Fences reduce habitat for a partially migratory ungulate in the Northern Sagebrush Steppe

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Abstract. Few studies have examined differential responses of partially migratory ungulates to human development or activity, where some individuals in a population migrate and others do not. Yet understanding how animals with different movement tactics respond to anthropogenic disturbance is key to sustaining global ungulate migrations. We examined seasonal resource selection of a partially migratory population of pronghorn (*Antilocapra americana*) in the Northern Sagebrush Steppe of Alberta, Saskatchewan, and Montana from 2003 to 2011. We developed step-selection functions (SSF) for migrant and resident pronghorn during the summer and winter at two spatial scales (second order and third order) and then integrated SSFs across scales to estimate pronghorn responses to fences and subsequent habitat loss from these features while accounting for responses to other resource use. Both migrant and resident pronghorn showed the strongest responses to natural and anthropogenic features at the second order and weaker responses at the third order. Selection responses of migrant and residents differed the most in response to normalized difference vegetation index, topography, and anthropogenic features. Seasonally, selection for intermediate greenness was strongest in summer, whereas avoidance of roads strongly influenced winter resource selection of both tactics. Both migrant and resident pronghorn showed strong avoidance of fencing at both spatial scales during summer and winter. Model predictions with complete removal of fences from the landscape (i.e., natural conditions) predicted an increase in the area of high-quality habitat of 16–38%. In contrast, doubling fence density on the landscape decreased the amount of high-quality habitat by 1–11% and increased low-quality habitat by 13–21%. Our results suggest that pronghorn winter and summer ranges can be improved by reducing the density of fences on the landscape, or mitigation measures to enhance fence crossings, to alleviate the indirect loss of habitat for this important endemic prairie species.

Key words: *Antilocapra americana*; connectivity; fences; habitat loss; movement barriers; movement tactic; pronghorn; resource selection.

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INTRODUCTION

The loss of migration has elicited steep declines in migratory birds and mammals worldwide (Wilcove and Wikelski 2008). Where migration still exists, mammalian movements are often restricted or limited by human disturbance. For example, Tucker et al. (2018) showed for 57 mammalian species that movements in areas of high human footprint averaged one-half to one-third the extent of their movements compared to areas of low disturbance. Migratory ungulates are especially vulnerable to anthropogenic impacts as they often travel across large and diverse landscapes of varying land ownership (Berger 2004, Harris et al. 2009, Seidler et al. 2015, Monteith et al. 2018). Declines in migratory ungulates can affect ecosystem function, including nutrient flow, predator–prey dynamics, and biodiversity processes (Berger 2004, Bolger et al. 2008). However, most ungulate populations are classified as partially migratory, where some individuals migrate between summer and winter ranges (migrants), while others (residents) do not (Kaitala et al. 1993, Dingle and Drake 2007, Chapman et al. 2011). Partial migration is common across taxa (Chapman et al. 2011) including ungulates, such as mule deer (*Odocoileus hemionus*; Nicholson et al. 1997), elk (*Cervus canadensis*; Hebblewhite et al. 2008), and pronghorn (*Antilocapra americana*; Barnowe-Meyer et al. 2017, Jakes et al. 2018a). Studies of partially migratory populations can provide key insights into behavioral and fitness consequences between movement tactics (Cagnacci et al. 2011, Hebblewhite and Merrill 2011, Middleton et al. 2013, Sawyer et al. 2016). These movement tactics can influence habitat selection patterns, demography, and the relative abundance of migrants and residents, and though warranted, few studies have quantified such differences (Ball et al. 2001, Hebblewhite et al. 2008).

Animals select resources in response to environmental heterogeneity across a sequence of hierarchically nested spatiotemporal scales (Johnson 1980, Boyce 2006, Meyer and Thuiller 2006, DeCesare et al. 2012). The two most commonly assessed spatiotemporal scales, or orders of selection (Johnson 1980), are second (selection of a home range) and third order (selection within a home range). Selection patterns have been shown to be scale dependent across species (Boyce 2006, Northrup et al. 2016) and, for ungulates, influenced by various anthropogenic features (i.e., roads and energy development). For example, mule deer consistently avoided energy development across multiple scales while responses to other resources were scale dependent (Northrup et al. 2016). Conversely, woodland caribou (*Rangifer tarandus*) exhibited scale-dependent responses to anthropogenic disturbances across spatial scales (DeCesare et al. 2012). Understanding scale dependence in response to anthropogenic structures and activities can reveal behavioral effects that may be evident at one scale, but not another, and may be especially important for highly mobile species (sensu Runge et al. 2014).

Although rarely studied, barbed and woven wire fences represent a dominant linear anthropogenic feature in agricultural regions across the globe, including the grasslands and shrub steppe of the Northern Plains of North America. For example, approximately 340,000 km of fences has been mapped in two large grassland areas of Alberta and Montana resulting in mean densities of 1.1 and 2.4 km/km^2, respectively (Seward et al. 2012, Poor et al. 2014). Fences are among the most dominant anthropogenic features and may far exceed road densities in these landscapes (Jakes et al. 2018b). Fences are an increasing feature of African pastoralist systems; border fences are expanding in North America and Europe and are listed as a contributing global threat to mammalian migration and movements (Berger 2004, Wilcove and Wikelski 2008, Flesch et al. 2009, Creel et al. 2013, Linnell et al. 2016). Despite the growing appreciation and call for greater attention to the impacts of fences on wildlife (Flesch et al. 2009, Jakes et al. 2018b), there have been few direct studies that quantify fence effects on partially migratory ungulate populations.

Pronghorn are the last remaining endemic ungulate to the grasslands and shrub steppe systems of western North America (Yoakum 2004). Anthropogenic features influence the selection patterns of pronghorn (Gavin and Komers 2006, Beckmann et al. 2012, Christie et al. 2015, 2017, Seidler et al. 2015). Pronghorn movements are often impacted by fences because of their propensity to crawl under, rather than jump over fences (Yoakum et al. 2014, Jones et al. 2018).

Fences can also cause direct and indirect mortality in pronghorn (Harrington and Conover 2006, Jones 2014). Understanding how fences alter pronghorn movement and seasonal resource selection among migratory and resident animals may be key to sustaining (or restoring) pronghorn populations throughout their range. Such information is especially timely in the United States because of the recent Secretarial Order 3362 from the Department of Interior (U.S. D.O.I. 2018) that directs agencies to conserve migration and winter habitat of pronghorn, mule deer, and elk in the western United States.

We examined the resource selection patterns of a partially migratory population of pronghorn in the Northern Sagebrush Steppe (NSS) from 2003 to 2011. The NSS is a transboundary grassland and sagebrush steppe ecosystem of global conservation significance (Forrest et al. 2004) straddling Alberta, Saskatchewan, and Montana. Specifically, we evaluated resource selection patterns between movement tactics (i.e., migrant and resident pronghorn) during summer and winter across two spatial scales (second order and third order). Our analysis framework allowed us to (1) evaluate the relative influence of anthropogenic features (i.e., roads, fences, and well pads) and natural landscape features on resource selection, (2) assess how fence density and number of fence crossings affected resource selection and the subsequent loss of habitat, and (3) predict changes in resource selection under various fence density scenarios. Very little is known about broad-scale patterns of pronghorn use and their response to human disturbance; therefore, we evaluated resource selection at multiple scales. We hypothesized that both migrant and resident pronghorn would exhibit similar seasonal selection patterns with the strongest patterns (selection for or avoidance of) occurring at the second order as previously documented for other species (Meyer and Thuiller 2006). A main objective of our study was to evaluate the influence of fences on pronghorn resource section; therefore, we predicted that pronghorn would avoid fences at both spatial scales in the first large-scale quantitative test of fencing effects on ungulates. This prediction is based on the fact that pronghorn have difficulty crossing from one side of a fence to the other (Yoakum et al. 2014,

Jones et al. 2018). If pronghorn avoided fences, we then predicted that this could lead to significant indirect habitat loss (sensu Boulanger et al. 2012), which we estimated using second-order mapped resource selection probabilities (i.e., which depict habitat).

