METHODS, TOOLS, AND TECHNOLOGIES

Behavior-specific habitat models as a tool to inform ungulate restoration

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Abstract. Across North America, many ungulate species that experienced historic population declines and range contractions are now broadly distributed across their native ranges after the implementation of successful restoration programs. The use of translocation continues to serve as an important restoration tool and is often informed through habitat models used to identify potential translocation areas based on biotic and abiotic landscape characteristics. Within the context of partially migratory wildlife populations, resident and migrant population segments can select for varying habitat characteristics, yet these population segments are often pooled when building habitat models. We used a large spatial dataset collected from eight bighorn sheep (*Ovis canadensis*) populations to build separate winter and summer resource selection models for migrant and resident animals with the purposes of (1) characterizing differences in seasonal selection patterns between resident and migrant population segments and (2) generating broad spatial predictions of bighorn sheep habitat to inform future translocations across western Montana, USA. Lastly, we used the model to inform two potential management scenarios, first to establish a new population in an unoccupied area and second to expand the distribution of existing populations through intra-mountain translocations. Selection patterns were generally similar among migrants and residents, especially in winter. Summer selection patterns varied between the two behaviors, with migrants selecting for higher elevations and residents selecting for lower elevations. Throughout the western Montana prediction area, bighorn sheep habitat was centered around mountain areas in all seasons. In the first management scenario, our model predicted that adequate resident and migratory bighorn sheep habitat existed in the restoration area, thus justifying the use of either resident or migrant source populations in translocation. In the second management scenario, our model predicted that there was broad potential for translocations into unoccupied areas adjacent to the current bighorn sheep distribution in western Montana. The behavior-specific approach to predicting bighorn sheep seasonal habitat captures the specific habitat characteristics of multiple migratory behaviors and may help to inform targeted and effective translocation programs.

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INTRODUCTION

Across North America, many ungulate species that experienced historic population declines and range contractions are now broadly distributed across their native ranges after the implementation of successful restoration programs (Kallman et al. 1987, Picton and Lonner 2008, IUCN/SSC 2013, Batson et al. 2015). Translocation, the intentional movement of animals from one area to another, has a long history in wildlife and fisheries management and is the foundation of native fauna restoration (Kallman et al. 1987, Griffith et al. 1989). The use of translocation continues to serve as an important tool in the restoration and augmentation of native taxa with varied management goals, including expanding the distribution of sensitive species (Brewer et al. 2014), increasing genetic diversity in small populations (Hedrick and Fredrickson 2010), increasing hunter, angler, and wildlife viewing opportunities (Kallman et al. 1987), bolstering population dynamics in small or declining populations (Griffith et al. 1989, Komers and Curman 2000), or reducing population abundance of source populations (Duka and Masters 2005, Wyoming Game and Fish Department 2016). Moreover, as climate change and other anthropogenic stressors continue to alter existing habitat conditions at a rate that exceeds the ability of species to change their distribution, there has been an increase in the use of translocation to help species track favorable habitat conditions (Thomas 2011, IUCN/SSC 2013).

Technological advances have provided managers tools to inform translocation programs and increase the probability of translocation success. For example, wildlife researchers and management practitioners routinely collect location data from devices on marked individuals to construct habitat models (Boyce and McDonald 1999, Johnson et al. 2006). Such models can identify covariates that influence habitat selection and be predicted spatially to generate habitat maps across large landscapes. Within the context of translocation, habitat selection models can help to identify unoccupied habitat or possible translocation sites (Niemuth 2003, Cianfrani et al. 2010) and are an effective tool to increase

the probability of translocation success (Griffith et al. 1989, Zeigenfuss et al. 2000).

The broad deployment of animal tracking devices also has highlighted the diversity of migratory behaviors both among populations and among individuals within a single population. For example, partial migration in which a population subset is migratory while the remaining individuals are resident on a shared winter range is common among migratory wildlife species (Chapman et al. 2011). Resident and migrant population segments can experience demographic trade-offs stemming from differing range conditions (Hebblewhite and Merrill 2009, 2011, Johnson et al. 2013), as well as varying selection patterns on shared winter ranges (Hebblewhite and Merrill 2009, Robinson et al. 2010, Barker et al. 2018). Although inter- and intraspecific differences in migration and selection patterns are being increasingly well described for many species (Cagnacci et al. 2011, Sawyer et al. 2016, Barker et al. 2018, Lowrey et al. 2019, 2020), these differences are not routinely included in habitat models used to inform translocation. Rather, location data from both residents and migrants are often pooled, resulting in an "average" habitat model that might not describe the more nuanced habitat characteristics of any single population segment (Lowrey et al. 2019, Spitz et al. 2020).

When selection patterns are strongly divergent among migratory behaviors, pooling location data across multiple migratory behaviors can produce a mismatch in which the models used to inform translocations do not reflect the migratory behavior of translocated individuals. For example, habitat models constructed from location data collected from migrants may misinform translocations where residents are used as the source population. By developing behavior-specific habitat models (i.e., separate models for each migratory behavior), managers can (1) evaluate possible differences in the habitat requirements of multiple migratory behaviors, (2) predict behavior-specific habitat selection models across the restoration area, and (3) strategically target source populations with specific migratory behaviors that best match the landscape attributes in the areas that are being restored. Additionally, when a restoration area has favorable

habitat conditions for multiple migratory behaviors, translocations from both resident and migrant source populations may help to build diverse migratory portfolios in restored populations (Lowrey et al. 2020), which can provide a buffer from the effects of interannual variation in environmental conditions or perturbations, and result in more stable populations through time (Schindler et al. 2015, Gilroy et al. 2016).

We used a large spatial dataset collected from eight bighorn sheep (*Ovis canadensis*) populations across western Montana to build behavior-specific habitat models with the purpose of characterizing differences in seasonal selection patterns between resident and migrant population segments and generating broad spatial predictions of bighorn sheep habitat to inform future translocations. Bighorn sheep are an iconic mountain ungulate that occur throughout western North America but have struggled to rebound to historic numbers despite extensive translocation and restoration efforts over the last century (Buechner 1960, Brewer et al. 2014). Bighorn sheep populations can be resident, migratory, or partially migratory, and previous translocation efforts have indicated that translocations of migratory animals were more successful than translocations of resident animals (Singer et al. 2000*b*). We expected to observe similar selection patterns between residents and migrants when sharing seasonal ranges in winter but different summer selection patterns specific to each behavior. Additionally, we expected to observe unoccupied habitat beyond the current distribution of bighorn sheep in western Montana, indicating broad restoration potential. Lastly, we used the model to inform two potential management scenarios, one to establish a new population in an unoccupied area and secondly to expand the distribution of existing populations through intra-mountain translocations into adjacent, unoccupied areas (Lula et al. 2020).

METHODS

Study area

Our study included eight bighorn sheep populations that were broadly distributed across mountainous regions of western Montana Fig.1). Migratory behaviors of study populations included elevational migrations in six populations (Castle Reef, Lost Creek, South Madison, Spanish Peaks, Stillwater, and the Upper Yellowstone) and resident behavior in two populations (Paradise and Petty Creek, see Lowrey et al. 2020 for additional details). All individuals within each population expressed the same migratory behavior (Appendix S1). In general, migrant populations had low-elevation winter ranges and high-elevation summer ranges, while residents remained at low elevations year-round. Migrant populations consisted of a combination of restored, augmented, and native management histories (Lowrey et al. 2019), and the two resident populations were both restored (MFWP 2013).

