distance to water	DistWater§'¶	Minimum distance to water (km)
Proportion Sagebrush	Sage†'‡'§'¶	For RSF modeling, proportion of sagebrush-dominated pixels within 0.5 km. For SSF modeling, binary variable representing whether pixel was sagebrush-dominant
Vegetation quality	INDVI§'¶	Integrated normalized difference vegetation index (https://phenology.cr.usgs.gov/methods_metrics.php)
Anthropogenic		
Distance to†'‡'§'¶		
Roads	DistRoad	Minimum distance to road (km)
Wells	DistWell	Minimum distance to oil and gas well (km)
Fences	DistFence	Minimum distance to fence (km)
Density of†'‡'§'¶		
Roads	RoadDens	Density of roads (km/km^2)
Wells	WellDens	Density of oil and gas wells (wells/km^2)
Fences	FenceDens	Density of fences (km/km^2)
Path overlap‡'¶		
Road intersection	RoadInt	Whether path along a step intersects road
Fence intersection	FenceInt	Whether path along a step intersects fence

† Used in RSF modeling for winter seasons.
‡ Used in SSF modeling for winter seasons.
§ Used in RSF modeling for summer seasons.
¶ Used in SSF modeling for summer seasons.

wells, and fences. Two additional binary anthropogenic variables were included in the SSF modeling approach that evaluated whether pronghorn steps crossed road or fence features (i.e., 0 = no intersection, 1 = intersection). All covariates were standardized with a z-score transformation with a mean of 0 and standard deviation of 1 prior to analyses. We computed Pearson correlation coefficients between all continuous covariates and retained the most informative of any correlated ($r \geq |0.7|$) variables. Extraction of covariate values and all subsequent analyses were performed using RStudio and Program R version 3.4.1 (R Development Core Team 2017) and ArcGIS 10.4 (ESRI 2016).

Environmental covariates.—Due to their small hoof area relative to body weight, pronghorn fare poorly in snow compared with other ungulate species (Telfer and Kelsall 1984); snow depths >30 cm severely hinder movement and are usually avoided (O'Gara and Yoakum 2004).

Additionally, trials using a control temperature of 21°C (a temperature considered to be within the thermoneutral zone for pronghorn) showed that fasting pronghorn begin to reach their lower critical temperature at roughly 0°C; this results in increased metabolic rate as animals attempt to raise their body temperature, becoming particularly costly when individuals experience increased activity levels and reduced forage intake (Wesley et al. 1973). The locomotive difficulty that deeper snow presents, combined with the energy required for self-maintenance in colder temperatures, ultimately increase the expense of winter survival in pronghorn, and in severe winters, die-offs can be extreme (Barrett 1982). These climatic conditions can influence pronghorn mortality (Reinking et al. 2018), and therefore likely influence resource use. We obtained daily snow depth (cm) and temperature (°C) data using SnowModel (Liston and Elder 2006*a*; InterWorks Consulting, Loveland,

Colorado, USA; 250-m resolution). SnowModel simulates processes related to snow, including but not limited to snow precipitation, blowing snow, snow-density evolution, and snow melt. The meteorological variables required to drive SnowModel were provided by MicroMet (Liston and Elder 2006*b*) and included temperature, precipitation, and other meteorological factors. We calculated a heat load index (HLI), which incorporates slope, aspect, and latitude to identify the warmest slopes (McCune and Keon 2002).

We used LANDFIRE Existing Vegetation Type raster data (LANDFIRE 2013) to assess pronghorn selection in relation to vegetation type (sagebrush or non-sagebrush-dominant pixels) and water. Pronghorn are often considered to be sagebrush obligates, relying heavily on this vegetation year-round as a source of dietary nutrition and cover (O'Gara and Yoakum 2004, Taylor et al. 2016). We classified a pixel as sagebrush-dominant when it was classified as Great Basin xeric mixed sagebrush shrublands, Intermountain basins big sagebrush shrublands, Columbia Plateau low sagebrush steppe, Intermountain basins big sagebrush steppe, or Intermountain basins montane sagebrush steppe (sensu Donnelly et al. 2017). We then evaluated the proportion of sagebrush-dominant pixels within 0.5 km of each pronghorn location for use in RSF modeling and assessed the potential role of sagebrush in SSF analyses with a binary covariate representing whether an area was sagebrush-dominant (i.e., 0 = not dominant, 1 = dominant; Fig. 2). These two different sagebrush variables were used in RSF and SSF analyses because the distance between temporally linked locations in SSF analyses was <0.5 km regardless of time of day or season. In addition to their reliance on sagebrush habitats, Poor (2010) found that habitat suitability for pronghorn fall and spring migrations increased closer to water. We estimated Euclidean distance to water from all water sources identified within LANDFIRE (2013). To evaluate vegetative quality, we included integrated normalized difference vegetation index (INDVI; 250 m resolution) for each year of our study; INDVI is related to growing season plant production and nutritional quality (Pettorelli et al. 2005, 2011).