METHODS

Study area

The study area encompasses 315,876 km^2 of the prairie regions of Alberta, Saskatchewan, Canada, and northern Montana, USA, referred to as the NSS (Fig. 1). The landscape is characterized as flat with open plains and rolling hills as a result of glacial recession and deposits. Badlands and deep coulees are prevalent throughout the region (Mitchell 1980). Habitat across the region is a mosaic of native prairie, pastures seeded to non-native forages, and irrigated and dryland agricultural fields. Native prairie species include June grass (*Koeleria cristata*), needle and thread grass (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), and blue grama (*Bouteloua gracilis*). Notable shrubs in upland settings include silver sagebrush (*Artemisia cana*), big sagebrush (*Artemisia tridentata*), horizontal juniper (*Juniperus horizontalis*), and western snowberry (*Symphoricarpos occidentalis*). A diverse forb assemblage flowers throughout the growing season, although it often comprises a relatively small percentage of the total annual herbaceous production. Major cultivated crops include peas, canola, wheat, mustard, and alfalfa hay (Mitchell 1980). A mix of land use is prevalent throughout the region, with cattle grazing being dominant in Alberta and Montana, whereas crop production is generally more prevalent in Saskatchewan. Oil and natural gas wells occur at high densities in Alberta and continue to be developed in Saskatchewan and Montana. Human population centers are relatively sparse with higher densities in Lethbridge and Medicine Hat, Alberta, Regina and Swift Current, Saskatchewan, and Havre and Glasgow, Montana. The region is considered semi-arid, receiving an annual mean of 39.2 cm of precipitation, with approximately 70% as rainfall (Environment Canada 2010). The study area experienced severe winter conditions from 2008 to 2011, especially during the winter of 2010–2011, when mean temperatures were below
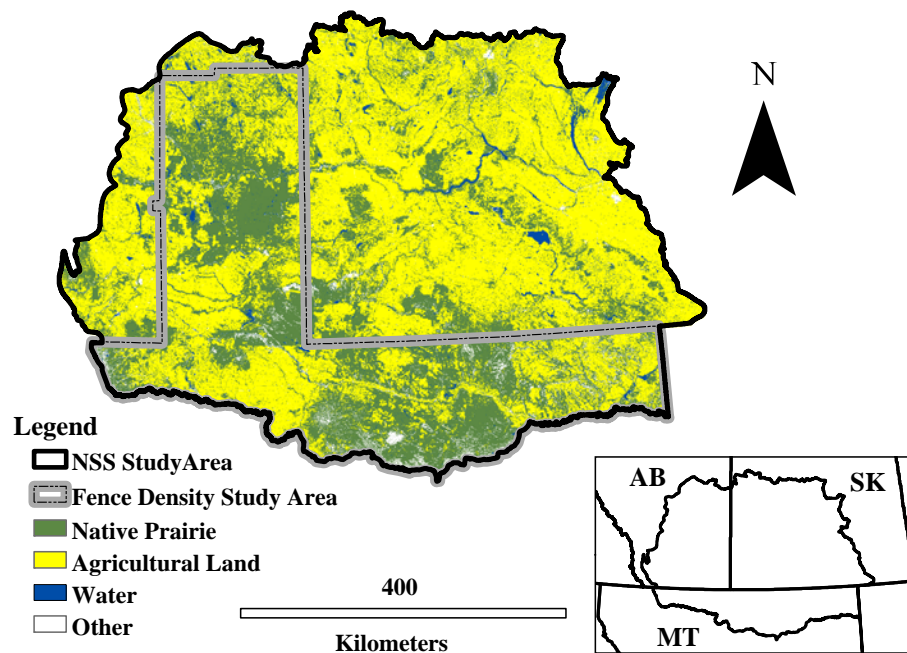
Fig. 1. Pronghorn study area within the Northern Sagebrush Steppe (NSS; solid black line) area of Alberta (AB) and Saskatchewan (SK), Canada, and Montana (MT), USA, 2003–2011. The gray truncated boundary within the NSS study area represents the area where fence data were available for analysis.

average and snow accumulation broke regional records (Jakes et al. 2018a).

Pronghorn capture

We captured female pronghorn using a net fired from a helicopter (Jacques et al. 2009) across the NSS from 2003 to 2010 and fitted each female with a Global Positioning System (GPS) collar (Lotek GPS 3300 and ARGOS 7000SA models; Lotek Wireless, Newmarket, Ontario, Canada). Capture protocols were approved by Alberta Fish and Wildlife (Alberta Sustainable Resource Development, Fish and Wildlife Research Permits 11861, 16707, and 20394), from the Montana Fish, Wildlife & Parks (approved by the Institutional Animal Care and Use Committee), and from the Saskatchewan Ministry of Environment. Of the 185 individuals captured, relocations were taken every 2 (*n* = 64 pronghorn) or 4 (*n* = 121 pronghorn) hours. We successfully retrieved data from 173 individuals. Habitat-induced GPS bias was negligible in our study as we obtained a 98% fix-success rate; we did not consider fix success to be a likely source of bias in our analyses (Frair et al. 2010). Our

data included 170 animal-years with 54 mortalities and 13 animals with multiple data years. We removed the first two days of data for each individual to address issues with post-capture movements not representing typical behavior (Jakes et al. 2018a). More details on capture and data collection methods were reported in Jones et al. (2015a) for Alberta, Canada, study animals and Jakes et al. (2018a) for Saskatchewan, Canada, and Montana, USA, study animals.

Analysis

Data processing.—Our objective was to estimate resource selection models for pronghorn within the NSS across two seasons, between the two movement tactics, and at two different spatial scales. We elected to use both second- and third-order selection scales to account for selection patterns at both coarse and fine scales (Johnson 1980, DeCesare et al. 2012). We first separated the data for modeling based on pronghorn movement tactics of migrant or resident for individual animal-years. Because some individuals did switch movement tactics between years, we use

animal-year as the sample unit. We classified pronghorn as a migrant if they moved between distinct seasonal ranges in a biological year, whereas a resident showed no movements between distinct seasonal ranges during a calendar year (Jakes et al. 2018a). We defined separate summer (March 22–October 30) and winter (October 31–March 21) seasons using non-linear models of net squared displacement (Bunnefeld et al. 2011) and used the graphical outputs to classify individuals as migrant or resident during each animal-year using each daily noon relocation for each pronghorn. See Jakes et al. (2018a) for more detail regarding pronghorn-specific migrant and resident classification.

Choice sets.—We applied a used-available resource selection function (RSF) design (Manly et al. 2002), comparing used (i.e., GPS relocation) and available point locations to estimate relative probability of selection for pronghorn and selection for, or avoidance of, spatiotemporal resources. We generated five available points at both the second- and third-order scales (Fig. 2) using a step-selection function (SSF) framework (Thurfjell et al. 2014). Because GPS fix rate is arbitrary, we used a time-lagged approach to approximate the second-order scale SSF by randomly selecting one used location every 4 d and connecting locations to determine the step length which represented a longer spatiotemporal scale of selection choices than scheduled collar GPS relocations (Thurfjell et al. 2014). We selected a 4-d interval following explanatory analysis (P. F. Jones et al., *unpublished data*) because it represented an even time interval and a longer spatiotemporal period than the daily relocation fix rate. We then buffered each used point using the 90th percentile from the step length distribution and randomly selected available points from within the buffered area. For the third-order scale, we calculated step lengths and turning angles between consecutive used points and applied those distributions to randomly select, with replacement, five step lengths and five turning angles for each used point. The distributions of step length and turning angles were animal specific to avoid issues of circularity (Thurfjell et al. 2014) and allow for the evaluation of selection between movement tactics. Hereafter, we use choice set to indicate a used point and its corresponding available points in a SSF framework and then estimated the SSF using conditional logistic regression (Hosmer and Lemeshow 2000).