All eight study populations were located in mountainous landscapes characterized by rugged topography. The populations experienced strong seasonal variation in annual climate typical of temperate latitudes. Winters were characterized by cold temperatures and moisture occurring as snow, while summers were characterized by relatively warm temperatures with snow persisting into the summer months at higher elevations. Climate varied among the populations with average annual precipitation ranging from 597 to 1013 mm and mean temperatures for July ranging from 12.3° to 18.9°C and for January ranging from −8.5° to −3.1°C (PRISM Climate Group 2016). Vegetation cover types were diverse across the populations and generally included alpine and subalpine meadows and mesic coniferous forests (e.g., subalpine fir [*Abies lasiocarpa*] and Engelmann spruce [*Picea engelmannii*]) at higher elevations, mixed coniferous forests (e.g., Douglas fir [*Pseudotsuga menziesii*] and lodgepole pine [*Pinus contorta*]) at mid-elevations, and a mosaic of grasslands, shrublands, and agricultural areas at lower elevations. Across all populations except the Paradise population, which was primarily within the Flathead Indian Reservation, land ownership was predominantly federal lands managed by the U.S. Forest Service or National Park Service with privately owned lands along the valley bottoms. Potential predators of bighorn sheep present in all populations included black bears (*Ursus americanus*), coyotes (*Canis latrans*), wolves (*C. lupus*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and golden eagles (*Aquila chrysaetos*).
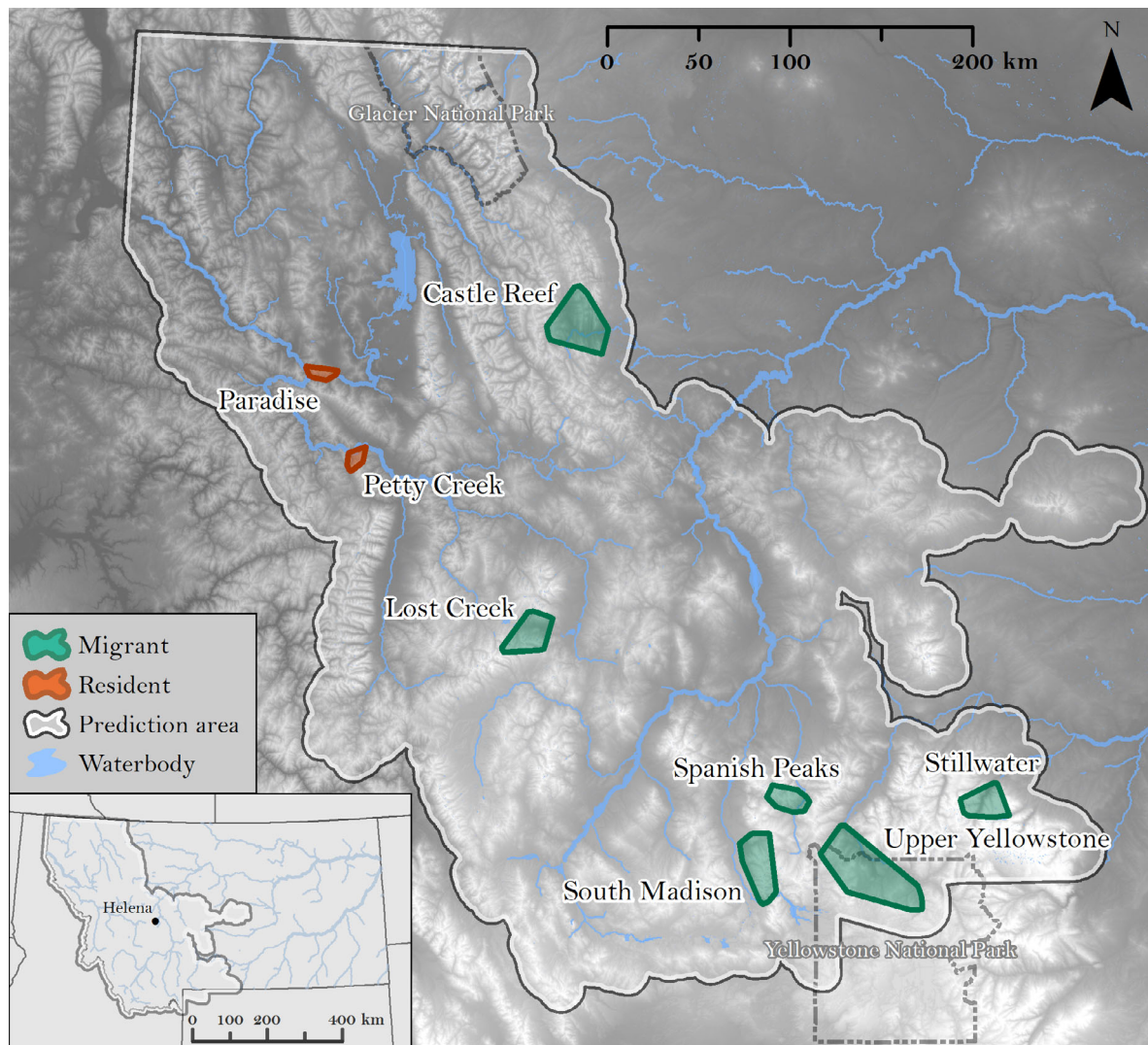
Fig. 1. The eight study populations used to model migratory and resident female bighorn sheep resource selection in the montane regions of western Montana, USA, 2012–2018. Migrant populations are shown in green, while the residents are shown in orange. The study areas were defined using an annual minimum convex polygon which we buffered by 2.5 km. Elevation is represented by the dark gray (low) to light gray (high) gradient.

Grizzly bears (*U. arctos horribilis*) were also present in all populations except Petty Creek and Lost Creek. All populations were sympatric with one or more additional ungulates, including mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), and mountain goats (*Oreamnos americanus*). Recent minimum population counts varied by population and ranged between 100 and 325 animals (Lowrey et al. 2019).

We defined the area for predicting habitat models as the mountain regions of western Montana that were within the Western Cordillera ecoregion designation and ≤500 km^2 (Fig.1). Additionally, we included portions of Yellowstone National Park in Wyoming that were occupied by the Upper Yellowstone population. The prediction area encompassed the historic distribution of bighorn sheep in montane areas of Montana (Couey 1950, Buechner 1960, Omernik

and Griffith 2014) and the current distribution of bighorn sheep in mountain areas of western Montana (i.e., we excluded the prairie areas of eastern Montana, see DeVoe et al. 2020).

Data collection

From 2012 to 2018, we used ground darting, drop nets, and helicopter net gunning to capture female bighorn sheep, primarily during winter. Collar model and programming varied among study populations. Most individuals were fitted with store-on-board GPS (TGW-4400-2 or TGW-4400-3; Telonics, Mesa, Arizona, USA) radio collars programmed to record a location at 4-, 5-, or 8-h intervals and release from the animal after 1–2 yr. A subset of animals was fitted with Iridium (TGW-4570; Telonics, Mesa, Arizona, USA) or Globalstar (Lotek LifeCycle and LifeCycle Pro 330) satellite-linked collars programed to record a location at 12-h intervals. All animals were captured and handled according to protocols approved by the Montana State University Institutional Animal Care and Use Committee (permits 2011–17, 2014–32, 2016–6). Where metrics were provided by the GPS collar manufacturer, we censored GPS locations with an HDOP > 10 (D'eon and Delparte 2005) and a horizontal error >100 m (Lowrey et al. 2019). After censoring, the mean fix success rate of individual bighorn sheep was 92% (SD = 17%).

Seasonal periods and resource covariates

We constructed separate winter (24 November–6 May) and summer (7 June–7 October) resource selection models for the migrant and resident populations. This approach allowed us to include season-specific covariates in our models and compare seasonal patterns in resource selection between resident and migratory populations (Johnson et al. 2000). While other methods are available when comparing habitat selection models (i.e., latent selection differences; Latham et al. 2011), creating separate behavior-season models best accommodated our varied sample size among the allopatric resident and migrant populations and also advanced our goals of generating spatial predictions for each behavior that could help inform future translocation. We defined the seasonal periods using migration parameters estimated from nonlinear regression modeling of population-mean elevation profiles of the migrant populations and then applied the seasonal periods to the resident populations (Appendix S2; Bunnefeld et al. 2011, Spitz et al. 2015).

We used non-collinear combinations of covariates that have been shown to influence bighorn sheep resource selection across multiple study populations within the inter-mountain region of the western United States and Canada Table 1; Wakelyn 1987, Turner et al. 2004, DeCesare and

Table 1. Covariate descriptions and hypothesized direction of selection for covariates used in modeling migratory and resident female bighorn sheep resource selection in the montane regions of western Montana, USA, 2012–2018.

Covariate	Abbreviation	Description	Form†	Migrants (summer, winter)	Residents (summer, winter)
Aspect	ASP	The inverse cosine of aspect minus 35 degrees. North-northeast to south-southwest (−1 to 1)	Li	pos, neg	pos, neg
Canopy cover	COV	Canopy cover	Li	neg, neg	neg, neg
Distance to steep terrain	DST	Euclidean distance from slopes ≥40 degrees	Li	neg, neg	neg, neg
Elevation	ELEV	Elevation (m)	Sq	pos, neg	neg, neg
NDVI amplitude	$NDVI_{Amp}$	Mean difference between max and baseline NDVI at start of growing season (May–October of 2012–2018)	Li	neg, na	neg, na
Slope	SLP	Slope (degrees)	Sq	pos, pos	pos, pos
Slope variance	SLP_{var}	Standard deviation² of SLP	Ps	pos, pos	pos, pos
Snow water equivalent	SWE	Mean Dec–Jan from 2011 to 2014	Li	na, neg	na, neg

† Li = linear, Sq = quadratic, and Ps = natural log/pseudothreshold.

Pletscher 2006, Poole et al. 2016, Lowrey et al. 2018, Lula et al. 2020). Terrain covariates included elevation (ELEV), slope (SLP), and slope variance (SLP$_{var}$) which characterized landscape ruggedness and was calculated as the squared standard deviation of slope within a 300 × 300 m neighborhood (DeVoe et al. 2015, Poole et al. 2016, Lowrey et al. 2017, 2018). We also included distance to steep terrain (DST) and defined steep as slopes ≥40° (DeCesare and Pletscher 2006, Poole et al. 2016). Although the definition of steep can be arbitrary (DeVoe et al. 2015), the relatively high slope angle helped to reduce collinearity with slope (Lowrey et al. 2018). We expected all models to indicate a positive relationship with moderate or high values of slope and ruggedness and a negative relationship with distance to steep terrain. We expected to observe a seasonal response to elevation for migrants with positive selection in summer and negative selection in winter and a negative relationship with elevation for residents in both seasons, resulting from their annual use of relatively low-elevation areas (Poole et al. 2016, Lowrey et al. 2018).

Vegetation covariates included canopy cover (COV) and normalized difference vegetation index amplitude (NDVI$_{Amp}$; Table 1). Canopy cover was sourced from the 2011 National Land Cover Database (Homer et al. 2015) and represented areas that bighorn sheep may avoid because of reduced visibility (Smith et al. 1991, Johnson and Swift 2000). NDVI amplitude was derived from 8-d surface reflectance images with 250 m resolution from moderate resolution imaging spectroradiometer (MODIS) Terra satellites (MODIS product MOD09Q1) and indexed the mean difference between the max NDVI and the baseline at the beginning of the growing season from 2012 to 2018. Although various NDVI metrics are commonly included in ungulate habitat models to represent forage and have shown a positive relationship for bighorn sheep (Pettorelli et al. 2007, Hoglander et al. 2015), the relationships are inconsistent. For example, multiple studies have documented bighorn sheep and other mountain ungulates avoiding higher NDVI values (Lowrey et al. 2017, 2018, Lula et al. 2020). While forage is an important component of bighorn sheep habitat, the relationship may be masked by strong selection for steep and rugged slopes at broad spatial scales, which are characteristically rocky and have relatively low NDVI values (Lowrey et al. 2017). Following regional work in the northern Rocky Mountains, we predicted that both resident and migrant populations would have a negative relationship with NDVI$_{Amp}$ in both seasons.