Anthropogenic covariates.—Pronghorn movement and resource selection may be severely altered by impermeable and permeable anthropogenic infrastructure, such as roads and fences (Sheldon 2005, Sawyer et al. 2013, Seidler et al. 2015), and natural gas wells (Beckmann et al. 2012). We used fence data obtained from the Wyoming Cooperative Fish and Wildlife Research Unit and 2009 National Agricultural Imagery Program Imagery-derived road data from the United States Geological Survey (O'Donnell et al. 2014). We obtained locations of producing oil and gas wells from the Wyoming Oil and Gas Conservation Commission (WOGCC 2017). Wells were filtered by spud date (the date when drilling activity began) to ensure they were present during the time when individual pronghorn locations were recorded. If spud date was not available, we used the completion date (the date of the first completion report filing).

Resource selection function

We used a two-stage approach (Fieberg et al. 2010) to evaluate selection within summer and winter seasonal ranges, where we estimated an RSF for each pronghorn during each season and year (hereafter referred to as an animal-season-year [ASY]) to generate population-level inference. For each ASY, we assessed environmental and anthropogenic covariates at used and 12,820 randomly generated available locations (10 times the average number of locations for each ASY) for each animal within 90% fixed kernels representing their seasonal home-range (default bivariate kernel smoothing parameter; Worton 1989). Prior to developing individual ASY models, we used global models to determine whether distance to or density of each anthropogenic feature (roads, wells, or fences) was a better explanatory covariate to use in ASY selection models for each season. Global models represented population-wide selection, rather than selection of individual pronghorn. We compared global models that contained all environmental covariates plus distance to with a global model that contained all environmental covariates plus density of each of the three anthropogenic variables. We used Akaike's information criterion (AIC) to assess model support and retained the form of the anthropogenic variable that had the most model support when included in a global model. Each individual ASY model, therefore, contained all
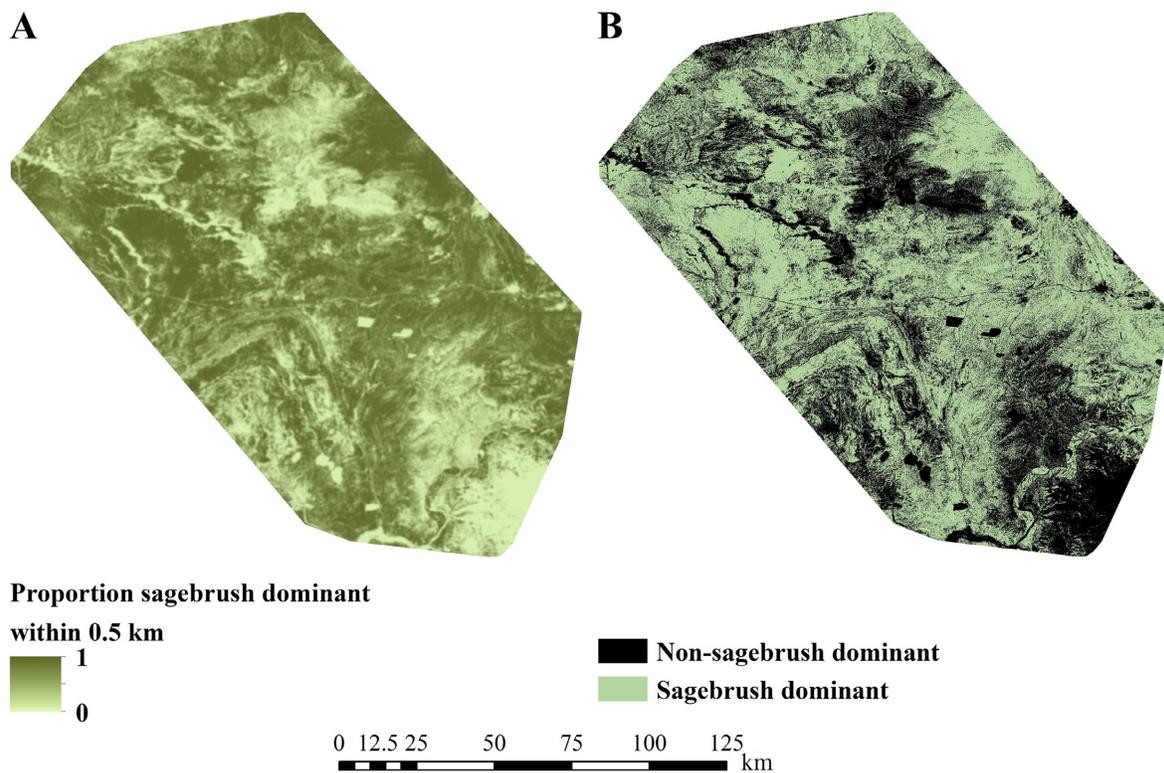
Fig. 2. Maps of sagebrush covariates in the Red Desert study area where third-order seasonal resource use of adult female pronghorn was evaluated across multiple scales in south-central Wyoming, USA, 2013–2016. To assess the potential role of sagebrush in resource selection at the seasonal home-range scale with a resource selection function, we used the proportion of sagebrush-dominant pixels within 0.5 km of pronghorn locations (A). To assess the potential role of sagebrush in resource selection at the seasonal patch-level scale using a step-selection function, we used a binary variable representing whether a pixel was sagebrush-dominant (B).