Habitat covariates.—We considered the following resource covariates for the summer season: all road density (i.e., paved and unpaved road density), paved road density, oil and gas well pad density, cosine of aspect (north–south gradient), vector ruggedness measure (VRM), large hydrographic feature density (1:1 million-meter scale), and normalized difference vegetation index (NDVI). We termed the models without a fence covariate as our No Fence model(s). The two road covariates were derived from a seamless GIS layer developed for the NSS that incorporated road layers from each jurisdiction (Jakes 2015). The all road covariate included roads with the attributes paved, gravel, and dirt surface, while the paved road covariate included those roads with the paved surface attribute. Well pad density was developed using the point location well pad layer for the NSS and consisted of active and inactive oil, gas, injection, water, and test wells. We used the digital elevation model decimal surface to derive our aspect and VRM covariates. We converted our aspect from degrees to radians according to Zar (1999) resulting in a north–south gradient where −1 represents south and +1 represents north. We used the Terrain Tools Toolbox developed by Sappington et al. (2007) to combine aspect and the gradient component of slope into a single terrain ruggedness index ranging from 0 (no terrain ruggedness–flat) to 1 (complete terrain ruggedness). We used the Nelson drainage file from the Government of Canada website at the 1:1 million-meter scale to represent hydrology features at a coarse scale (Jakes 2015). The hydrology features included major rivers, streams, creeks, and canals (Jakes 2015). We used NDVI as a surrogate for both forage quality and landcover type (e.g., native prairie or agricultural land) in our models because habitat and landcover were represented by categories that produce complicated models for interpretation. In addition, previous studies have shown strong correlations between NDVI and forage biomass and forage quality, especially in grassland systems (Hebblewhite et al. 2008, Borowik et al. 2013). We used the 16-d composite NDVI imagery from the MODIS satellite from 2000 to 2011 (MOD13Q1). We assigned NDVI values to choice sets based on the
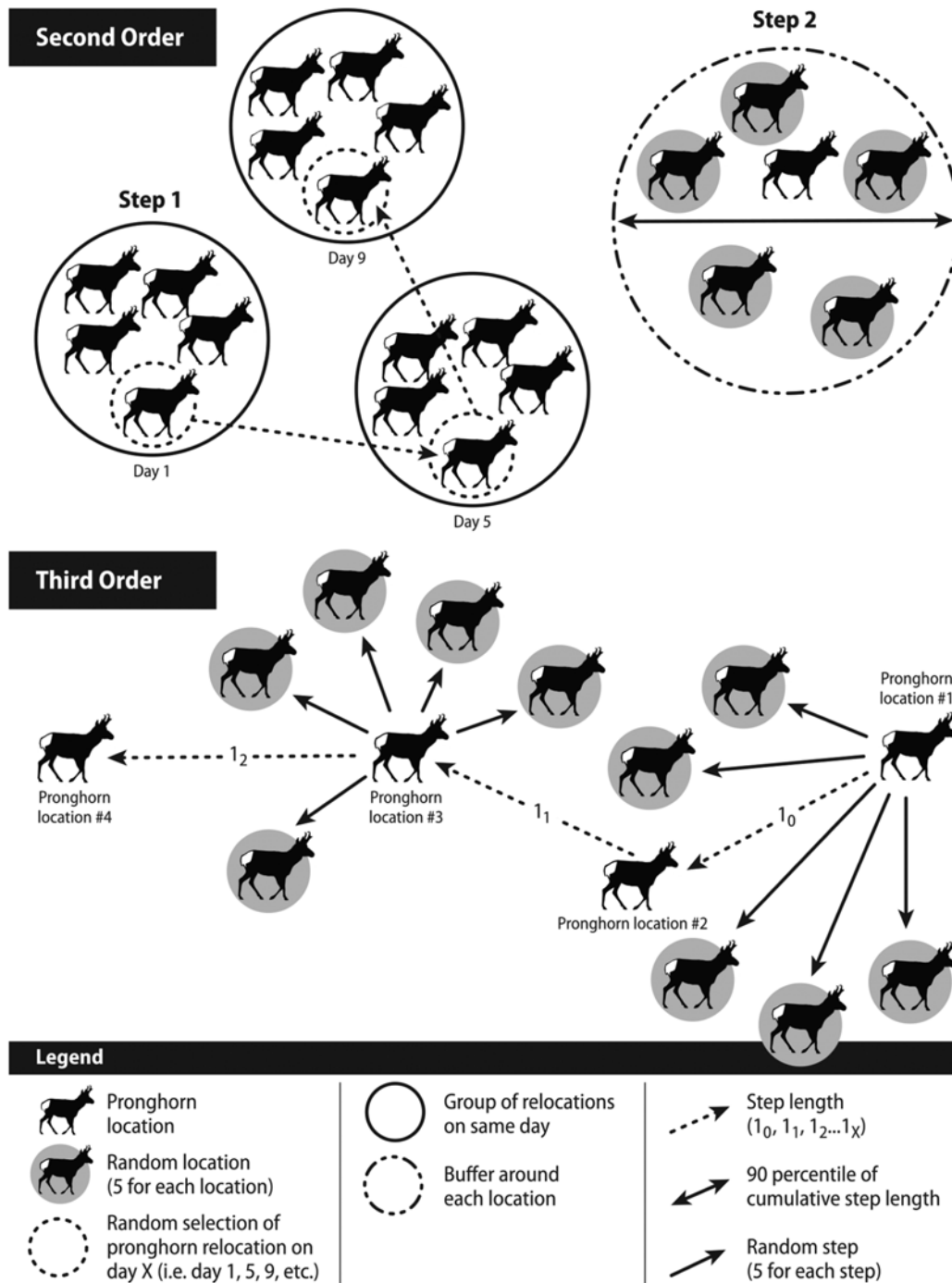
Fig. 2. Conceptual diagram of step-selection function sampling design at the second and third order for migrant and resident pronghorn in the Northern Sagebrush Steppe, 2003–2011. At the second order, the buffer around each used and available point was equal to the 90th percentile from the step length distribution. At the third order, we calculated step lengths and turning angles between consecutive used Global Positioning System points and used those distributions to randomly select, with replacement, five step lengths and five turning angles for each used point.

date of the use location for a given choice set resulting in NDVI being assigned spatiotemporally. For example, if the pronghorn location was for January 15 of a given year, it would be assigned to the first 16-d composite tile (January 1–January 16); if the location was for 18th January, it would be assigned to the second 16-d tile (January 17–February 1), and so on (Jakes 2015). Potential covariates differed slightly for the winter season No Fence model. We used maximum NDVI instead of standard NDVI in the winter models because maximum NDVI represents standing biomass outside of the growing season (Borowik et al. 2013). We developed maximum NDVI by using the maximum NDVI value for a given raster cell across all time periods in the dataset. We also included snow duration as a potential covariate in the winter models using 8-d composite MODIS data (MOD10A, Hall et al. 2002). We clipped, interpolated, and evaluated MODIS imagery to create 8-d composite tiles for snow presence/absence from 2000 to 2011. We then calculated the cumulative number of 8-d images containing snow cover for a particular pixel and assigned these snow duration values to each used and random location for a given choice set. We included the hydrological features covariate in the winter model (as well as summer) because the classification within hydrological features is not limited to just the incised water channel but also includes areas up to the high-water mark. The area up to the high-water mark may contain silver sagebrush, a quasi-riparian species (Jones et al. 2005), that is an important forage species for pronghorn during the winter (Yoakum et al. 2014). See Appendix S1 for data source information for all resource covariates.

We specifically evaluated the effects of fences on pronghorn when we added a unique fence covariate to the No Fence models at each spatial scale. We applied two separate measures of fences at each scale to better biologically assess potential pronghorn scale-dependent response to fences. We merged a spatial fence layer for a portion of the Alberta study area (Seward et al. 2012) and a map output of predicted fence locations for the Montana portion of our study area (Poor et al. 2014) to create our seamless layer of fence locations. Fence locations were unavailable in the Saskatchewan portion of our study area. At the second-order scale, we developed fence density rasters by calculating line density within a variety of search radii in ArcGIS 10.4 (Esri 2016). We termed the second-order models that included fence density along with the other covariates the Fence Density model(s). We developed a fence crossing covariate by drawing a line (i.e., step lines) from each of the used and available points for a given choice set back to the used point from the prior choice set in an SSF framework to better reflect how pronghorn encounter fences at the third-order scale. We counted the number of intersections between a given pronghorn step (line) and the fence location layer (i.e., number of fence crossings). Fence crossings greater than 10 were capped at 10 using a histogram of fence crossings (P. F. Jones et al., *unpublished data*). We used the fence crossings covariate to assess variance between how many fences were crossed where the animal chose to move (i.e., used point) or could have moved (i.e., available point). We termed the third-order models that included fence crossing along with the other covariates the Fence Crossing model(s). We fit these two fence models in the subset of the study area for which fence data were available (Fig. 1). We restricted data used for Fence Density and Fence Crossings models to choice sets occurring within 1 km of the fence layer. These scale-dependent fence models allowed us to assess the relative effect fences had on seasonal selection patterns of pronghorn.

At the second order, we assessed multiple radii for each covariate to determine at which spatial scale pronghorn showed the strongest univariate response (Hebblewhite et al. 2014). At the second order for each covariate (e.g., density of fences), we calculated the density of the covariate using 50, 100, 200, 300, 400, 500, 750, 1000, 1500, and 2000 m radii. We then compared the univariate models using Bayesian Information Criterion (BIC; Burnham and Anderson 2002), because of the stronger penalty term that accounts for the number of locations (n) in this context, as well as number of parameters, and selected the density spatial resolution model with lowest BIC score for each covariate. We used results from our previous work for pronghorn covariates at the third order where we similarly evaluated the spatial resolution for other point and linear covariates which pronghorn showed the strongest selection responses to (Jakes 2015).

Model building and model selection

We used SSFs to estimate the relative probability of seasonal selection by pronghorn (Thurfjell et al. 2014). We fit all models across animals within a given selection season, order, and movement tactic. We did not use mixed-effects SSF models because of challenges of interpreting random slopes/coefficients in such models and instead adopted a single clogit model across all animals (Fieberg et al. 2009). We used model selection and external cross-validation as the ultimate measure of model goodness of fit. We assumed that the probability of an animal selecting the *j*th resource unit on the *i*th choice set was

$$p_{ij} = \frac{\exp(\beta_1 x_{1_{ij}} + \beta_2 x_{2_{ij}} \cdots + \beta_p x_{p_{ij}})}{\sum_{k=1}^{N_i} \exp(\beta_1 x_{1_{ik}} + \beta_2 x_{2_{ik}} \cdots + \beta_p x_{p_{ik}})} \quad (1)$$

where there are *n* sets of resource units of size N_i ($i = 1, 2, \ldots, n$), $\beta_1, \ldots, \beta_p$ are estimated coefficients, $x_{1_{ij}}, \ldots, x_{p_{ij}}$ are covariate values for the *j*th unit of the *i*th choice set, and *p* is the number of covariates in the model. We note that the SSF formulation yields a relative probability of selection (Lele et al. 2013, Thurfjell et al. 2014). We used R statistical software to fit the models (R Development Core Team 2018), specifically, the Survival R package which fits the conditional logit model using the Cox-proportional hazards approximation (Therneau 2015).

Prior to modeling, we performed Pearson's pairwise correlation analysis to identify potential collinearity issues. None of the covariates considered during model selection exhibited strong correlation ($|r| > 0.6$). Additionally, we examined coefficients and their standard errors during the modeling process and inspected for large changes in coefficient estimates coinciding with the addition of a particular covariate which can indicate multi-collinearity (Hosmer and Lemeshow 2000). As a result, we determined that some covariates would best approximate pronghorn selection if both linear and quadratic terms were included in the model selection process (e.g., NDVI and well pad density). For example, optimal NDVI for pronghorn selection appeared in the middle of the range of NDVI values with selection being lower at both the lowest and highest extents of NDVI. Lastly, two road covariates were included in our modeling approach of which one (paved roads) is nested within the other (all roads). Both covariates were included in potential models after determining that these covariates had very weak collinearity (tested across seasons and scale), and when one road covariate was removed, the beta coefficients remained stable (within 17%; Hosmer and Lemeshow 2000) and there was a large change in ΔBIC (P. F. Jones et al., *unpublished data*). Importantly, retaining both road covariates in modeling efforts captured potential behavioral variances exhibited by pronghorn, thereby increasing the utility of models and spatial predictions to managers (see results and marginal plots in appendices).