To characterize heat load, we transformed aspect into a biologically interpretable covariate by taking the inverse cosine of the angle −35° (Table 1; ASP; Cushman and Wallin 2002). This transformation changed the axis from north-south to north-northeast–south-southwest and ranged from −1 to 1, respectively. We predicted both migrant and resident populations would select for relatively warm aspects in winter and relatively cool aspects in summer. Lastly, we used annual accumulated snow water equivalent (SWE; NOHRSC 2004) from 2012 to 2018 to calculate mean SWE, which served as an index of winter severity. We predicted both migrant and resident populations would have a negative relationship with SWE in winter.

While covariate functional forms were largely assumed to be linear, we included quadratic forms of elevation and slope, allowing selection for these resources to peak at intermediate values, and a pseudothreshold (natural log) form for slope variance, allowing selection for rugged terrain to asymptote at a threshold value (Table 1). These functional forms consistently outperform linear forms of the same covariate when used in bighorn sheep or other mountain ungulate habitat models (Gross et al. 2002, DeVoe et al. 2015, Poole et al. 2016, Lowrey et al. 2017, 2018, Lula et al. 2020).

Statistical framework, model selection, and model validation

For all models, we employed a used-available design (i.e., Design II; Manly et al. 2002) where values associated with individual GPS locations represented the used set and availability was sampled from pixel values associated with random locations that were cast using a 1:10 (used:available) ratio within population annual ranges. The 1:10 ratio ensured a sufficient sample to avoid numerical integration error and convergence issues within the mixed-model framework (Northrup et al. 2013). Annual ranges were defined using a minimum convex polygon (MCP)

which we buffered by 2.5 km, the 95% distribution quantile of all individual daily step lengths between a single randomly selected location for each day. We identified individuals nested within populations as the sample unit and accounted for the autocorrelation within each group (e.g., population and individual) and unbalanced sample size among groups by specifying a random intercept for each population and individual (Fieberg et al. 2010, Rayl et al. 2019). We fit generalized linear mixed-effect models with an inverse link function and scaled and centered the covariates using the mean and one standard deviation (Gillies et al. 2006, Fieberg et al. 2010).

We evaluated aspect, canopy cover, distance to steep terrain, elevation, slope, and slope variance in all models and included $NDVI_{Amp}$ in summer and SWE in winter. When two or more covariates were collinear (i.e., $r > |0.7|$), we used an information criteria (AIC) to select a single covariate using univariate models (Burnham and Anderson 2002). When fitting univariate models, we pooled data for residents and migrants within a season in order to have the same covariate structure when fitting the full models separately for each behavior. We validated the final behavior-specific models using a modified k-fold cross-validation where k indexed a population rather than a random data fold (Boyce et al. 2002, Ranglack et al. 2017). More specifically, for each behavior-specific model we used an iterative process to withhold the locations for all individuals in a population, 1 through k, fit an exponential resource selection function (RSF) with the populations that were retained, and then predicted the fitted values for the observations that were withheld. We then summed the occurrence of used locations within 10 equal-area RSF bins and evaluated the correlation between the frequency of occurrence and the relative RSF score using the Spearman's rank correlation (Boyce et al. 2002). This approach allowed us to evaluate predictive performance across populations for each model.

Spatial predictions and validation

To better understand our limitations in predicting the behavior-specific models across the montane areas of western Montana, we first evaluated the similarities between the covariate conditions within the study area and the prediction area for both resident and migrant populations

(Appendix S3). Because of the relatively small sample of resident populations ($N = 2$) and their limited distribution, we were unable to spatially predict the resident seasonal models due to the narrow distribution of covariate values relative to the broad prediction area (Appendix S3). For the seasonal migrant models, we generated predictions using the exponential RSF:

$$\hat{w}(x) = \exp\left(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \ldots + \hat{\beta}_n x_n\right) \qquad (1)$$

where β's are the coefficients of the effects of the covariates and X_i, on $\hat{w}(x)$, the relative probability of selection. Within the prediction area, we defined our inference space as the areas within the range of covariate values used in model building, yet also provide predictions for areas beyond the range of observed data (Appendix S3). While the majority of areas outside of the observed data range were not occupied by bighorn sheep or generally considered bighorn sheep habitat, we urge caution in interpreting predictions in areas characterized by covariate values beyond those observed in the study areas (Appendix S3).

We performed two independent validations of our predictions of the seasonal migrant models. First, because we were unable to spatially predict the resident seasonal models, we performed a cross-validation of the winter migrant model with the resident annual used GPS locations. This approach allowed us to quantify the correlation between the migrant winter model and annual resident use. We were specifically interested in the winter migrant model because of the potential similarities between migrant selection patterns during winter and the annual patterns of residents, which often share low-elevation ranges. Similar to the methods of Boyce et al. (2002), we extracted the migrant winter model predictions to resident annual locations, summed the number of points in each RSF bin (1–10), and used the Spearman rank correlation coefficient to assess correlation between the migrant winter predictions and annual resident use.

Second, we used seasonal bighorn sheep distribution polygons generated from expert opinion (Appendix S4) to validate the migrant predictions. More specifically, for each seasonal range polygon within the prediction area, we summed the number of each RSF bin (1–10) and used the

Spearman rank correlation coefficient to assess the correlation between the frequency of occurrence and each RSF bin. Following Boyce et al. (2002), our expectation was that we would observe a larger proportion of high bin values in each polygon if the model performed well. However, model performance was also influenced by the accuracy of the generalized distribution polygons, which varied by season. For example, while winter polygons were often well defined and covered specific core areas, summer polygons were broad and encompassed large areas of diverse landscapes that were suspected summer range (Appendix S4). Because of the broad and varied nature of bighorn sheep summer range (Lowrey et al. 2018), we expected to observe better predictive performance within the relatively confined winter polygons when compared to summer.

Model management application scenarios

We demonstrated two examples of how the model predictions could be used to inform bighorn sheep translocations with the purposes of (1) establishing a new population within unoccupied historic range and (2) expanding the distribution of existing populations through within-mountain range translocations. For the first example, we focused on the restoration of bighorn sheep in the Tendoy Mountains in southwest Montana. After the historic native population was extirpated, bighorn sheep were restored with multiple translocations totaling 53 individuals in the mid-1980s. The restored population experienced multiple die-offs associated with both lungworm and pneumonia, resulting in poor demographic performance and low success of continued translocation efforts (Montana Fish, Wildlife and Parks 2010). In response, the state wildlife management agency depopulated the Tendoy population and plans to restore the range with animals that are free of respiratory pathogens. We used the model predictions of relative habitat quality in the Tendoy Mountains to (1) identify areas with a relatively high probability of translocation success based on landscape characteristics and (2) identify the most appropriate migratory behavior(s) to target as a source population that best matches the landscape attributes of the Tendoy Mountains.

The second example explored the potential to expand current distributions of bighorn sheep through short-distance translocations from a single population to unoccupied, adjacent areas in the same mountain range. This approach can be an effective translocation strategy to promote a broader distribution of bighorn sheep with spatially structured subpopulations that may interact throughout the year but also occupy distinct seasonal ranges (Bleich et al. 1996, Singer et al. 2000a). These intra-mountain translocations have reduced risk of introducing novel pathogens or pathogen strains and have shown positive results in California and Montana bighorn sheep restoration programs, but require habitat near or adjacent to extant populations (Epps et al. 2010, Montana Fish, Wildlife and Parks 2013). We characterized bighorn sheep habitat, as indexed by the RSF bin values, adjacent to extant populations in western Montana by summing the frequency of each RSF bin value within a 15 km buffer surrounding (but not including) each seasonal polygon. The 15 km distance represented the 95th quantile of Euclidean distances between individual seasonal range centroids (Lowrey et al. 2019) and provided a buffer distance derived from movement data. In this scenario, we used the model predictions of relative habitat quality to (1) evaluate the potential for broad implementation of intra-mountain translocations across western Montana and (2) identify and discuss existing populations that provided examples of possible restoration scenarios with abundant habitat adjacent to winter and summer ranges, abundant habitat adjacent to only the winter range, or little habitat adjacent to both seasonal ranges.

We performed data processing and analyses using the sf (Pebesma 2018), raster (Hijmans 2017), tidyverse (Wickham 2017), and lme4 (Bates et al. 2015) packages in the R environment for statistical computing (R Core Team 2019).

Results

We monitored 194 female bighorn sheep across eight study populations with an average of 24 individuals (range = 10–52) in each population. Individuals were monitored for an average of 488 (SD = 231) d. We obtained a total of 518,748

GPS locations with an average of 2674 (SD = 1586) locations collected from each individual.

Elevation and SWE were highly collinear in winter (r = 0.80), with SWE being top ranked when competing univariate models of the two covariates (ΔAIC_c = 63,347.38). The final winter model for both migrants and residents contained aspect, canopy cover, distance to steep terrain, slope, slope variance, and SWE. Collinearity was not a concern (i.e., $r < 0.5$) in summer where the final model for both migrants and residents contained aspect, canopy cover, distance to steep terrain, elevation, slope, slope variance, and $NDVI_{Amp}$.

Although there were differences in strength of selection, specifically in summer, selection patterns were generally similar among migrants and residents within each season Fig.2). The notable exception was elevation in summer, where residents selected for low elevations while migrants selected for relatively high elevations, as expected. This was the strongest difference between the two migratory behaviors and the only covariate for which migrants and residents had an opposite direction of selection. The strength of the negative association with canopy cover and distance to steep terrain was similar across both migratory behaviors and seasons. In winter, both migrants and residents selected for relatively warm south-southwest aspects, while the relationship with aspect was negligible to slightly positive (i.e., selection for cool north-northwest aspects) for residents and migrants in summer, respectively. As predicted, we observed a negative relationship with $NDVI_{Amp}$ for both migrants and residents, although there was variation in the strength of avoidance, which was stronger for residents than for migrants. All behaviors selected relatively rugged and steep slopes but varied in the optimal slope angle which was less steep in winter than in summer (winter migrants = 48°, winter residents = 42°, summer migrants = 64°, summer residents = 58°). Both residents and migrants avoided high SWE in winter.