environmental covariates and the most predictive form of each anthropogenic covariate. We used generalized linear models to maximize the use-availability likelihoods with an exponential link function for each ASY (McDonald 2013). Because individual pronghorn were represented in more than one ASY, we took a random sample of model coefficients from ASYs for each pronghorn, to avoid issues of lack of independence of ASYs with the same individual for population-level inference (sensu Ladle et al. 2018). We bootstrapped coefficients by sampling coefficients for each individual, not ASY, at a rate of two times the number of total ASYs to generate mean coefficient values. We repeated this 5000 times for each coefficient to generate median and confidence interval estimates (2.5th and 97.5th quantiles; Ladle et al. 2018). The RSF took

the following form:

$$w(x) = \exp[\beta_1 h_1(x) + \beta_2 h_2(x) + \cdots + \beta_n h_n(x)]$$

where $w(x)$ was proportional to the probability of pronghorn selection, and representative of the relative probability of selection for covariates (h_n), at location x in environmental space, and B_n's were coefficients estimated for each covariate.

Step-selection function

We employed an SSF (Fortin et al. 2005) to evaluate patch-scale resource selection during summer and winter. We also assessed potential differences in selection between day and night because ungulates exposed to anthropogenic development may behave differently during nighttime hours in an effort to ameliorate the negative effects of altered resource use that may be

caused by daytime human activity (Lendrum et al. 2012, Buchanan 2015). We categorized locations as occurring either during daylight or darkness based on daylight hours for Wamsutter, Wyoming, USA, near the centroid of our study area. For each ASY, we randomly selected one daytime and one nighttime location on each day for which an individual had movement data. We paired each used location with 10 random available locations, generated from the distribution of step length and absolute and relative turning angles of used locations observed in all sample animals (Fortin et al. 2005, Thurfjell et al. 2014). For each used and available endpoint of a given step, we determined the values of environmental and anthropogenic covariates (Table 1). In addition, we evaluated whether paths along used or available steps intersected roads and fences. Using similar methodology to that employed in our RSF modeling, we determined which anthropogenic variable (distance to or density of each feature) to use in SSF modeling by ranking single-variable models with AIC. For each feature (roads, wells, or fences), the variable used in the model with the lower AIC value was retained and evaluated in the SSF for each unique season and time of day.

We used the survival package in Program R (Therneau 2015) to apply a conditional logistic regression to compare covariate values at used and available locations. This allowed us to estimate an SSF of the following form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n)$$

where β_1 represents the estimated coefficient describing the strength of selection for variable x_1.

RESULTS

We used data from 164 adult female pronghorn captured and released during three events (113 adult female pronghorn in November 2013, 13 in February 2014, and 38 in November 2014). Eighteen individuals (11.0%) were excluded from analyses because they had fewer than 500 total locations (and therefore had fewer than 500 locations in a given season) and four transmitters (2.4%) were never recovered. We thus evaluated resource selection for $n = 142$ adult female pronghorn from 882,169 recorded locations. We filtered location data by summer and winter seasons, using 306,023 summer locations and 242,405 winter locations from 479 unique ASY combinations (229 summer animal-year and 250 winter animal-year combinations). For each ASY, we censored individuals with fewer than 500 locations, resulting in 442 unique ASY datasets (215 summer animal-year and 227 winter animal-year datasets) from 2013 to 2016. We found that summer home-ranges were roughly half the size of winter home-ranges. Across all animal-year datasets, the average summer home-range was 73.4 km^2 (range: 3.0–1851.6 km^2), whereas the average winter home-range was 156.7 km^2 (range: 11.0–1582.7 km^2). During summer daytime, pronghorn moved an average of 220.4 m/h (95% CI: 219.3–221.5), while at night they moved an average of 146.7 m/h (95% CI: 145.4–147.9). In winter daytime, pronghorn moved an average of 245.6 m/h (95% CI: 244.1–247.2) but moved an average of only 93.1 m/h (95% CI: 92.3–93.9) at night.

Resource selection function modeling

After the removal of ASY combinations for which models failed to converge, we utilized 144 summer animal-year models and 196 winter animal-year models to evaluate seasonal selection at the home-range scale. Once we removed the less predictive anthropogenic covariates, Pearson's correlation coefficients for remaining covariates were <0.7 in any season, and thus, we retained all covariates for analyses.