We obtained final models by using forward stepwise model building and BIC to assess relative fit. Models were fit stepwise until either the BIC value did not improve by a value of 2.0 or the global model was reached (Burnham and Anderson 2002). Our forward stepwise model building process began with univariate models and added additional covariates to the best model at a given tier of models assuming the addition of the covariate improved relative fit. After top models were selected, we calculated standardized coefficients by normalizing the data and refitting the models to aid in the direct comparison between covariates. Once a final top model was estimated for the entire NSS study area, we then refit this top model (the No Fence model) to the reduced study area where the fence covariate data were available and re-estimated the model accounting for the effects of fence density (second order) or the number of fence crossings (third order). These second sets of models with fence covariates were termed the Fence models. We tested for coefficient similarity between the No Fence and Fence models to ensure no confounding was caused by different spatial extents of the two analyses (Fig. 1) and then used the fence models to estimate indirect loss of habitat specifically from fences.

Model validation

We withheld 20% of the animals at random from both the migrant and resident pronghorn groups for model validation. We validated the final models using the Johnson et al. (2006) method as follows: (1) Using the top model, we predicted the relative probability of selection across sampling units and reclassified units into

twenty equal-area rank bins (e.g., the twentieth bin containing the highest predicted 5% of the study area), (2) determined the median prediction $w(x_i)$ for each bin i, (3) determined the utilization $U(x_i)$ value for each bin i using the formula

$$U(x_i) = \frac{w(x_i)}{\sum_{k=1}^{20} w(x_k)} \qquad (2)$$

(4) summed the count of use points of the withheld animals within each bin, (5) estimated the sum of use points within each bin j, using

$$N_i = N \times U(x_i) \qquad (3)$$

where N_j is the total number of use points, (6) compared expected selection (from step 5) to observed selection (from step 4) using Spearman's rank correlation analysis. We considered scores >0.9 to indicate excellent model fit, 0.8–0.89 to indicate good model fit, 0.7–0.79 to indicate adequate model fit, 0.6–0.69 as satisfactory, and 0.5–0.59 to indicate a model that barely explains more than random by chance (Hosmer and Lemeshow 2000). We were unable to validate fence crossing models (third order) due to the conditional nature of the fence crossing covariate. The number of fence crossings was contingent upon the pronghorn movement direction and step length and developing an underlying spatial prediction that represented simulated fence crossings added an additional level of complexity (e.g., simulation modeling, Singer et al. 2017) and was beyond the scope of our analysis. Thus, our fence analyses focused just on results from the second order and likely underestimated the effects of fences at the third-order scale (see *Results*).

Model predictions

We mapped the spatial predictions of the relative probabilities of selection from the top SSF model (i.e., a spatial map of habitat) for each season, order of selection, and pronghorn group at a 1-km^2 spatial resolution. We multiplied the predicted probability of selection for a given grid cell across orders (DeCesare et al. 2012) to yield a habitat probability map that combined second- and third-order model predictions for just the No Fence models. We could not integrate the Fence models because of different covariates assessed at the second (fence density) and third (fence crossings) orders. We then assigned each grid cell a prediction value of 1 (low use) to 5 (high use) based on prediction percentiles that represented approximately the same amount of area (i.e., each prediction class contained approximately 20% of the predictions).

Fence density scenarios

We used the fitted fence density models to assess the change in relative probability of selection by pronghorn based on changes in fence density. We first simulated removing fences from the landscape by setting fence density to zero in the fence density raster used for predictions. This simple scenario represents historical, pre-settlement conditions. We then applied fitted models to the adjusted fence density data to develop use predictions in the absence of fences. We took the same approach to simulate increased fence density. We doubled fence density in the fence density raster used for predictions and applied fitted models. We then looked at the percent change between predicted relative probability of selection for the original predictions and those developed using adjusted fence density (i.e., removal of fences and doubled fence density). We calculated the area and percent change for each of the five bins, where bin 1 represents low-quality habitat and bin 5 represents the best-quality habitat.

Results

We classified 94 and 76 of 170 animal-years as migrant and resident, respectively. Our univariate analysis determined the following spatial resolution best explained pronghorn selection at the second order. Pronghorn showed the strongest response to fence density at 100 m, to all roads at 200 m, paved roads at 100 m, well pad density at 400 m, and hydrographic features at 500 m radii. Based on Jakes (2015), at the third-order scale, pronghorn showed the strongest response to all roads at 100 m, paved roads at 100 m, well pad density at 1000 m, and hydrographic features at 750 m radii. These resolutions were used in the modeling of resource selection. At the second order, we used a 6746-m buffer around the used points for the placement of the available points based on the 90th percentile determined from the step length distribution (Fig. 2).

Table 1. Standardized parameter estimates for the top models during the summer at the second and third order for migrant and resident pronghorn in the Northern Sagebrush Steppe, 2003–2011.

Pronghorn group by model	Fence crossings	Fence density	All roads	Paved roads	Well density	Well density^2	NDVI	NDVI^2	Aspect	VRM	Hydro
Second											
No fence											
Migrant	NA	NA	−0.13	−0.07	0.02	0.001	0.02	−0.03	−0.10	−0.02	−0.13
Resident	NA	NA	−0.13	−0.08	NA	NA	−0.07	−0.04	−0.07	−0.08	NA
Fence density											
Migrant	NA	−0.12	−0.11	−0.05	0.01	0.001	0.03	−0.06	−0.11	−0.01*	−0.10
Resident	NA	−0.09	−0.12	−0.09	NA	NA	−0.06	−0.04	−0.07	−0.08	NA
Third											
No fence											
Migrant	NA	NA	−0.07	−0.05	NA	NA	0.02	−0.02	−0.05	NA	−0.03
Resident	NA	NA	−0.07	−0.06	NA	NA	NA	NA	−0.06	−0.05	NA
Fence crossing											
Migrant	−0.31	NA	−0.06	−0.04	NA	NA	0.03	−0.02	−0.05	−0.02	−0.02
Resident	−0.29	NA	−0.05	−0.05	−0.03	NA	NA	NA	−0.07	−0.05	NA

Notes: NDVI, normalized difference vegetation index; VRM, vector ruggedness measure. The following values (second order/third order) are the spatial resolution at the two spatial scales used to determine the density covariates: fence crossings (NA/number of), fence density (100 m/NA), all roads (200 m/100 m), paved roads (100 m/100 m), well density (400 m/1000 m), and hydro (500 m/750 m). Unless otherwise noted, our parameter estimates are significant at $P < 0.001$. We standardized the parameters by subtracting the mean from each value and dividing by 1 SD.

* Significant at $P = 0.01$.

Summer models

Second-order models.—During summer at the second order, migrant and resident pronghorn displayed different selection patterns in terms of which covariates were the strongest in the final models (Table 1). In general, based on standardized β coefficients, migrants showed stronger avoidance of anthropogenic features at the second order than the third order (Table 1). For the No Fence model (no fence covariate included), both migrant and resident pronghorn avoided (i.e., showed less use than expected based on availability) all roads and paved roads (Table 1). Migrant pronghorn selected for well pad density with a quadratic relationship (Table 1), while for resident pronghorn well pad density was not a covariate in the final second-order model. Both migrant and resident pronghorn selected for south-facing aspects, flat terrain, while migrants avoided hydrographic features (Table 1). Hydrographic features were not a covariate in the final No Fence model for resident pronghorn. Both migrant and resident pronghorn had a quadratic relationship to NDVI (greenness), with migrant pronghorn peaking at 0.4 and resident pronghorn peaking at 0.2 (Table 1; Appendix S2). Marginal plots for the No Fence models during summer at the second order are provided in Appendix S2. When fence density was included (Fence Density model, Table 1) with the other covariates it was the strongest covariate in the final model for migrant but not resident pronghorn. Both migrant and resident pronghorn showed avoidance of areas with high fence density (Fig. 3). Pronghorn resource selection responses to other covariates did not change appreciably when fence density was included (see standardized β coefficients for each covariate in Table 1).