The interpolations within the study areas validated well for all models using k-folds cross-validation. The average Spearman's rank correlation among the model validations was 0.99 (SD = 0.01) and 0.95 (SD = 0.07) for migrants and resident in summer, respectively, and 0.97 (SD = 0.02) and 0.99 (SD = 0.002) for migrants and residents in winter, respectively. Additionally, the winter migrant model was strongly correlated with resident annual use for both Petty Creek (r = 0.96) and Paradise (r = 0.70) populations, with >95% of the used resident annual locations within the highest ranked habitat (i.e., bin 10) of the migrant winter model. There were mixed results when validating the seasonal migrant predictions with the general bighorn sheep distribution polygons (Appendix S4). In winter, we observed strong correlation with an average Spearman's rank correlation coefficient of r = 0.75 (SD = 0.47) among all winter polygons, and an average of 61% (SD = 33%) of each polygon was associated with relatively good habitat quality with an RSF bin value ≥ 9. In contrast, the summer model validation was low with an average Spearman's rank correlation coefficient of r = 0.52 (SD = 0.49) among all summer polygons, and an average of 32% (SD = 28%) of each polygon was associated with relatively good habitat quality with an RSF bin value ≥ 9. For both seasons, there was a wide range of variation in model performance among the seasonal polygons (Appendix S4).

Throughout the prediction area, bighorn sheep habitat was centered around mountainous areas in all seasons Fig.3). Habitat for migrants in summer was broadly distributed across rugged and steep areas at high elevations. Winter migrant and resident habitat were broadly dispersed throughout the prediction area at mid- to low elevations proximal to steep and rugged slopes.

Model management application scenarios

Our predictions within the Tendoy Mountain restoration area indicated widespread seasonal habitat with relatively large percentages of preferred habitat areas associated with high RSF bin values for both seasons Fig.4). We identified winter ranges within the northern, central, and southern parts of the restoration area which could be used as release sites to place animals into the highest quality habitat. Each of these potential wintering areas was adjacent to high-quality summer habitat in the high mountain areas. Given the broad expanses of seasonal habitat for migrants, sourcing individuals from migrant populations would be appropriate for
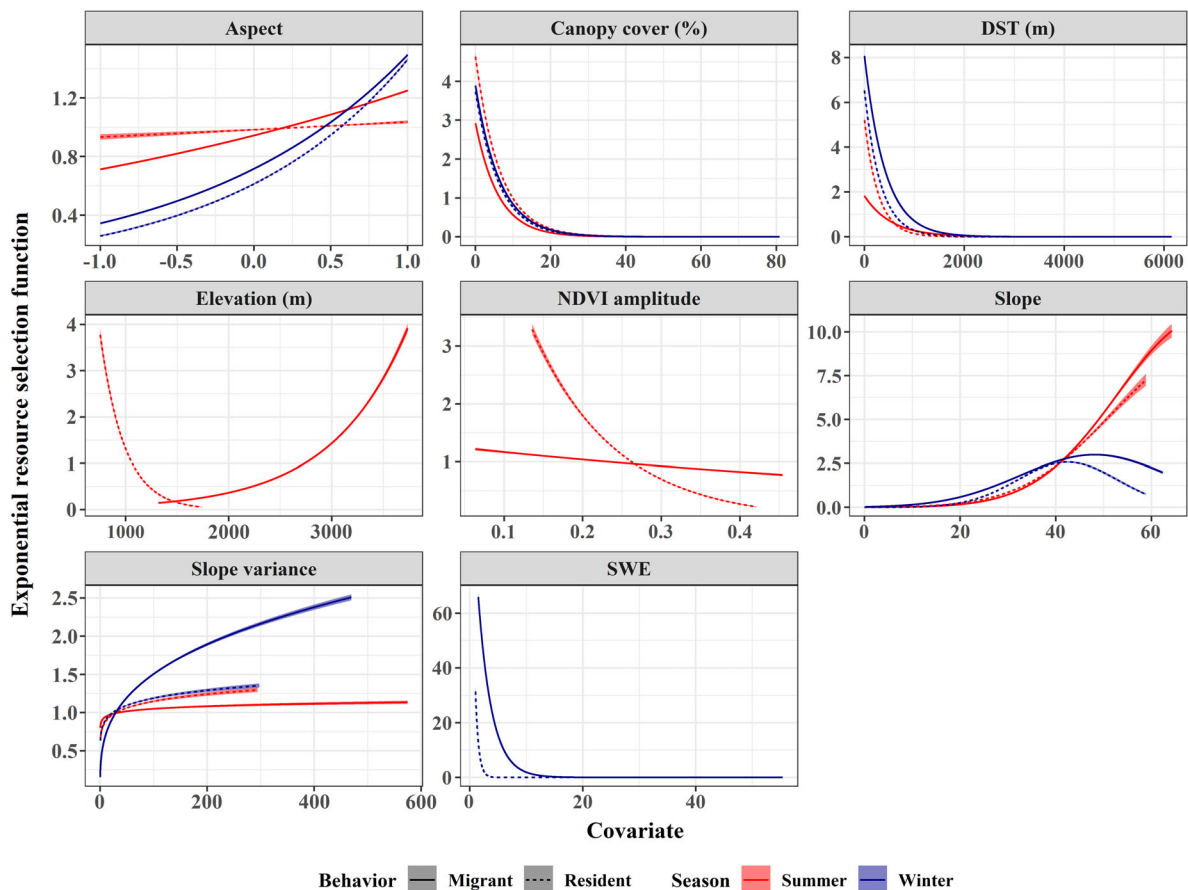
Fig. 2. Prediction plots showing the relationship with the exponential resource selection function (±95% CI) for the seasonal behavior-specific habitat models (summer, red; winter, blue; migrant, solid line; and resident, dashed line) developed for female bighorn sheep, western Montana, USA, 2012–2018. DST, distance to steep terrain and SWE, snow water equivalent.

future translocations. Additionally, because of the strong correlation between migrant selection patterns in winter and resident annual use, resident individuals could also be considered in future translocation efforts.

Our characterization of bighorn sheep habitat adjacent to extant populations in western Montana generally indicated a positive relationship between the RSF bin values and their relative abundance surrounding the extant populations Fig.5). Although the proportion of each bin value was relatively small and did not exceed 15% on average for any single bin, there was a larger proportion of relatively high RSF bin values within the 15 km buffer surrounding existing populations, indicating a larger proportion of

preferred habitat areas. Across the extant populations, many showed potential for intra-mountain translocations to expand the current distribution, while for others, this restoration strategy would not be recommended because our models predicted little habitat adjacent the current populations (Appendix S5). For some populations, over 25% of the area adjacent to both summer and winter ranges was classified as bin 10 indicating high restoration potential through intra-mountain translocations and broad possibilities for range expansion on both summer and winter ranges. For example, the summer and winter range of the Stillwater population and winter range of the Beartooth WMA population were embedded within a broad distribution of

bighorn sheep habitat Fig.6; Appendix S5). For other populations, for example, Ural Tweed in northwest Montana, there was relatively little habitat adjacent to the existing distribution of animals.

DISCUSSION

We developed habitat models for migratory and resident bighorn sheep to understand differences in selection patterns between resident and migrant population segments and demonstrated applications for informing future translocation efforts throughout the montane areas of western Montana. We observed similar selection patterns for residents and migrants during the winter period when animals expressing each of the behaviors predominantly used mid- to low-elevation areas proximal to steep and rugged terrain. Selection patterns were more variable in summer with differential selection for elevation. While residents tended to remain within rugged areas at relatively low elevations for the summer months, migrants traveled to high elevations, yet continued to select steep and rugged areas on their high-elevation summer ranges. Although both residents and migrants selected for similar landscape attributes with respect to terrain, they were doing so at different elevations. Given the similarity in winter selection patterns between the two behaviors, the traditional methods of aggregating residents and migrants in habitat model development would likely have produced similar models as the behavior-specific approach. However, aggregating residents and migrants in summer habitat model development would have obscured the behavior-specific relationship with elevation and missed the specific habitat characteristics of each migratory behavior (Appendix S6).

Combining the behavior-specific approach with a broad GPS dataset, our models provided several improvements over the existing habitat models available in Montana. Our models (1) provide separate summer and winter habitat predictions, (2) were constructed with a large sample of GPS locations from collared individuals as opposed to management data collected from annual surveys, and (3) were validated using multiple methods and data sources that span western Montana. When paired with other

habitat models for bighorn sheep throughout the state, there is now a state-wide habitat map to help inform restoration in both mountain and prairie (DeVoe et al. 2020) regions of Montana. Additionally, the behavior-specific approach allows managers to match the migratory behavior of source populations with landscape characteristics of the area being restored. In the Tendoy Mountain scenario, our models indicated that both resident and migrant source populations are appropriate for translocation given the predicted habitat available. This gives managers increased versatility in identifying a source population and could potentially allow managers to introduce both resident and migrant animals to increase migratory diversity in restored populations (Lowrey et al. 2020).