Environmental covariates.—The 95% confidence intervals generated by bootstrapping individual selection coefficients indicated that at the population level, during summer, pronghorn on average selected areas with higher proportions of sagebrush and higher INDVI (Fig. 3; Appendix S1: Table S1). They also selected areas farther from water, but confidence intervals around the coefficient for this covariate overlapped 0. During winter, pronghorn response to environmental covariates included selection for lower HLI and higher proportions of sagebrush (Fig. 3; Appendix S1: Table S1). We found a trend for selection of lower snow depth, but this was not a significant finding based on 95% confidence intervals around the coefficient overlapping 0.

Anthropogenic covariates.—On average, pronghorn selected areas farther from fences and with increased road density during summer. They also selected areas with increased well density, but 95% confidence intervals overlapped 0.
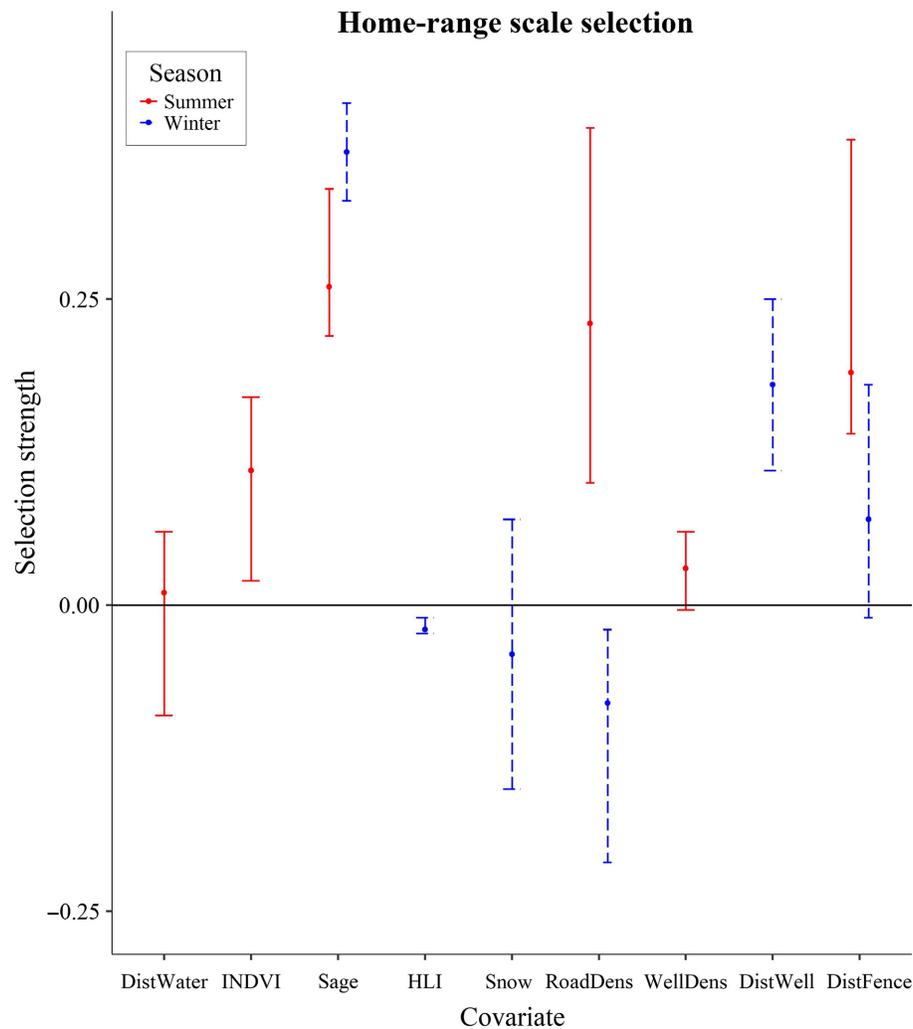
Fig. 3. Seasonal selection strength and 95% confidence intervals as modeled through the use of a resource selection function in relation to environmental and anthropogenic covariates used in home-range scale resource selection analysis of pronghorn in the Red Desert, Wyoming, USA, 2013–2016. Environmental covariates included distance to water (DistWater), vegetation quality as indexed by integrated normalized difference vegetation index (INDVI), proportion of sagebrush-dominant pixels within 0.5 km (Sage), heat load index (HLI), and snow depth (Snow). Anthropogenic covariates included densities of roads (RoadDens) and oil and natural gas wells (WellDens), and distances to nearest oil or natural gas well (DistWell) and fence (DistFence). Confidence intervals with values >0 indicate selection, <0 indicate avoidance, and spanning 0 indicate neither selection nor avoidance. Selection coefficients represent population-level medians.

During winter, pronghorn selected areas farther from wells and with lower road densities. They also tended to select areas farther from fences; however, coefficients for this covariate had confidence intervals that overlapped 0.