Third-order models.—At the third order, both migrant and resident pronghorn exhibited similar selection patterns (No Fence model, Table 1). Both migrant and resident pronghorn avoided all roads and paved roads (Table 1), while both tactics did not select for or against areas with high well pad densities. Both migrant and resident pronghorn selected for south-facing aspects, while only resident pronghorn selected for flat terrain (Table 1). Migrant pronghorn avoided hydrographic features, while resident pronghorn showed no selection for hydrographic features. Migrant pronghorn showed a quadratic relationship to NDVI with peak relative probability of selection occurring at
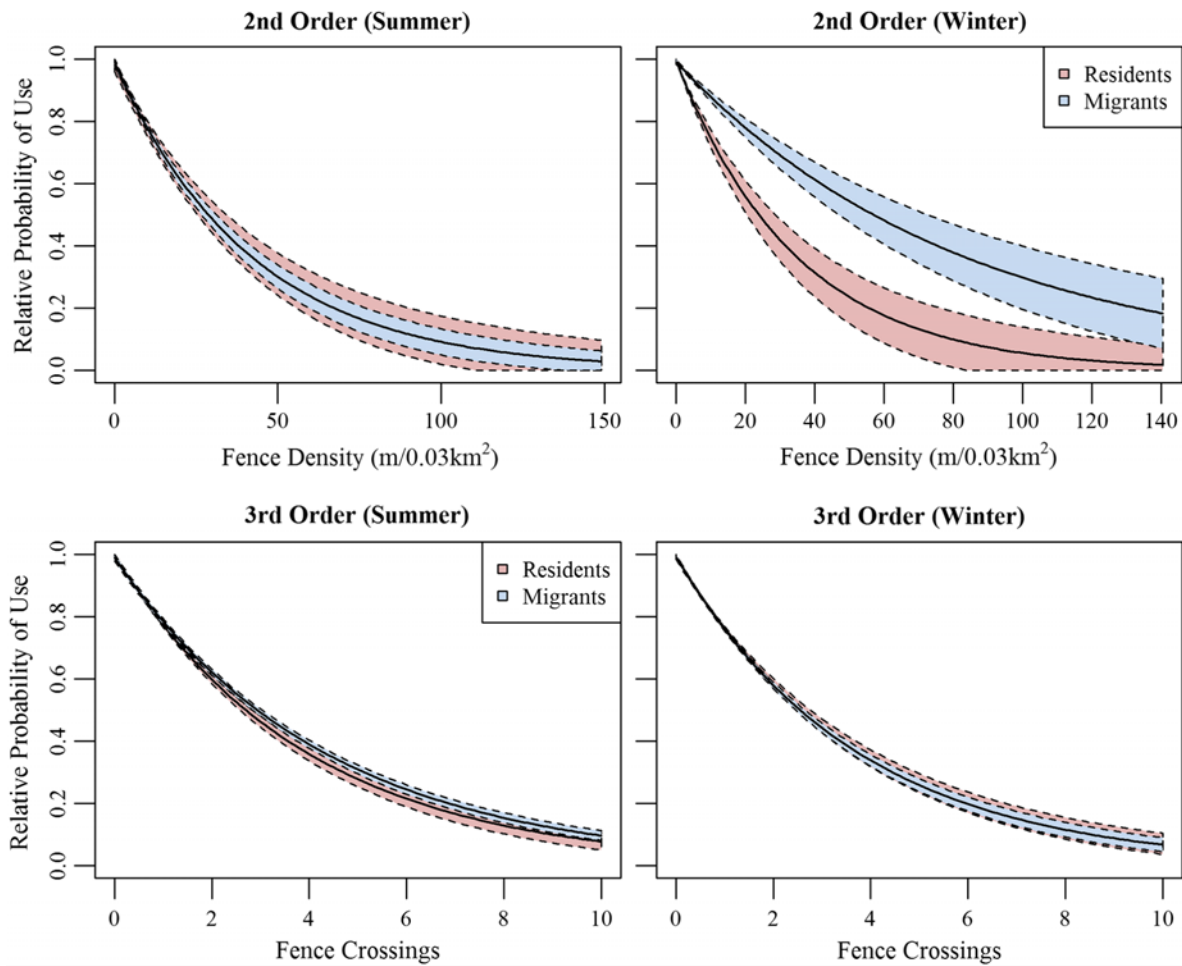
Fig. 3. Marginal plots for fence density (second order) and fence crossing (third order) during summer and winter for migrant and resident pronghorn in the Northern Sagebrush Steppe, 2003–2011.

approximately 0.5 (Appendix S3), while NDVI was not a covariate in the final model for resident pronghorn. Marginal plots for summer at the third-order No Fence models are provided in Appendix S3. When the number of fence crossings was included (Fence Crossing model, Table 1) with the other covariates, it was the strongest covariate in the final model for both migrant and resident pronghorn (Table 1). Both migrant and resident pronghorn showed strong avoidance to crossing fences (Fig. 3). The exceptions were for migrant pronghorn where terrain ruggedness was a covariate in the Fence Crossing model but not the No Fence model and for resident pronghorn a linear relationship to well pad

density was included in the Fence Crossing model but not the No Fence model (Table 1).

Summer model validation and predictions.—Summer models performed well with models for resident pronghorn consistently validating better than the models for migrant pronghorn at the second order (Table 2). The Fence Density model validated better than the No Fence model for migrants at the second order, with the opposite occurring for resident pronghorn where the No Fence model validated better than the Fence Density model (Table 2). At the third order, the No Fence model for migrant pronghorn validated well, while the No Fence model for resident pronghorn did not validate well. When the

Table 2. Spearman's rank correlation values for the top no fence and fence density models during the summer and winter at the second order, third order, and integrated (second order × third order) for migratory and resident pronghorn in the Northern Sagebrush Steppe, 2003–2011.

Season	Model	Pronghorn group	Spearman's rank correlation values		
			Second	Third	Second × Third
Summer	No fence	Migrant	0.71	0.89	0.81
Summer	No fence	Resident	0.89	0.45	0.90
Summer	Fence density	Migrant	0.85	NA	NA
Summer	Fence density	Resident	0.86	NA	NA
Winter	No fence	Migrant	0.95	0.86	0.95
Winter	No fence	Resident	0.63	0.21	0.66
Winter	Fence density	Migrant	0.93	NA	NA
Winter	Fence density	Resident	0.53	NA	NA

No Fence models at the second order and third order were integrated, models performed better than single-scale models. The integrated relative probability of selection (second-order × third-order model predictions) by migrant and resident pronghorn across the NSS during summer using the No Fence model and the probability of selection at the second-order for the Fence Density model are depicted in Fig. 4a, b, respectively. We were unable to provide an integrated Fence model relative probability of selection due to the conditional nature of the fence crossing covariate (third order).

Winter models

Second-order models.—During winter at the second order, migrant and resident pronghorn displayed similar patterns in terms of the coefficient signs but did show different patterns in terms of which covariates were the strongest in the final No Fence models (Table 3). Both migrant and resident pronghorn avoided all roads and paved roads (Table 3), with resident pronghorn showing a slightly stronger avoidance. Migrant pronghorn avoided areas with high well pad density, while resident pronghorn selected for areas with high well pad density (Table 3). Both migrant and resident pronghorn selected for south-facing aspects and against rugged terrain. Migrant pronghorn selected for hydrographic features, while resident pronghorn avoided hydrographic features. Both migrant and resident pronghorn showed a quadratic relationship to maximum NDVI, with peak relative probability of selection occurring at 0.3 and 0.0, respectively

(Appendix S4). For migrant pronghorn, snow duration was not a covariate in the final model, while resident pronghorn avoided areas with greater snow persistence. Marginal plots for the winter No Fence models at the third order are provided in Appendix S4. When fence density was included with the other covariates (Fence Density model, Table 3), both migrant and resident pronghorn avoided areas with high fence density (Fig. 3), but in both cases, fence density was not the strongest covariant in the final models (Table 3). Resident pronghorn showed a slightly stronger avoidance of high fence density areas compared to migrant pronghorn. When fence density was included, pronghorn resource selection responses to other covariates did not change appreciably for most covariates (see standardized β coefficients for each covariate in Table 3). Notable exceptions were for migrant pronghorn where in the Fence Density model, paved roads were no longer a covariate in the final model and for resident pronghorn, the relationship changed from a quadratic in the No Fence model to linear in the Fence Density model for both well pad density and maximum NDVI (Table 3).