As an alternative to starting new populations, previous work in the Madison Range of southwest Montana indicated that the availability of adjacent habitat does not constrain bighorn sheep restoration (Lula et al. 2020). As a result, the state wildlife agency has been conducting a multi-year intra-mountain translocation to assist the expansion of bighorn sheep northward to areas identified as habitat but that have remained unoccupied (Montana Fish, Wildlife and Parks 2013). By characterizing unoccupied areas that are adjacent to the known distribution of bighorn sheep across western Montana, our work expanded on Lula et al. (2020) in evaluating the potential of habitat to limit bighorn sheep distributions more broadly across the state. We observed a larger proportion of preferred habitat areas, as indexed by the relative RSF bin values, within the 15 km buffer surrounding many existing populations and suggest there is broad restoration potential through intra-mountain translocations. Nonetheless, our intent with this restoration scenario was to broadly characterize the potential for implementing the intra-mountain translocation approach across western Montana using the RSF values within the 15 km buffer as a standard index of relative habitat quality across all populations. As a result, our interpretations are specific to the areas within the 15 km buffer of existing populations. While the buffer approach enabled us to generally characterize the surrounding landscape, it may not adequately capture the broader
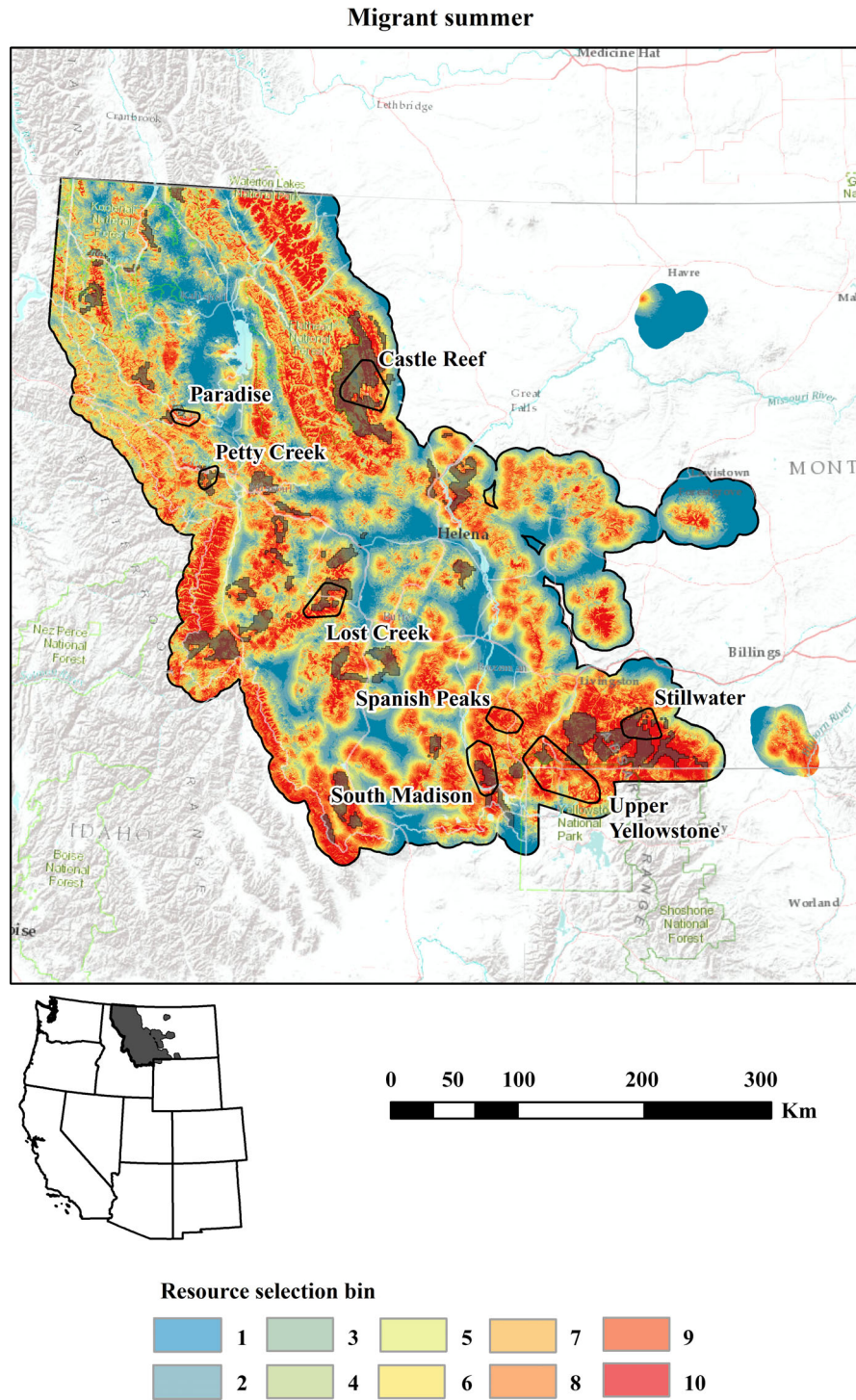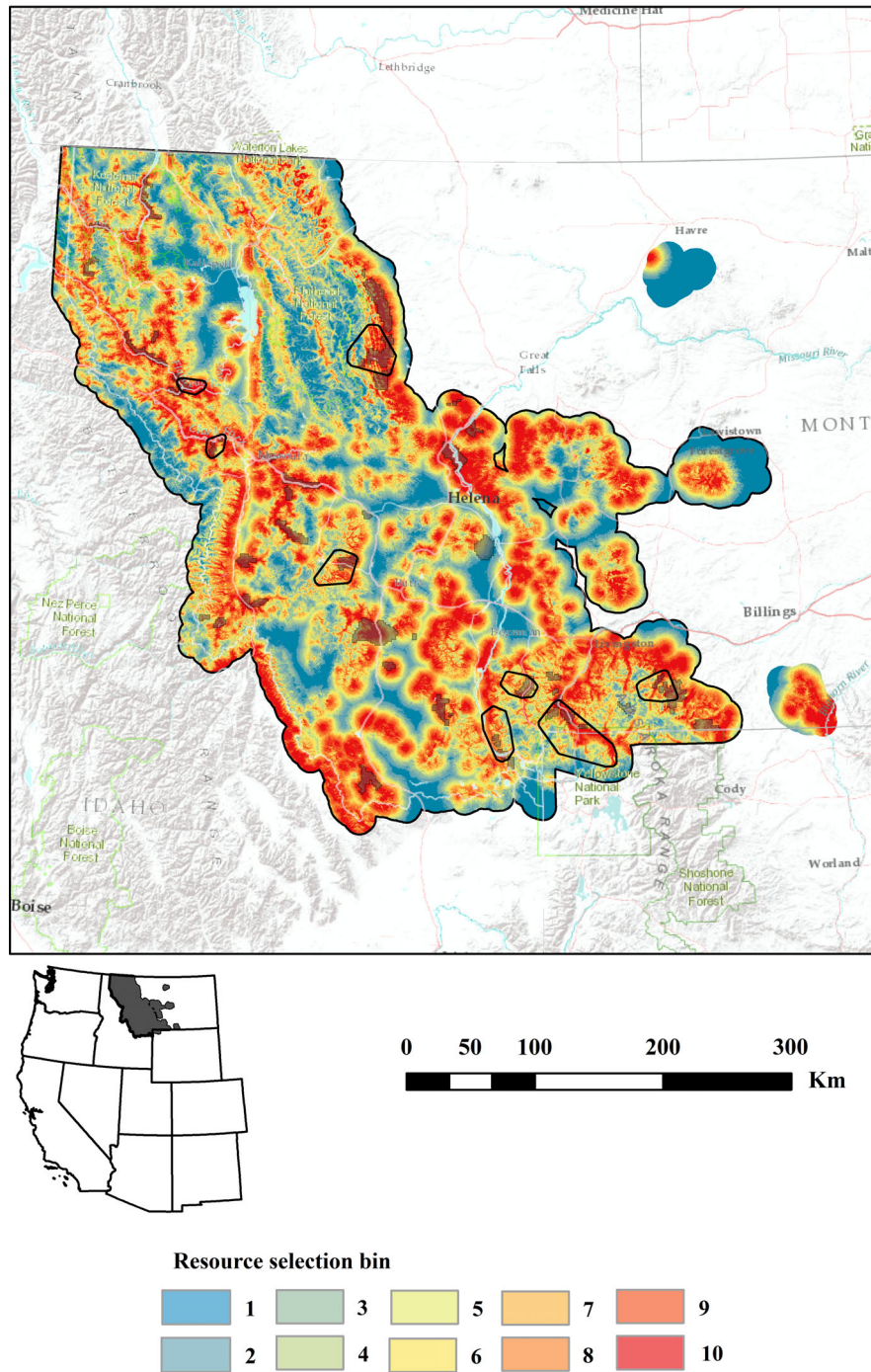
Migrant summer

Fig. 3. Seasonal resource selection model predictions for migratory bighorn sheep, which in winter also characterizes resident annual use, western Montana, 2012–2018. Resource selection bins are numbered 1–10 (blue–red). The population annual minimum convex polygons (black) are shown as are the generalized expert opinion bighorn sheep seasonal ranges (dark gray).