In the summer and winter season, 75.6% and 89.7% of individuals displayed positive selection for proportion of sagebrush, respectively. In summer, 56.3% of pronghorn showed positive selection for areas with higher INDVI values. Selection for areas farther from fences and with greater road density was evident in 62.5% and 59.7% of individuals during this season, respectively. In winter, 60.7% of pronghorn selected

areas with lower HLI. We also observed selection for areas farther from wells and with lower road densities in 56.6% and 57.1% of individuals, respectively, during this season.

Step-selection function modeling

We utilized 1,009,154 used and available steps (283,756 summer daytime, 280,121 summer nighttime, 221,357 winter daytime, and 223,920 winter nighttime steps) in our step-selection analyses. We evaluated correlation coefficients between covariates after the removal of the less predictive variable (distance to or density of) for each anthropogenic feature (roads, wells, and fences). In SSF modeling of winter daytime selection, density of fences and distance to wells, the most predictive fence and well variables, were highly correlated ($r = 0.73$). For this season and time of day, we removed density of fences from consideration, as distance to wells was more informative, based on its lower AIC value. All other variables were retained, as no other Pearson correlation coefficients of continuous variables were $\geq |0.7|$ for covariates during any season, daytime or nighttime.

Environmental covariates.—Across seasons and times of day, results indicated that at the 95% confidence level, pronghorn selected for sagebrush-dominant areas (Figs. 4, 5; Appendix S1: Tables S2 and S3). They also displayed selection for areas closer to water and with lower INDVI values during both daytime and nighttime in summer, but 95% confidence intervals around the coefficients for these variables at both times of day overlapped 0 (Fig. 4; Appendix S1: Table S2). During winter days, pronghorn selected for warmer areas, but this result was not significant at the 95% confidence level (Fig. 5; Appendix S1: Table S3). At nighttime in winter, pronghorn selected for areas with lower temperatures. During both daytime and nighttime, pronghorn avoided greater snow depths, but confidence intervals around this coefficient overlapped 0 for both times of day (Fig. 5; Appendix S1: Table S3).

Anthropogenic covariates.—Pronghorn avoided crossing fences in all seasons and at all times of day (Figs. 4, 5; Appendix S1: Tables S2 and S3). We also found that pronghorn avoided fences in winter nighttime and both summer daytime and nighttime, when they selected areas farther from

these features; however, this avoidance was only significant at the 95% confidence level during the daytime in summer. Pronghorn selected paths that intersected road features during both seasons in daytime but avoided paths that intersected roads during both seasons at nighttime. Avoidance of anthropogenic features at the patch scale was also evident during winter daytime, when pronghorn selected for areas farther from roads and oil and natural gas wells; during winter nighttime, they also selected for lower well densities, but 95% confidence intervals around the coefficient for this variable overlapped 0 (Fig. 5; Appendix S1: Table S3). Interestingly, pronghorn selected for greater densities of roads and wells during daytime in summer (Fig. 4; Appendix S1: Table S2). They also displayed selection for greater well densities during the nighttime in summer, but this result was not significant at the 95% confidence level. Pronghorn selected for areas closer to roads during summer nights and showed selection for increased road density during nighttime in winter, though the 95% confidence intervals around the selection coefficient for road density in winter nighttime overlapped 0 (Figs. 4 and 5; Appendix S1: Tables S2 and S3).

DISCUSSION

We sought to identify resource selection of adult female pronghorn in the Red Desert of south-central, Wyoming, USA, particularly as it related to the recent expansion of anthropogenic infrastructure in the region. To accurately capture the scale of pronghorn selection relative to both environmental and anthropogenic variables, we used two analysis techniques, each addressing different scales of selection within third-order resource use (Johnson 1980): a traditional RSF to evaluate selection at the seasonal home-range scale and an SSF to assess selection as the animal moved through the landscape at the seasonal patch-scale within home-ranges. In addition to evaluating fine-scale differences in selection behavior between seasons, our SSF analyses allowed us to assess how pronghorn resource use may vary across times of day.

Unexpectedly, we observed selection for colder areas during winter at both the broader, home-range scale, where pronghorn selected for areas