Third-order models.—During winter at the third order, migrant and resident pronghorn displayed similar patterns in terms of the coefficient signs but did show different patterns in terms of which covariates were the strongest in the final No Fence models (Table 3). Both migrant and resident pronghorn avoided all roads and paved roads, while only migrant pronghorn avoided areas with high well pad density (Table 3). Both migrant and resident pronghorn selected for
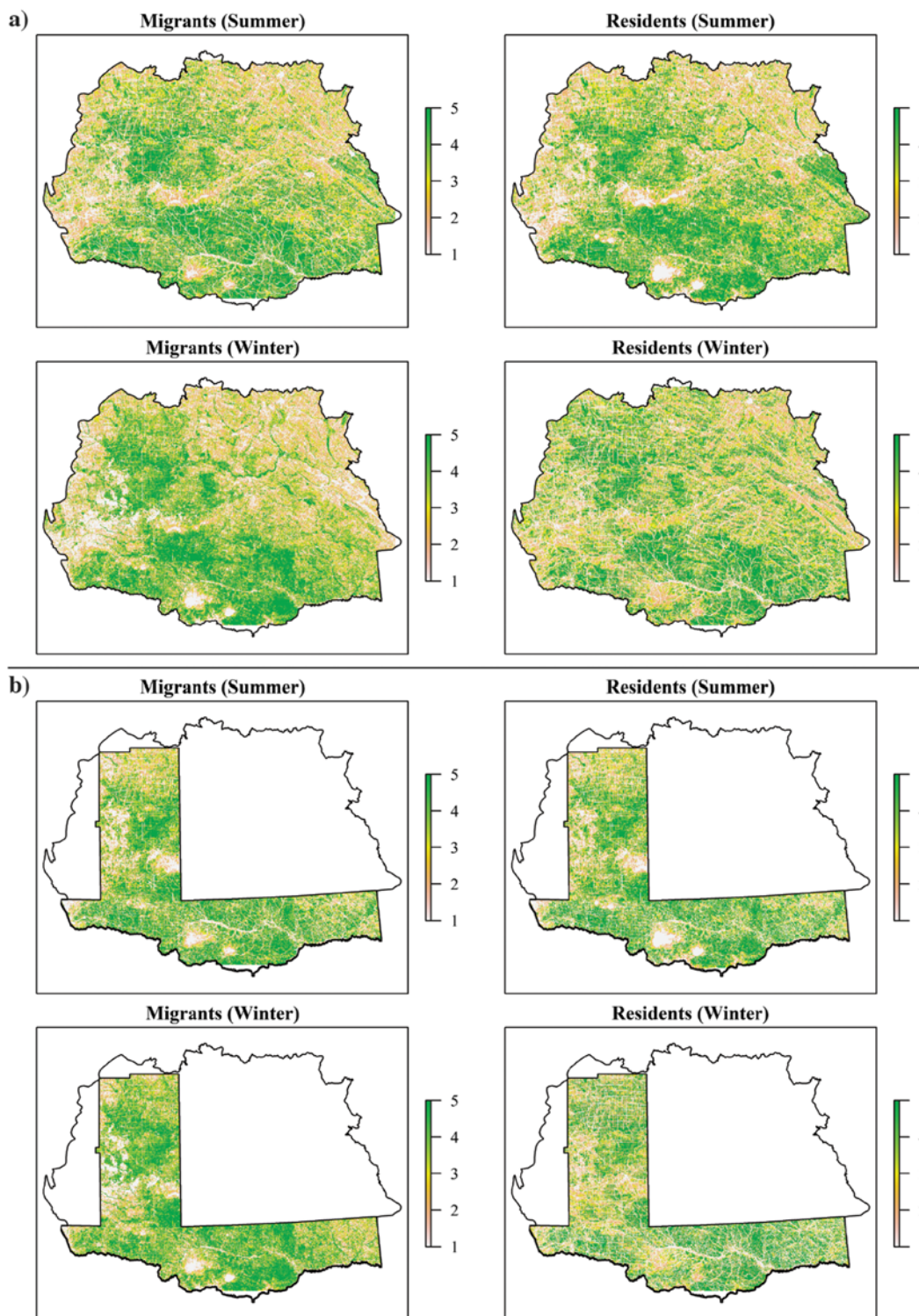
Fig. 4. The scale-integrated predicted probability of selection and second-order predicted probability of selection for the No Fence (a) and Fence Density (b) models, respectively, for migrant and resident pronghorn during the summer (top row) and winter (bottom row) in the Northern Sagebrush Steppe, 2003–2011.

Table 3. Standardized parameter estimates and P values for the top models during the winter at the second order and third order for migrant and resident pronghorn in the Northern Sagebrush Steppe, 2003–2011.

Pronghorn group by model	Fence crossings	Fence density	All roads	Paved roads	Well density	Well density^2	Max NDVI	Max NDVI^2	Aspect	VRM	Hydro	Snow
Second												
No fence												
Migrant	NA	NA	−0.11	−0.04	−0.02	NA	−0.14	−0.02	−0.09	−0.12	0.07	NA
Resident	NA	NA	−0.15	−0.07	0.002*	−0.01	−0.05	0.02	−0.07	−0.07	−0.09	−0.02
Fence density												
Migrant	NA	−0.06	−0.12	NA	−0.03	NA	−0.14	−0.04	−0.08	−0.12	0.10	NA
Resident	NA	−0.11	−0.14	−0.06	−0.04	NA	−0.04	NA	−0.07	−0.06	−0.10	−0.03
Third												
No fence												
Migrant	NA	NA	−0.05	−0.04	−0.003$^+$	NA	−0.03	NA	−0.04	−0.07	NA	NA
Resident	NA	NA	−0.10	−0.04	NA	NA	NA	NA	−0.07	NA	−0.04	NA
Fence crossing												
Migrant	−0.34	NA	−0.03	−0.02	−0.03	NA	0.0003^{++}	−0.01	−0.04	−0.08	NA	NA
Resident	−0.28	NA	−0.10	−0.04	−0.04	NA	NA	NA	−0.07	NA	−0.04	NA

Notes: NDVI, normalized difference vegetation index; VRM, vector ruggedness measure. The following values (second order/third order) are the spatial resolution at the two spatial scales used to determine the density covariates: fence crossings (NA/number of), fence density (100 m/NA), all roads (200 m/100 m), paved roads (100 m/100 m), well density (400 m/1000 m), and hydro (500 m/750 m). Unless otherwise noted, our parameter estimates are significant at $P < 0.001$. We standardized the parameters by subtracting the mean from each value and dividing by 1 SD.

* $P = 0.79$, $^+P = 0.47$, $^{++}P = 0.96$.

south-facing aspects while only migrant pronghorn selected for flat terrain and resident pronghorn avoided hydrographic features. Migrant pronghorn had a linear relationship for maximum NDVI with higher relative probability of selection occurring near 0 (Appendix S5). Maximum NDVI was not a covariate in the final model for residents. Snow duration was not a covariate in the final models for migrant or resident pronghorn. Marginal plots for the No Fence third-order models during winter are provided in Appendix S5. When the number of fence crossings was included with the other covariates (Fence Crossing model, Table 3), it was the strongest covariate in the final models, with both migrant and resident pronghorn showing a reluctance to cross fences (Fig. 3). When fence crossing was included, pronghorn resource selection responses to other covariates did not change appreciably for most covariates (see standardized β coefficients for each covariate in Table 3). The exceptions were for migrant pronghorn that showed a stronger relationship to well pad density in the Fence Crossing model, the relationship for maximum NDVI changed from linear in the No Fence model to quadratic in the Fence Crossing model, and for resident pronghorn where well pad density became a significant covariate in the Fence Crossing model (Table 3).

Winter model validation and predictions.—Overall models for migrant pronghorn consistently validated better than the models for resident pronghorn (Table 2). During winter, the second-order No Fence model performed similar to the Fence Density model for migrants, with the No Fence model for residents performing better than the Fence Density model. At the third order, the No Fence model performed well for migrant pronghorn but not resident pronghorn. When the No Fence model scales were integrated, the model performed exceptionally well for migrant pronghorn but did not perform well for resident pronghorn. The integrated relative probability of selection (second-order × third-order model predictions) by migrant and resident pronghorn across the NSS during winter using the No Fence model and the probability of selection at the second order for the Fence Density model are mapped in Fig. 4a, b, respectively.

Fence density scenarios

When we examined the relative effects of fence density on ranked categories of pronghorn
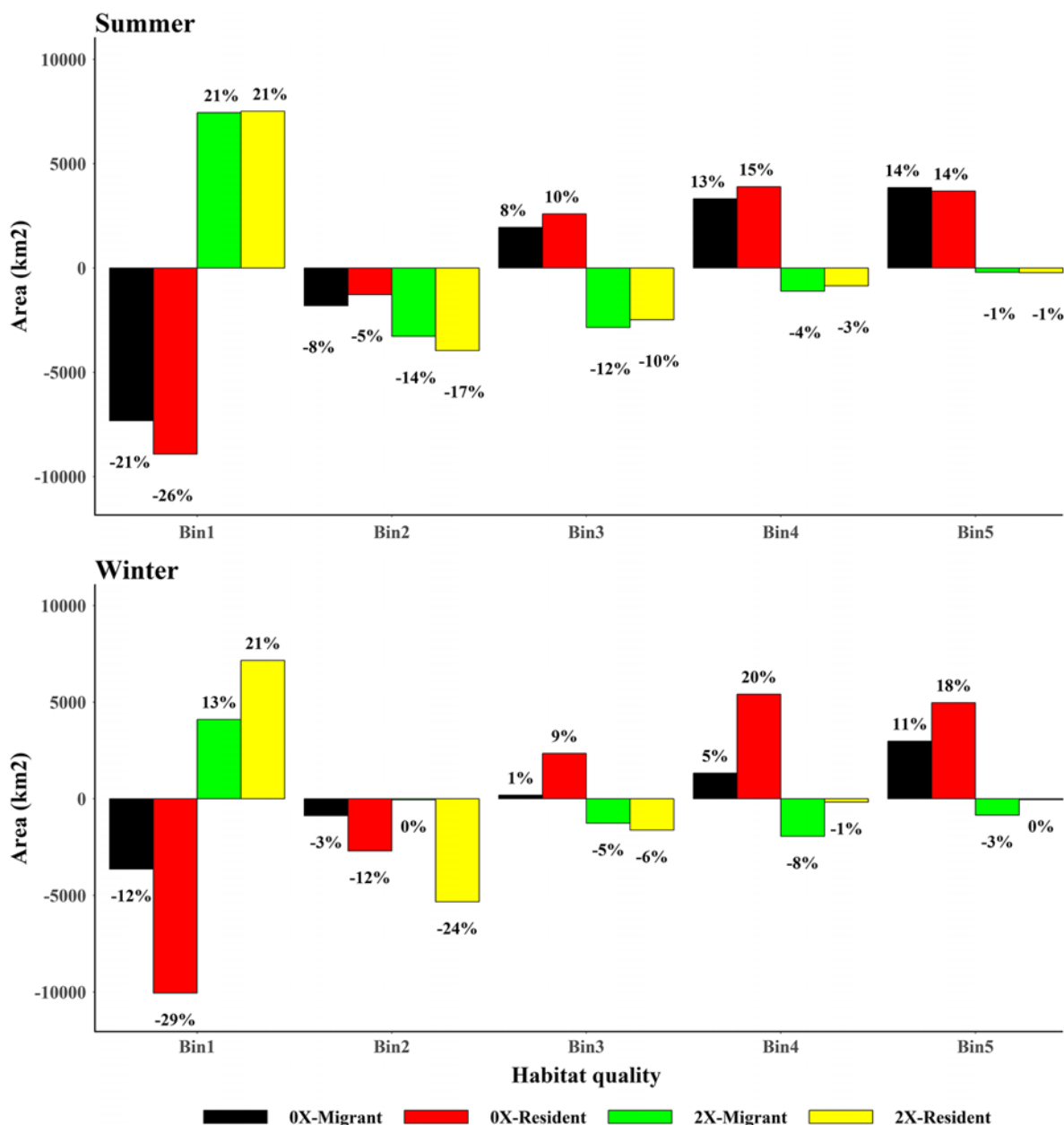
Summer