Migrant winter and resident annual

Resource selection bin

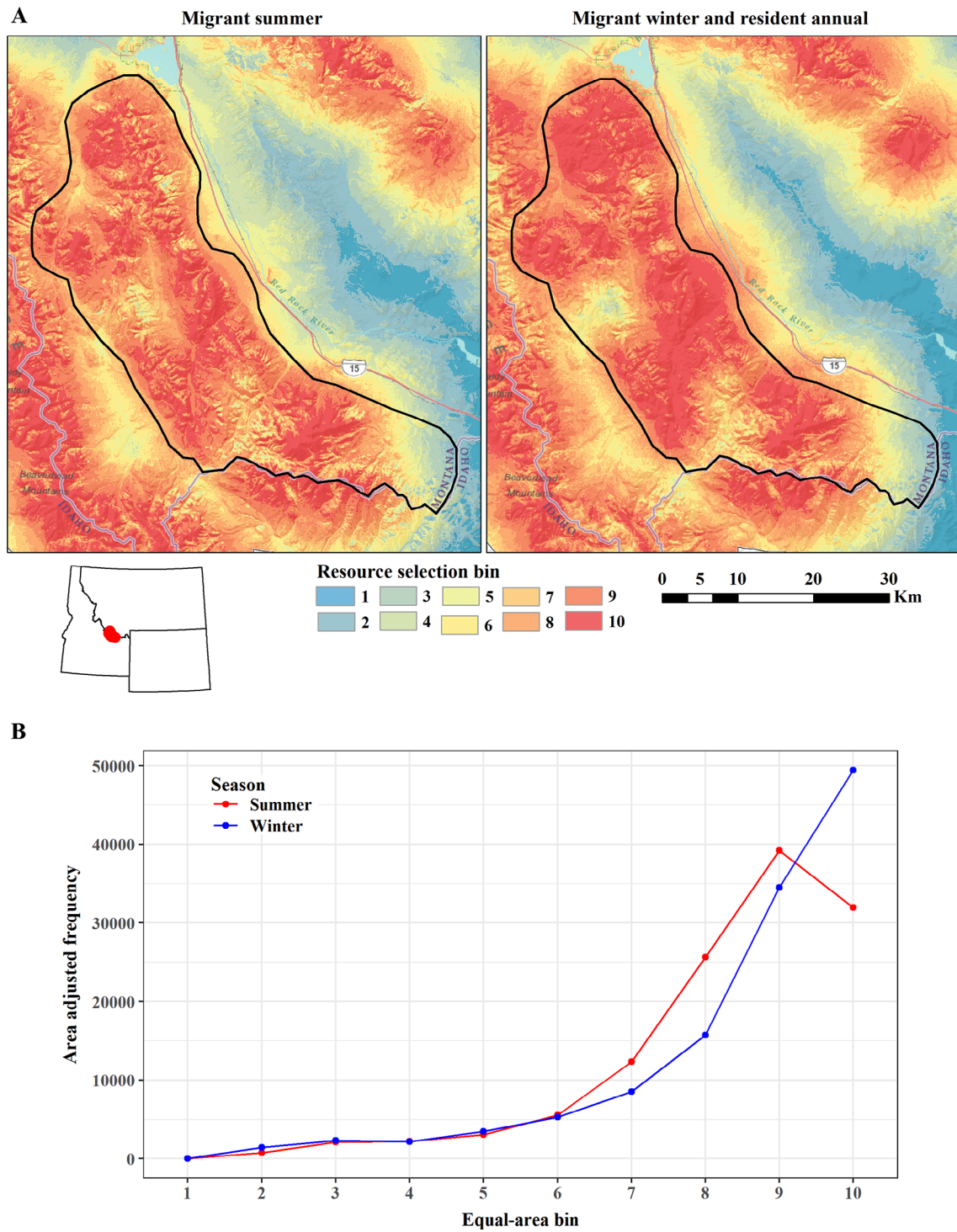|					
▢ 1	▢ 3	▢ 5	▢ 7	▢ 9
▢ 2	▢ 4	▢ 6	▢ 8	▢ 10

(Fig. 3. *Continued*)

A

Fig. 4. (A) Summer and winter migrant model predictions in the Tendoy Mountains, southwest Montana, USA, 2012–2018. Because of the strong correlation between winter selection of migrants and resident annual use, we interpreted the winter model for both migrants in winter and residents annually. (B) The frequency of occurrence of RSF bin values from the seasonal migrant models predicted across the Tendoy Mountains.
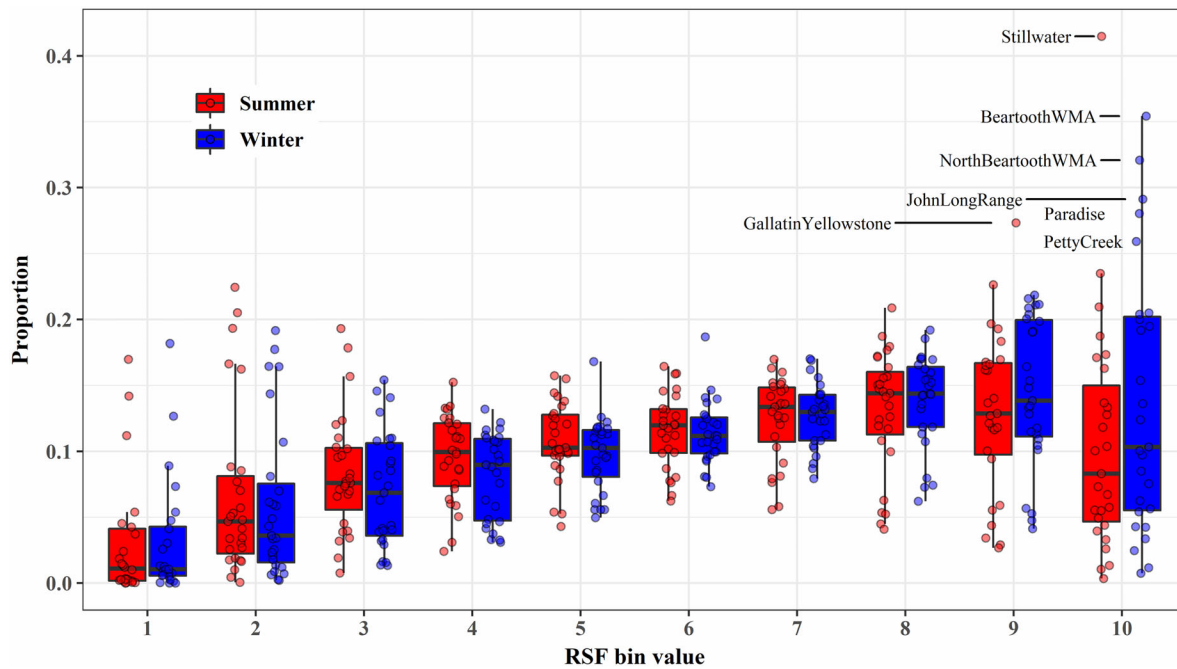
Fig. 5. Boxplots (and raw data points) summarizing the seasonal distribution of the proportion of each RSF bin within the 15 km buffer surrounding the general bighorn sheep distribution polygons. The points with a proportion >0.25 are labeled with the population name for reference.

landscape where restorations could occur, for example, in the Stillwater population example (Fig. 6). We encourage local working groups to further evaluate the restoration potential of these areas beyond the 15 km buffer distance included in our analysis.

Our work was conducted with both resident and migrant populations with little variation among individuals within a population (Appendix S2). Recent work however has highlighted the diversity of migratory behaviors and that a single ungulate population can contain residents as well as short-, mid-, and long-distance migrants (Cagnacci et al. 2011, Sawyer et al. 2016, Barker et al. 2019, Lowrey et al. 2020). Moreover, residency, which occurred exclusively on low elevations in our study populations, can also occur at high elevations where bighorn sheep remain at elevations ≥3000 m annually (Courtemanch et al. 2017, Spitz et al. 2020). The relative lack of intraspecific migratory diversity in our study populations likely minimized the differences in selection between the resident and migrant behaviors. Expanding from our binary

comparisons between residents and migrants, the behavior-specific modeling approach we used can be applied to populations with diverse migratory portfolios to better understand potential differences in selection patterns among individuals with varying migratory behaviors. In particular, models of high-elevation winter or resident ranges may help to restore bighorn sheep into these historic ranges where there is reduced risk of overlap with domestic livestock and associated deleterious pathogens (Wyoming Game and Fish Department 1980, Lowrey et al. 2020).

The purpose of our study was to implement a behavior-specific approach to developing and predicting habitat models that could inform future translocation across western Montana. While the difference in selection with respect to elevation for residents and migrants was expected, the behavior-specific approach provided a framework for explicitly modeling differences in selection between the two migratory behaviors. In our study, incorporating the behavior-specific relationships resulted in
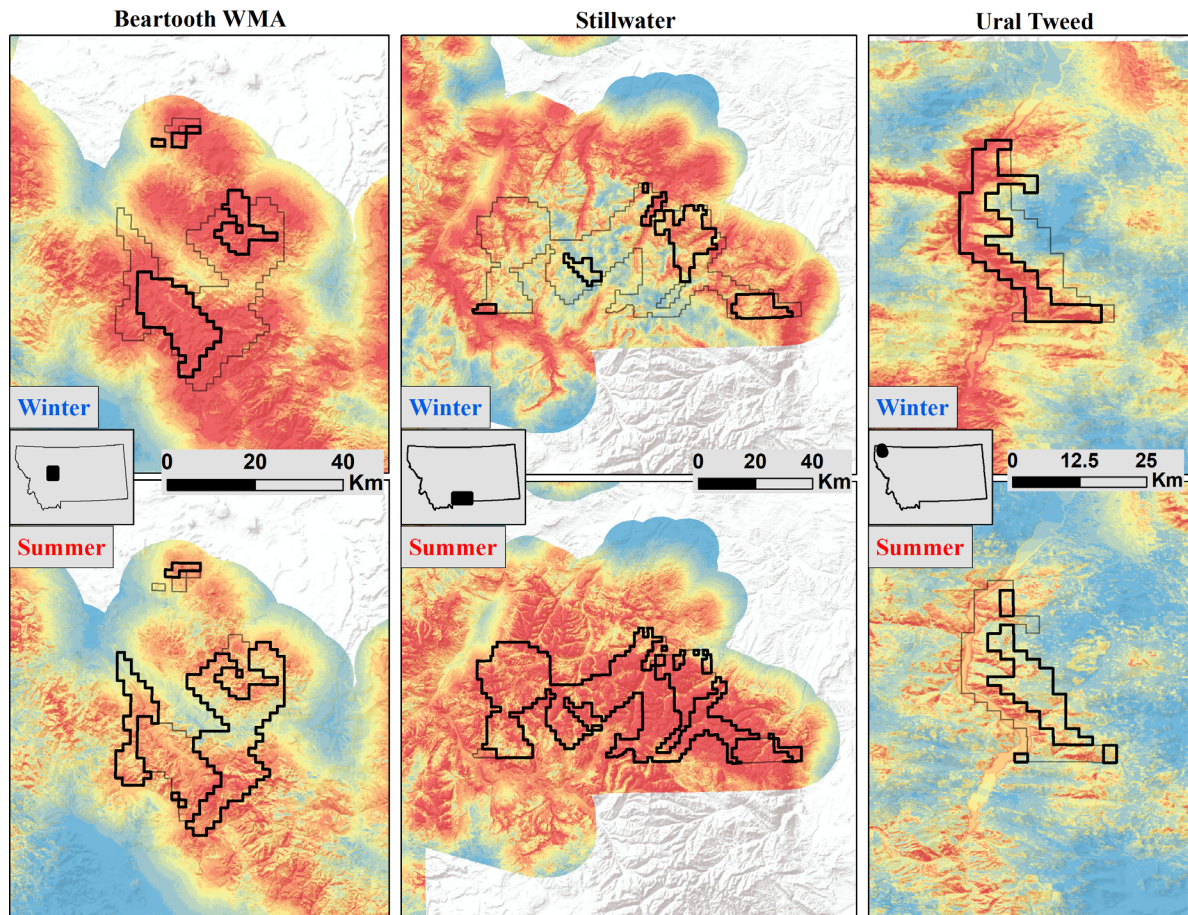
Fig. 6. Seasonal model predictions for three example extant populations in which there was predicted habitat beyond the winter range (Beartooth WMA), beyond both seasonal ranges (Stillwater), and relatively limited adjacent habitat (Ural Tweed). For each population, the top and bottom panels represent winter and summer, respectively. Both winter and summer ranges are shown in all panels but are in bold for the respective season. Note the different scale for the Ural Tweed population.