Summer patch-level selection
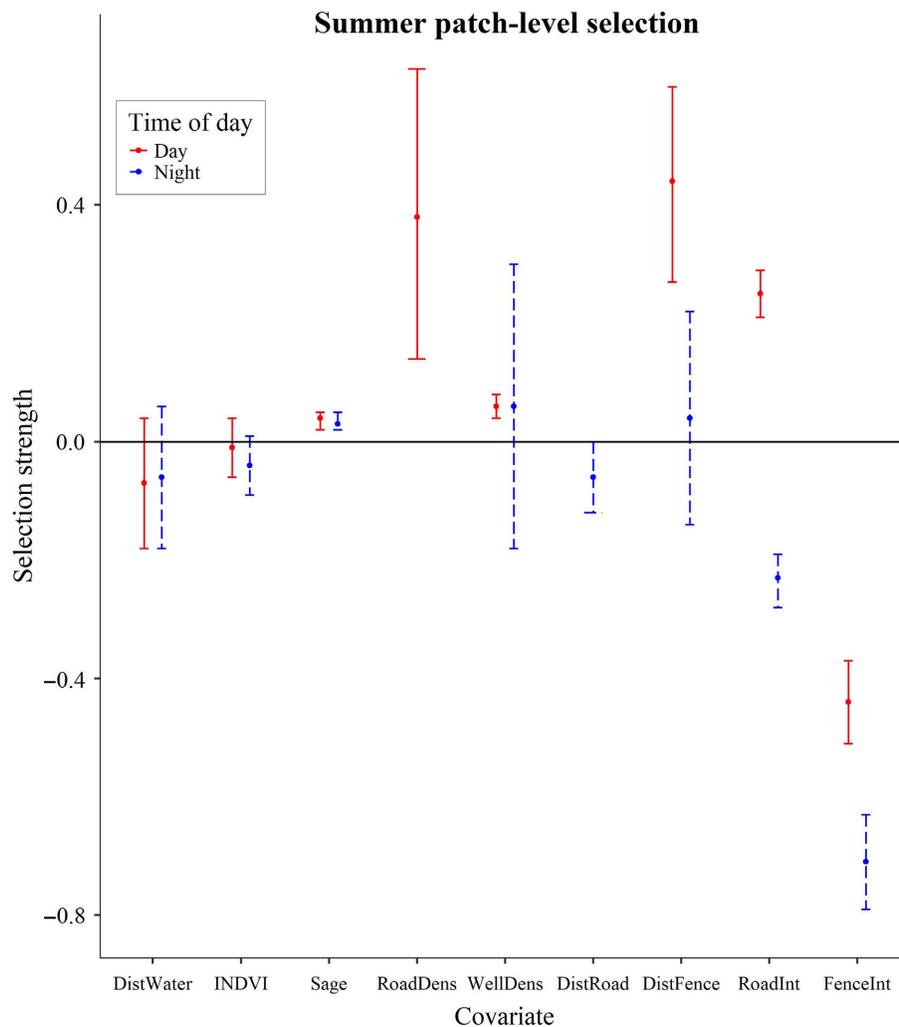
Fig. 4. Daytime and nighttime step-selection strength as a function of environmental and anthropogenic covariates used in summer patch-scale resource selection modeling of pronghorn in the Red Desert, Wyoming, USA, 2013–2016. Environmental covariates included distance to water (DistWater), vegetation quality as indexed by integrated normalized difference vegetation index (INDVI), and whether a pixel was sagebrush-dominant (Sage). Anthropogenic covariates included densities of roads (RoadDens) and oil and natural gas wells (Well-Dens), distances to nearest road (DistRoad) and fence (DistFence), and two binary variables representing whether pronghorn steps intersected roads (RoadInt) or fences (FenceInt). Confidence intervals with values >0 indicate selection, <0 indicate avoidance, and spanning 0 indicate neither selection nor avoidance.