Winter

Fig. 5. Predicted probability of selection change in area (km^2) of bin 1 (low) to bin 5 (high) quality habitat for migrant and resident pronghorn during the summer (top panel) and winter (bottom panel) under two fence scenarios (no fences [0×] and doubling of fences [2×]) in the Northern Sagebrush Steppe, 2003–2011. Values below or above bars are the percent change for that category.

habitat (i.e., spatial predictions from the top SSF models), we determined that during the summer removing all fences would result in an approximately 27% and 29% increase in the availability of top-quality habitat (bin 4 and 5) for migrant and resident pronghorn, respectively (Fig. 5). An opposite pattern held true when we doubled the existing fence densities. When we doubled the existing fence density, we determined a loss of approximately 5% and 4% in the availability of

top-quality habitat (bin 4 and 5) for migrant and resident pronghorn, respectively (Fig. 5). An increase of 21% in the availability of the lowest quality habitat (bin 1) was observed for both migrant and resident pronghorn when the fence density was doubled. During winter when we removed fences from the landscape, we saw an increase of 16% and 38% in the availability of top-quality habitat (bin 4 and 5) for migrant and resident pronghorn, respectively (Fig. 5). When we doubled the fence density during the winter, the impact on available habitat was greater for migrant than resident pronghorn (Fig. 5). The doubling of fencing resulted in a decrease in the availability of top-quality habitat (bin 4 and 5) of 11% for migrant pronghorn and only a decrease of 1% for resident pronghorn. We also saw an increase in the availability of low-quality habitat (bin 1) of 13% and 21% for migrant and resident pronghorn, respectively.

Discussion

Anthropogenic disturbance affects animal movements across the globe (Gaynor et al. 2018, Tucker et al. 2018). Barbed and woven wire fences are laced throughout the agricultural regions of the world, including the prairies and intermountain valleys of western North America (Linnell et al. 2016, Jakes et al. 2018b). For example, our Alberta and Montana study regions contained enough fence to circle the earth eight times (Seward et al. 2012, Poor et al. 2014). Despite the widespread abundance of fences, their impacts on wildlife have received far less attention than any other anthropogenic feature (Flesch et al. 2009, Jakes et al. 2018b). Until the public becomes aware of an event where ungulates become either entangled or their movement is severely restricted resulting in mass mortalities, fences are essentially invisible in terms of their broad-scale impacts (Jakes et al. 2018b). Our long-term study shows the strong negative effects that fences have on the movement, distribution, and resource selection of migrant and resident pronghorn in the northern plains. Regardless of season or movement tactic, pronghorn avoided areas of high fence density and were reluctant to cross fences. These effects were only identified with the use of data developed from broad-scale mapping studies across our study area (Seward et al. 2012, Poor et al. 2014). Without a clear understanding of where fences are on the landscape, it becomes impossible to manage the impacts fences have on ungulates and ensure that functional connectivity between seasonal ranges persists.

Our results have added current implications due to recent cabinet-level policies in the United States and the growing recognition toward conserving connectivity by the IUCN connectivity working group (https://www.iucn.org/theme/protected-areas/wcpa/what-we-do/connectivity-conservation). The recent Secretary of the Interior's Order No. 3362 directs the Department of Interior to work with 11 western states to enhance and improve the quality of big-game (elk, mule deer, and pronghorn) winter range and migration corridor habitat to increase or maintain sustainable big-game populations (U.S. D.O.I. 2018). The identification, improvement, and enhancement of pronghorn winter (and summer) range can be achieved by reducing fence densities or modifying existing fence designs to facilitate pronghorn movement. By delineating the preferred seasonal ranges of pronghorn, our study also allows managers to prioritize or target fence management and modification efforts to ensure effective outcomes (Jones et al. 2018). Further, our model outcomes quantify the magnitude of habitat improvement possible on winter or summer ranges by fence mitigation efforts. Removal or modifying existing fences will benefit mule deer as fencing has been shown to influence mule deer crossing decisions (Burkholder et al. 2018) and will address a recommendation for enhancing connectivity for mule deer in the western states and provinces (Wakeling et al. 2015). However, the level of fencing on landscapes across the world is not static but continues to proliferate (Linnell et al. 2016, Li et al. 2017, Løvschal et al. 2017). For example, to support higher stocking rates, improve range health, and increase profitability, there is a movement to expand fencing to support multi-pasture and/or rotational grazing systems (Briske et al. 2011, Teague et al. 2013). Even though it is expensive to install and maintain fences for a landholder (Knight et al. 2011), these costs can be offset through currently available landholder incentive programs throughout the world (Frank and Ekilund 2017). If such increases in fencing are to be

encouraged, it must be accompanied by agency policy that directs new (and existing) fencing to be wildlife friendly to allow ungulate passage (Burkholder et al. 2018, Jones et al. 2018).

Both fence density and number of fence crossings were among the strongest covariates in our models (Tables 1, 3, Fig. 3) and highly influenced the selection patterns of both migrant and resident pronghorn. Our results indicated that both migrant and resident pronghorn selected areas with lower fence densities at the second-order scale, and selected movement paths with a lower number of fence crossings than available at the third-order scale while on seasonal range. In all cases, both movement tactics responded similarly to fences, except during winter at the second order where residents responded more strongly to fences than migrants. The difference between migrant and resident pronghorn in relationship to avoidance of fences during winter at the second order is likely due to two potential factors. First, our resident pronghorn group contained some animals that resided in agricultural landscapes during the winter, while all migrants wintered on native prairie. Agricultural landscapes are likely to have lower fence density than native range, though this need quantifying (Seward et al. 2012, Poor et al. 2014), which would translate to lower fence densities during the winter for resident animals compared to migrants. Alternatively, during winter snow can accumulate along fences making a once permeable fence impassable. To avoid fences acting as potential predator traps (golden eagles [*Aquila chrysaetos*], Jones et al. 2015a; coyotes [*Canis latrans*], P. F. Jones, *unpublished data*), resident pronghorn may move to areas of their home range that have a lower density of fences during the winter. Migrants avoid these potential predator traps by moving significantly more than resident animals, especially during the winter period (Jones et al. 2017). Further research is required to assess these two factors to determine which is driving the difference between movement tactics.

Our results of low number of fence crossings at the third order by both migrant and resident pronghorn were not surprising. Examination of consecutive GPS locations determined that locations were in proximity to mapped fences but did not actually cross the fence. This reluctance to cross fences was consistent with Reinking

(2017) who found that pronghorn in Wyoming rarely crossed fences when she included a fence crossing covariate similar to our third-order fence covariate. A pronghorn's propensity to cross under a fence, as opposed to jumping, over is well documented and has potential negative ramifications such as hair loss, wounds (and associated infections), and frostbite (Jones 2014). Our work highlights how simple efforts of modify existing fences to make them permeable for pronghorn can substantially increase available habitat (Jones et al. 2018).

It is well documented that many temperate migrating ungulates worldwide surf the green wave, following vegetation green-up during spring migration to maximize exposure to high-quality forage (Hebblewhite et al. 2008, Mueller et al. 2008, Gaidet and Lecomte 2013). Greenness as measured by NDVI was found to be the driving factor in migration for pronghorn in our study area during spring (Poor et al. 2012, Jakes 2015) and indicated that females followed the green wave (Middleton et al. 2018) in preparation of fawning. While we assumed we would observe differences in the selection of NDVI between movement tactics, as is well documented for other ungulates during the spring (Hebblewhite et al. 2008, Monteith et al. 2011, Middleton et al. 2018), we had predicted both tactics would show similar selection patterns while on summer range. However, migrant pronghorn consistently selected for intermediate NDVI in summer at the two spatial scales examined, while resident pronghorn selected for NDVI at the second order and not the third order. Based on selection of NDVI by migrants at the third order, it appears that migrant pronghorn continue to move in search of higher quality forage, while resident pronghorn do not, even though both tactics occupy similar areas during the summer. This difference in selection lends support to the forage maturation hypothesis, where migrants find higher quality forage as they move but they expend greater energy and potentially face higher adult predation rates, whereas residents conserve energy but do not have access to the highest nutritional forage, which could lead to lower reproductive rates (Fryxell and Sinclair 1988, Mysterud 2013). Migrants show consistently higher monthly movement rates throughout the year than

resident pronghorn (Jones et al. 2017), which was similar for nomadic Mongolian gazelles (*Procapra gutturosa*) in the eastern steppes of Mongolia who showed continuous movements in search of intermediate range of NDVI values (Mueller et al. 2008).