models with additional biological relevance and utility in informing future translocation, for example, enabling managers to match the migratory behavior of source populations with the landscape attributes of the area being restored. Just as generating sex-, age-, or season-specific models is common practice in wildlife research, our study extends these principles to generating models for population components with unique migratory behaviors where selection patterns vary among individuals. While evaluating the need for multiple habitat models for different migratory behaviors may not always result in behavior-specific models, such evaluations are

an important aspect of the modeling approach with broad implications for ecology, conservation, and management.

Within the broad context of our study, we were unable to incorporate local factors which can influence habitat selection behaviors and translocation success. For example, areas with low predator densities are often prioritized as translocation sites as predation can negatively impact translocation success (Rominger et al. 2004, Frair et al. 2007). Although predators can have important local influences, the dynamics are complex and often involve additional domestic or wildlife species through apparent

competition (Rominger et al. 2004, Johnson et al. 2013). As a result, the effects of predator populations and the responses by their ungulate prey are highly variable (Elbroch and Wittmer 2013) and unable to be captured in a broad spatial covariate. The broad nature of our work may have also missed some of the more nuanced relationships with NDVI, which are varied for mountain ungulates regionally (Lowrey et al. 2017). More targeted research on the role of local landscape features (i.e., geology and canopy cover) on the NDVI signal would help to better define bighorn sheep's association with NDVI when used as an index of forage.

Disease is an additional important factor to consider in animal translocation (Woodford and Rossiter 1994, Singer et al. 2000*a*). For bighorn sheep, mitigating the effects of disease often follows a policy of separating bighorn sheep from domestic sheep and not translocating bighorn sheep within a threshold distance of known domestic sheep allotments or smaller hobby flocks (Singer et al. 2000*c*, Montana Fish, Wildlife and Parks 2010, Wild Sheep Working Group 2012, U.S. Forest Service 2015). Accurate data on domestic livestock densities and distribution are not available across western Montana and in particular for private lands, where domestic livestock distribution can be more dynamic. Consequently, we were unable to evaluate the effect of domestic sheep on habitat availability throughout the prediction area based on current separation distance policies. Recognizing the importance of local knowledge regarding the distribution of domestic sheep and other factors which we were unable to incorporate into the broad analysis (i.e., access, local politics, or public opinion), our habitat models are intended to serve as a tool to be used in combination with local knowledge and resources to guide specific translocation projects.

Although many species have greatly benefited from the use of translocations, the successes are not ubiquitous. Bighorn sheep have struggled to rebound to historic numbers and distributions after nearly a century of concerted restoration effort (Buechner 1960, Gross et al. 2000). The use of bighorn sheep translocations as a management tool has been widespread, resulting in nearly 1500 restoration and augmentation efforts and the translocation of more than 21,500 bighorn sheep throughout North America (Brewer et al. 2014).

Although these efforts have been foundational in the historic successes over the last century, alternative translocation practices may be needed to bolster existing bighorn sheep populations and establish new populations throughout their historic range. More broadly, as climate and anthropogenic disturbance continue to place an increasing strain on wildlife populations, the need for translocations will continue to increase (Thomas 2011, IUCN/SSC 2013). The behavior-specific approach builds from the existing tools, yet provides enhanced utility in the ability to compare selection patterns among migratory behaviors of partially migratory species, evaluate the need for multiple behavior-specific habitat models, and match source population migratory behavior with the landscape attributes of the area being restored. As the need for translocations increases across taxa, novel tools and practices will help to ensure that the efficacy of translocations meets the growing demand for their implementation.

ACKNOWLEDGMENTS

LITERATURE CITED

Barker, K. J., M. S. Mitchell, and K. M. Proffitt. 2019. Native forage mediates influence of irrigated agriculture on migratory behavior of elk. Journal of Animal Ecology 88:1100–1110.

Barker, K. J., M. S. Mitchell, K. M. Proffitt, and J. D. DeVoe. 2018. Land management alters traditional nutritional benefits of migration for elk. Journal of Wildlife Management 83:167–174.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, G. Grothendieck, and P. Green. 2015. lme4: linear mixed-effects models using "Eigen" and S4. Journal of Statistical Software 67:1–48.

Batson, W. G., I. J. Gordon, D. B. Fletcher, and A. D. Manning. 2015. Translocation tactics: a framework to

support the IUCN guidelines for wildlife translocations and improve the quality of applied methods. Journal of Applied Ecology 52:1598–1607.

Bleich, V. C., J. D. Wehausen, R. R. Ramey, and J. L. Rechel. 1996. Metapopulation theory and mountain sheep: implication for conservation. Pages 353–373 *in* D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington, D.C., USA.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology & Evolution 14:268–272.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Brewer, C. E., V. C. Bleich, J. A. Foster, T. Hosch-Hebdon, D. E. McWhirter, E. M. Rominger, M. W. Wagner, and B. P. Wiedmann. 2014. Bighorn sheep: conservation challenges and management strategies for the 21st century. Wild Sheep Working Group, Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. Wildlife Monographs 4:3–174.

Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, Heidelberg, Germany.

Cagnacci, F., et al. 2011. Partial migration in roe deer: Migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790–1802.

Chapman, B. B., C. Brönmark, J.-Å. Nilsson, and L.-A. Hansson. 2011. The ecology and evolution of partial migration. Oikos 120:1764–1775.

Cianfrani, C., G. Le Lay, A. H. Hirzel, and A. Loy. 2010. Do habitat suitability models reliably predict the recovery areas of threatened species? Journal of Applied Ecology 47:421–430.

Couey, F. M. 1950. Rocky Mountain bighorn sheep of Montana. Bulletin No. 2, Montana Fish and Game Commission, Helena, Montana, USA.

Courtemanch, A. B., M. J. Kauffman, S. Kilpatrick, and S. R. Dewey. 2017. Alternative foraging strategies enable a mountain ungulate to persist after migration loss. Ecosphere 8:1–16.

Cushman, S. A., and D. O. Wallin. 2002. Separating the effects of environmental, spatial and disturbance factors on forest community structure in the

Russian Far East. Forest Ecology and Management 168:201–215.

DeCesare, N. J., and D. H. Pletscher. 2006. Movements, connectivity, and resource selection of Rocky Mountain bighorn sheep. Journal of Mammalogy 87:531–538.

D'eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383–388.

DeVoe, J. D., R. A. Garrott, J. J. Rotella, S. R. Challender, P. J. White, M. O'Reilly, and C. J. Butler. 2015. Summer range occupancy modeling of non-native mountain goats in the greater Yellowstone area. Ecosphere 6:1–20.

DeVoe, J. D., B. Lowrey, K. M. Proffitt, and R. A. Garrott. 2020. Restoration potential of bighorn sheep in a prairie region. Journal of Wildlife Management 84:1256–1267.

Duka, T., and P. Masters. 2005. Confronting a tough issue: fertility control and translocation for overabundant koalas on Kangaroo Island, South Australia. Ecological Management & Restoration 6:172–181.

Elbroch, L. M., and H. U. Wittmer. 2013. The effects of puma prey selection and specialization on less abundant prey in Patagonia. Journal of Mammalogy 94:259–268.

Epps, C. W., J. D. Wehausen, P. J. Palsbøll, and D. R. McCullough. 2010. Using genetic tools to track desert bighorn sheep colonizations. Journal of Wildlife Management 74:522–531.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:2233–2244.

Frair, J. L., E. H. Merrill, J. R. Allen, and M. S. Boyce. 2007. Know thy enemy: Experience affects elk translocation success in risky landscapes. Journal of Wildlife Management 71:541–554.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals: random effects in resource selection. Journal of Animal Ecology 75:887–898.

Gilroy, J. J., J. A. Gill, S. H. M. Butchart, V. R. Jones, and A. M. A. Franco. 2016. Migratory diversity predicts population declines in birds. Ecology Letters 19:308–317.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477–480.