with lower HLI values, and the finer, patch-level scale, where they selected for areas with lower temperatures at night. However, an evaluation of summary statistics for these covariates showed that while selection strength was statistically informative, the difference between average winter HLI values or temperatures in used locations compared with available locations was minute and unlikely to be biologically significant. At the home-range scale, pronghorn in winter used locations with an averaged HLI value of 0.74 (standard error [SE] < 0.01), while available locations averaged an HLI value of 0.74 (SE < 0.01). Similarly, at the patch scale, nighttime used locations of pronghorn in winter averaged a temperature of −5.04°C (SE = 0.04), and available
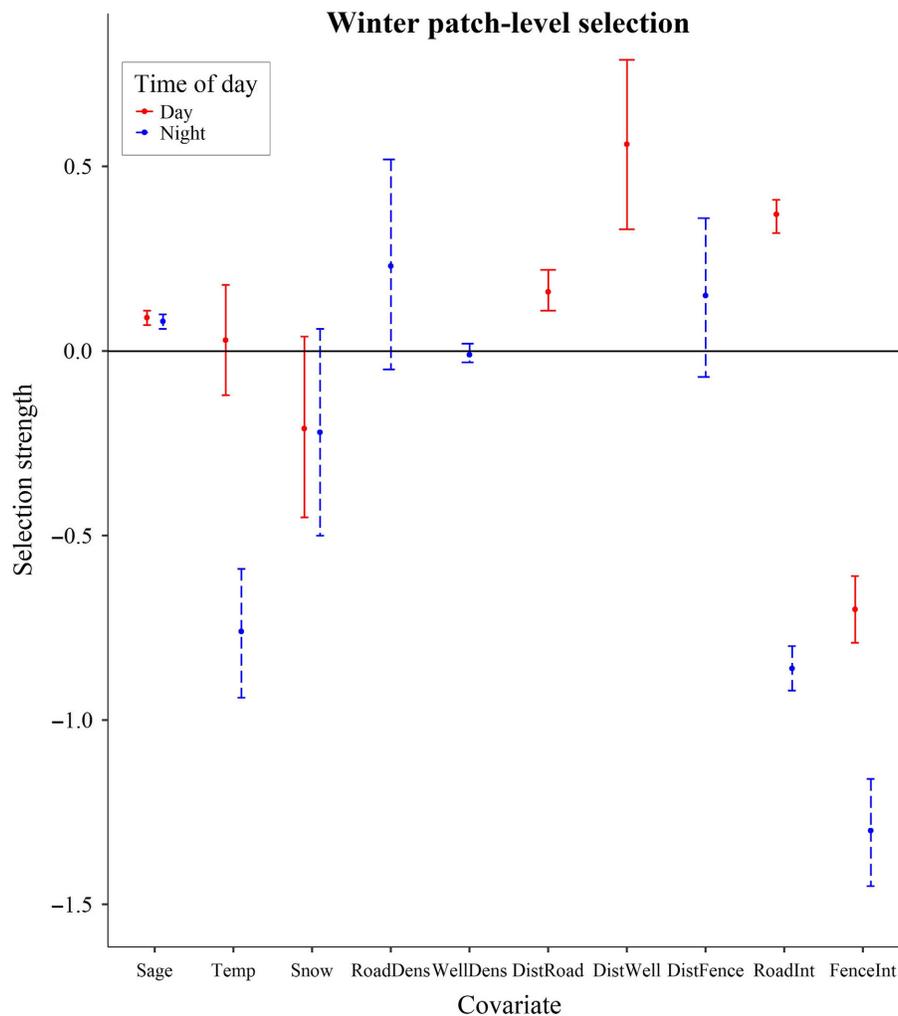
Fig. 5. Daytime and nighttime step-selection strength as a function of environmental and anthropogenic covariates used in winter patch-scale resource selection modeling of pronghorn in the Red Desert, Wyoming, USA, 2013–2016. Environmental covariates included whether a pixel was sagebrush-dominant (Sage), temperature (Temp), and snow depth (Snow). Anthropogenic covariates included densities of roads (RoadDens) and oil and natural gas wells (WellDens), distances to nearest road (DistRoad), oil or natural gas well (DistWell), and fence (DistFence), and two binary variables representing whether pronghorn steps intersected roads (RoadInt) or fences (FenceInt). We reduced winter step-selection coefficient and error values for the temperature covariate by 1 power of 10 to improve ease of interpretation. Confidence intervals with values >0 indicate selection, <0 indicate avoidance, and spanning 0 indicate neither selection nor avoidance.

locations averaged a temperature of −5.03°C (SE = 0.01). While we found statistically significant selection for colder areas in winter across scales, these results are likely reflective of the tight range in HLI values and nighttime temperatures throughout our study area, rather than true selection driven by ecological processes.

Our RSF results indicated that at the broader, seasonal home-range scale, pronghorn selected for greater proportions of sagebrush in both summer and winter, a trend which was further supported by our finer-scale, patch-level SSF, which demonstrated that pronghorn selected for sagebrush-dominant areas at all times of day in both seasons.

Pronghorn in Wyoming rely heavily on sagebrush habitats for nutrition year-round; in the Red Desert, their diets can be composed of 62–97% shrub species, including sagebrush, with percent composition of shrubs being highest in winter (Taylor 1972, O'Gara and Yoakum 2004). In relation, we observed positive selection for areas with higher INDVI values during summer at the seasonal home-range scale. Normalized difference vegetation index-based indices of vegetative quality have been identified as important parameters in pronghorn habitat suitability models and resource selection studies, and selection for areas with higher INDVI values likely contributes to improved acquisition of high-quality energetic resources (Dalton 2009, Poor et al. 2012, Seidler et al. 2015). In addition to its role in pronghorn nutrition, sagebrush structure also provides thermoregulatory benefits and shelter from wind (O'Gara and Yoakum 2004), as well as hiding cover and bed site habitat for fawns (Alldredge et al. 1991). Sagebrush communities are one of the most highly imperiled ecosystems in North America, becoming increasingly fragmented and experiencing rapid declines in forage production as a result of energy development, its associated infrastructure, and other anthropogenic features (Copeland et al. 2009, Davies et al. 2011). In this context, the pronghorn's strong reliance on high-quality sagebrush habitat for survival and reproductive success, which is supported by the positive selection that we observed across seasons and spatial scales, emphasizes the importance of sagebrush conservation in the management of this species.