In addition to differences related to NDVI during summer, we also saw differences in the selection of maximum NDVI during the winter between movement tactics. Migrants responded more strongly to maximum NDVI at both scales during the winter, while resident pronghorn selected for lower maximum NDVI at the second order and not at all at the third order. We used the maximum NDVI value for the year in our analysis of NDVI in winter. Maximum NDVI values would represent total forage biomass achieved in an area during the peak growing season (June and July; Thoma et al. 2002). The differences we observed between movement tactics may be related to landscape configuration and the composition of animals within the movement tactic. As previously mentioned the resident group contained some animals that resided year-round in agricultural landscapes dominated by non-native vegetation types, while the migrant group contained animals that only wintered on native range. Native prairie plants tend to have higher NDVI values than introduced non-native species (Olimb et al. 2018). Differences in NDVI values based on plant type (native or non-native) are likely reflected in the variation in the selection patterns of the two movement tactics during the winter. These differences in maximum NDVI values between migrants and residents may contribute to the fact that pronghorn in more agriculturally dominated landscapes are considered sink populations with high fawn production but low population growth (Sheriff 2006).

Another contrast between migrant and resident resource selection was their response to well pad density during summer. Specifically, resident pronghorn did not select for or against well pad density whereas migrant pronghorn selected for well pad density; that is, the probability of selection increased with well pad density. Our results support those of Christie et al. (2017) who found pronghorn did not avoid well pads in North Dakota. The NSS, especially the Alberta portion, is highly developed with oil and gas wells, with a tendency for well pads to be on

native habitat, which is also important habitat for pronghorn and mule deer. The tendency for pronghorn to not select against well pads was previously noted because of a propensity for well pads to be placed on native prairie, which is high-value ungulate habitat (Beckmann et al. 2012, Christie et al. 2017). Though it appears that pronghorn select for areas with well pads, an assessment of how they distance themselves from the well pads, especially as well pads are under production, is warranted to assess the scale-dependent impact of energy development on pronghorn (Jakes 2015). Migratory mule deer in Wyoming did not show habituation to natural gas development after 15 yr but instead continued to distance themselves from well pads resulting in indirect habitat loss and reduced size of available winter range (Sawyer et al. 2006, 2017). However, mule deer are less gregarious than pronghorn and show stronger fidelity to their winter ranges. Nonetheless, our results suggest competing interests between pronghorn and energy development in the selection of native prairie, with potential implications related to the cumulative effects of energy development on ungulate habitat and, ultimately, population dynamics (Hebblewhite 2010, Sawyer et al. 2017).

We acknowledge that our results may have been influenced by intra-annual variation in winter severity over time during our study. We first captured study animals in Alberta between 2003 and 2006, followed by Saskatchewan and Montana between 2008 and 2010. Study animals in Alberta experienced typical winter conditions, while those in Saskatchewan and Montana experienced extreme conditions including cold temperatures and snow accumulation (Jakes et al. 2018*a*). We are aware that the extreme winter conditions did alter the movement patterns of the animals in Saskatchewan and Montana, with these animals completing facultative migrations from one winter range to another (in the same winter) due to extreme snow conditions (Jakes et al. 2018*a*). Nonetheless, we did attempt to capture differences in winter severity while pronghorn were on winter ranges in our models using temporally matched MODIS snow duration data. However, snow duration was rarely retained in final models, which may be because pronghorn are more responsive to snow depth,

not just how long snow is present. Pronghorn have a high foot-loading index and low mean chest height (Telfer and Kelsall 1984) and are known to avoid areas with deep snow (Bruns 1977, O'Gara 2004). Unfortunately, neither local snow depth measurements nor modeled snow depths (i.e., SNODAS; e.g., Brennan et al. 2013) were available across our large study area. We believe any potential effects of intra-annual weather variation were captured in our averaged models which represented average weather conditions over the 6 yr of our study. The fence crossing covariates during winter were the strongest covariates in the model for both movement tactics with pronghorn avoiding crossing fences. However, this result may underestimate the potential interactive effects of snow depth and the negative effects of fences. For example, Bruns (1977) documented the difficulty of pronghorn to move during the winter because of fences becoming a barrier to their movement (i.e., they can no longer move underneath), which is exacerbated by the accumulation of snow along fences (P. F. Jones, *personal observation*). Future studies of fence effects on wildlife may benefit from developing study area-specific snowscape mapping products that specifically quantify aspects of snow depth and quality to use in wildlife resource selection studies (Mahoney et al. 2018).

The hierarchical habitat selection hypothesis states finer scale selection is conditional on broader scale selection and that the most important resources are selected or avoided the strongest at the largest scales of selection (Rettie and Messier 2000, Boyce 2006). Previous results for other ungulates (Kie et al. 2002, Northrup et al. 2016) showed individuals responded more strongly to resources at broader than finer spatial scales (Rettie and Messier 2000, DeCesare et al. 2012). We had predicted that pronghorn would also show stronger patterns of selection at the second order (based on Spearman's rank correlation value) which was the case. Pronghorn are selecting seasonal ranges first and then their distribution within the seasonal range being governed by the location of the seasonal range. However, though selection for or against certain resources is likely to occur at broader scales one cannot discount their selection at finer scales. To account for selection at multiple scales, DeCesare et al. (2012) recommended that resource selection should be examined at multiple scales and the probabilities from each scale combined into a single scale-integrated function map. DeCesare et al. (2012) reported better model fit using the scale-integrated resource selection model over individual scale models based on Spearman rank correlation values. When we applied this approach and combined the second- and third-order probabilities of selection into a single scale-integrated function model, performance improved or was equivalent to second-order model performance. This single integrated function map will allow managers to instantaneously view important seasonal habitat for pronghorn across the NSS (DeCesare et al. 2012).

Our modeling approach of first assessing resource selection at the second order without fence density (potential habitat), then refitting the model including fence density (realized habitat), followed by comparing the resultant relative probability of selection change under two fence density scenarios effectively quantifies the amount of indirect habitat loss (sensu Polfus et al. 2011). Our results showed up to an 11% decline in the area of high-quality habitat (habitat rank bin 4 and 5; Fig. 5) when fence density was doubled, but likely underestimated the true loss of habitat if we had been able to model the loss of habitat because of fence crossings (third order). This is because the response by pronghorn to the effects of fences was even stronger at the third-order scale than at the second order. Even so, the level of indirect habitat loss estimated at the second order was comparable to Polfus et al. (2011), who showed a 2–8% reduction of high-quality habitats because of indirect habitat loss associated with caribou avoiding roads. More serious impacts of human infrastructure were demonstrated by Northrup et al. (2015), who showed a 50% loss of winter range by mule deer due to avoidance of oil and gas development. Other studies generally showed indirect habitat loss for ungulates because of anthropogenic disturbances ranged from 5% to 30% across species (Johnson et al. 2005, Hebblewhite 2010, Polfus and Krausman 2012, Sawyer et al. 2017). Although difficult to measure, these indirect habitat losses can presumably result in population declines, as less habitat generally equates to a decreased ability to support larger

numbers of animals. For example, a mule deer population in Wyoming declined by 36% concurrent with long-term avoidance of energy development where previous studies had shown similar levels of indirect habitat loss due to avoidance of infrastructure (Sawyer et al. 2017).

Our results quantify differences in resource selection between migrant and resident animals, particularly regarding green wave surfing/NDVI selection and selection behavior associated with energy development, and provide much-needed insight into the behavioral differences between movement tactics. The next step is to assess how the differences in resource selection between the movement tactics translate into overall fitness and population size. Previous studies have used a habitat-based RSF model (Boyce and McDonald 1999) to estimate population size (Boyce and Waller 2003, Patthey et al. 2008, Heinrichs et al. 2010, DeCesare et al. 2014, Hebblewhite et al. 2014). If population abundance data were readily available for our study area, we could test and quantify the resultant population effects with removal or doubling of fence density as proposed by our scenarios. For example, if we predict an 11% decrease in high-quality habitat when fence density is doubled, is a corresponding 11% decline in pronghorn populations observed? An assessment of the correlation between recruitment and population size with varying densities of fences across their range would reveal the true impact fences have on this and other species. Our results suggest that there may be underappreciated negative effects of fences on population abundance. To conserve partially migratory populations, efforts need to be made to reduce the negative effects of fencing through either complete or temporary removal (e.g., reduce permanent interior fencing and use semipermanent electric fencing) of fences and/or widespread adoption of fence modification approaches that mitigate the negative effects of fences on wildlife habitat and movements. For pronghorn, modifications should include either double-stranded smooth wire on the bottom or using clips to attach the bottom wire to the wire above to create a larger space between the wires and the ground, and lastly ensure the bottom wire is a minimum of 46 cm from the ground (Jones et al. 2018).

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