In addition to selection for sagebrush habitats, our results indicated that pronghorn avoid fencing at multiple scales. At the seasonal home-range scale, pronghorn selected areas farther from fences in summer, while the finer-scale SSF analysis showed that pronghorn selected areas farther from fencing during daytime in summer and avoided paths that intersected fence features at all times of day in both seasons. The Red Desert region is marked by a vast network of relic net-wire fencing largely associated with a boom in livestock ranching operations in the early 1960s (Sheldon 2005), though new fencing has also been erected for modern ranching operations, along roadways, and around energy development. Fences can serve as a source of direct mortality for pronghorn (Harrington and Conover 2006, Kolar et al. 2012), and indirectly alter habitat use through their effect as permeable or impermeable barriers to movement and through their potential to be perceived as a source of risk (Frid and Dill 2002, Sawyer et al. 2013). Fences may represent an even greater source of risk during winter, when depressions under fences fill with snow, often causing wildlife-friendly fencing to become impassable (Bruns 1977, Sheldon 2005, Yoakum et al. 2014). To maintain pronghorns' ability to acquire high-quality energetic resources, particularly during times of seasonal stress, connectivity across large landscapes is essential (O'Gara and Yoakum 2004). Modifying fences to increase permeability through measures such as raising the bottom wire to a minimum height of 16 in. from the ground (Yoakum et al. 2014), or removing fences altogether where feasible, are important management tools that facilitate pronghorn access to crucial nutrition and seasonal ranges.

During winter, when pronghorn are faced with increased thermoregulatory and locomotive costs (Wesley et al. 1973, Barrett 1982, Telfer and Kelsall 1984, Reinking et al. 2018), they may be more risk-averse in an effort to avoid the loss of crucial energy reserves. Indeed, we observed avoidance of development during winter at both scales, with animals selecting areas farther from wells and with lower road densities at the home-range scale, and farther from roads and wells during daytime at the patch scale. It is interesting to note, however, that animals displayed somewhat opposite responses in summer, instead selecting for increased road density at the seasonal home-range scale and selecting for increased road and well density in daytime at the patch-scale. The multi-scale selection for anthropogenic infrastructure that we observed in pronghorn during summer could indicate an improved ability to offset the potential negative physiological effects that these features can induce, such as increased stress and reduced time spent accruing energetic reserves through foraging (Gavin and Komers 2006, Wasser et al. 2011), with increased consumption of high-quality forage during this season. This is potentially supported by the positive selection for higher vegetation quality (as indexed by INDVI) that we observed at the home-range scale in summer. Regardless of this possible ability to reduce negative impacts of

exposure to anthropogenic infrastructure in summer, the avoidance response that we observed toward these features in winter across scales suggests that restrictions on human activity and energy development during this season, particularly in crucial winter range and areas dominated by high-quality sagebrush, would be beneficial for pronghorn populations.

In addition to differential responses toward anthropogenic infrastructure during summer and winter, we also saw varied responses between daytime and nighttime selection of road features. At the patch level, pronghorn selected for areas closer to roads during the nighttime in summer. This result suggests that individuals may be able to take advantage of resources in areas with anthropogenic infrastructure during night that would otherwise not be utilized during the day, potentially because of the risk-avoidance response that can be elicited by these features and their associated activity (Frid and Dill 2002, Lendrum et al. 2012). However, pronghorn appeared to select for crossing roads during daylight hours but selected against crossing roads during nighttime in both seasons. It is possible that pronghorn may avoid crossing roads at night, when there is an increased risk for wildlife–vehicle collision (Mastro et al. 2010, Diaz-Varela et al. 2011, Hothorn et al. 2015), but this result may also be reflective of the decreased pronghorn movement we observed during nighttime hours in summer and winter.

Conclusions

Our results indicate that high proportions of sagebrush are crucial for pronghorn, regardless of season and scale. In addition, adult female pronghorn in Wyoming's Red Desert showed avoidance of fences at both home-range and patch-level scales during all times of day and in all seasons, selecting for areas farther from fences during summer at the seasonal home-range scale, and avoiding paths that intersect fences at the patch-level scale during both summer and winter. Results of SSF modeling also indicated that pronghorn selected areas farther from fencing during daytime in summer. Pronghorn would therefore benefit from the conservation of areas with large proportions of sagebrush, and we recommend that development be limited in

important summer and winter ranges. Moreover, increased permeability in fencing, as well as fence removal where possible, would reduce the risk of direct mortality and could mitigate the loss of high-quality habitat resulting from altered resource selection (Sheldon 2005, Gates et al. 2012, Yoakum et al. 2014). Finally, we found that during winter, pronghorn selected for areas farther from wells and with lower road densities at the seasonal home-range scale and for areas farther from both roads and wells during daytime hours at the seasonal patch-level scale. It is possible that during winter, risk-avoidance behavior is elevated given the potential in ungulate species to lose crucial energy reserves (Parker et al. 1984, Monteith et al. 2013). We thus recommend limiting human activity during winter and minimizing anthropogenic disturbance in pronghorn crucial winter range.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2722/full