Gross, J. E., M. C. Kneeland, D. F. Reed, and R. M. Reich. 2002. GIS-based habitat models for mountain goats. Journal of Mammalogy 83:218–228.

Gross, J. E., F. J. Singer, and M. E. Moses. 2000. Effects of disease, dispersal, and area on bighorn sheep restoration. Restoration Ecology 8:25–37.

Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

Hebblewhite, M., and E. H. Merrill. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. Oikos 120:1860–1870.

Hedrick, P. W., and R. Fredrickson. 2010. Genetic rescue guidelines with examples from Mexican wolves and Florida panthers. Conservation Genetics 11:615–626.

Hijmans, R. J. 2017. raster: geographic data analysis and modeling. R package version 2.6-7. https://CRAN.R-project.org/package=raster

Hoglander, C., B. G. Dickson, S. S. Rosenstock, and J. J. Anderson. 2015. Landscape models of space use by desert bighorn sheep in the Sonoran Desert of southwestern Arizona. Journal of Wildlife Management 79:77–91.

Homer, C., J. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. Herold, J. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States–representing a decade of land cover change information. Photogrammetric Engineering & Remote Sensing 81:345–354.

IUCN/SSC. 2013. Guidelines for reintroductions and other conservation translocations. IUCN Species Survival Commission, Gland, Switzerland.

Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. Journal of Wildlife Management 64:685–697.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. Mcdonald, and M. S. Boyce. 2006. Resource selection functions based on use–availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Johnson, H. E., M. Hebblewhite, T. R. Stephenson, D. W. German, B. M. Pierce, and V. C. Bleich. 2013. Evaluating apparent competition in limiting the recovery of an endangered ungulate. Oecologia 171:295–307.

Johnson, T. L., and D. M. Swift. 2000. A test of a habitat evaluation procedure for rocky mountain bighorn sheep. Restoration Ecology 8:47–56.

Kallman, H., C. R. Agee, W. R. Goforth, and J. P. Lin-Duska, editors. 1987. Restoring Americas wildlife 1937–1987: the first 50 years of the federal aid in wildlife restoration (Pittman-Robertson) act. U.S. Government Printing Office, Washington, D.C., USA.

Komers, P. E., and G. P. Curman. 2000. The effect of demographic characteristics on the success of ungulate re-introductions. Biological Conservation 93:187–193.

Latham, A. D. M., M. C. Latham, and M. S. Boyce. 2011. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. Canadian Journal of Zoology 89:267–277.

Lowrey, B., et al. 2019. Characterizing population and individual migration patterns among native and restored bighorn sheep (*Ovis canadensis*). Ecology and Evolution 9:8829–8839.

Lowrey, B., R. A. Garrott, D. E. McWhirter, P. J. White, N. J. DeCesare, and S. T. Stewart. 2018. Niche similarities among introduced and native mountain ungulates. Ecological Applications 28:1131–1142.

Lowrey, B., R. A. Garrott, H. M. Miyasaki, G. Fralick, and S. R. Dewey. 2017. Seasonal resource selection by introduced mountain goats in the southwest Greater Yellowstone Area. Ecosphere 8:1–20.

Lowrey, B., D. E. McWhirter, K. M. Proffitt, K. L. Monteith, A. B. Courtemanch, P. J. White, J. T. Paterson, S. R. Dewey, and R. A. Garrott. 2020. Individual variation creates diverse migratory portfolios in native populations of a mountain ungulate. Ecological Applications 30:1–14.

Lula, E. S., B. Lowrey, K. M. Proffitt, A. R. Litt, J. A. Cunningham, C. J. Butler, and R. A. Garrott. 2020. Is habitat constraining bighorn sheep restoration? A case study. Journal of Wildlife Management 84:588–600.

Manly, B. F., L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic, Dordrecht, The Netherlands.

Montana Fish, Wildlife and Parks. 2010. Montana bighorn sheep conservation strategy. Montana Fish, Wildlife & Parks, Wildlife Division, Helena, Montana, USA.

Montana Fish, Wildlife and Parks. 2013. Draft environmental impact statement assessment for the potential reintroduction of bighorn sheep into Indian or Wolf creek, Madison mountain range. http://fwp.mt.gov/news/publicNotices/environmentalAssessments/developmentImprovementsAndEnhancements/pn_0319.html

Niemuth, N. D. 2003. Identifying landscapes for greater prairie chicken translocation using habitat models and GIS: a case study. Wildlife Society Bulletin 31:145–155.

NOHRSC. 2004. National operational hydrologic remote sensing center snow data assimilation system (SNODAS) data products at NSIDC. National Snow and Ice Data Center, Boulder, Colorado, USA.

Northrup, J. M., M. B. Hooten, C. R. Anderson, and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use–availability design. Ecology 94:1456–1463.

Omernik, J. M., and G. E. Griffith. 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management 54:1249–1266.

Pebesma, E. 2018. sf: simple features for R. R package version 0.6-3. https://CRAN.R-project.org/package=sf

Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Côté. 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390.

Picton, H. D., and T. N. Lonner. 2008. Montana's wildlife legacy: decimation to restoration. Media Works, Bozeman, Montana, USA.

Poole, K., R. D. Serrouya, I. E. Teske, and K. Podrasky. 2016. Bighorn sheep winter habitat selection and seasonal movements in an area of active coal mining. Canadian Journal of Zoology 94:733–745.

PRISM Climate Group. 2016. Oregon State University. http://prism.oregonstate.edu

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ranglack, D. H., K. M. Proffitt, J. E. Canfield, J. A. Gude, J. Rotella, and R. A. Garrott. 2017. Security areas for elk during archery and rifle hunting seasons. Journal of Wildlife Management 81:778–791.

Rayl, N. D., K. M. Proffitt, E. S. Almberg, J. D. Jones, J. A. Merkle, J. A. Gude, and P. C. Cross. 2019. Modeling elk-to-livestock transmission risk to predict hotspots of brucellosis spillover. Journal of Wildlife Management 83:817–829.

Robinson, B. G., M. Hebblewhite, and E. H. Merrill. 2010. Are migrant and resident elk (Cervus elaphus) exposed to similar forage and predation risk on their sympatric winter range? Oecologia 164:265–275.

Rominger, E. M., H. A. Whitlaw, D. L. Weybright, W. C. Dunn, and W. B. Ballard. 2004. The influence of mountain lion predation on bighorn sheep translocations. Journal of Wildlife Management 68:993–999.

Sawyer, H., A. D. Middleton, M. M. Hayes, M. J. Kauffman, and K. L. Monteith. 2016. The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. Ecosphere 7:1–11.

Schindler, D. E., J. B. Armstrong, and T. E. Reed. 2015. The portfolio concept in ecology and evolution. Frontiers in Ecology and the Environment 13:257–263.

Singer, F. J., V. C. Bleich, and M. A. Gudorf. 2000a. Restoration of bighorn sheep metapopulations in and near western national parks. Restoration Ecology 8:14–24.

Singer, F. J., M. E. Moses, S. Bellew, and W. Sloan. 2000b. Correlates to colonizations of new patches by translocated populations of bighorn sheep. Restoration Ecology 8:66–74.

Singer, F. J., C. M. Papouchis, and K. K. Symonds. 2000c. Translocations as a tool for restoring populations of bighorn sheep. Restoration Ecology 8:6–13.

Smith, T. S., J. T. Flinders, and D. S. Winn. 1991. Habitat evaluation procedure for Rocky Mountain bighorn sheep in the Intermountain West. Western North American Naturalist 51:205–225.

Spitz, D. B., M. Hebblewhite, and T. R. Stephenson. 2015. 'MigrateR': extending model-driven methods for classifying and quantifying animal movement behavior. Ecography 40:788–799.

Spitz, D. B., M. Hebblewhite, and T. R. Stephenson. 2020. Habitat predicts local prevalence of migratory behavior in an alpine ungulate. Journal of Animal Ecology 89:1032–1044.

Thomas, C. D. 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. Trends in Ecology & Evolution 26:216–221.

Turner, J. C., C. L. Douglas, C. R. Hallum, P. R. Krausman, and R. R. Ramey. 2004. Determination of critical habitat for the endangered Nelson's bighorn sheep in southern California. Wildlife Society Bulletin 32:427–448.

U.S. Forest Service. 2015. Bighorn sheep risk of contact tool v2 user guide. U.S. Forest Service/U.S. Bureau of Land Management Bighorn Sheep Working Group. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd527641. pdf

Wakelyn, L. A. 1987. Changing habitat conditions on bighorn sheep ranges in Colorado. Journal of Wildlife Management 51:904–912.

Wickham, H. 2017. tidyverse: easily install and load the 'Tidyverse'. R package version 1.2.1. https://CRAN.R-project.org/package=tidyverse

Wild Sheep Working Group. 2012. Recommendations for domestic sheep and goat management in wild sheep habitat. Western Association of Fish and Wildlife Agencies. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5385708. pdf

Woodford, M. H., and P. B. Rossiter. 1994. Disease risks associated with wildlife translocation projects.

Pages 178–200 *in* P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. Creative Conservation: interactive management of wild and captive animals. Springer, Dordrecht, The Netherlands.

Wyoming Game and Fish Department. 1980. Bighorn sheep Darby Mountain job completion report. Wyoming Game and Fish Department, Jackson, Wyoming, USA.

Wyoming Game and Fish Department. 2016. Bighorn sheep Cody Job completion report. Wyoming Game and Fish Department, Cody, Wyoming, USA. https://wgfd.wyo.gov/WGFD/media/content/PDF/Hunting/JCRS/JCR_BGCODY_SHEEP_2016.pdf

Zeigenfuss, L. C., F. J. Singer, and M. A. Gudorf. 2000. Test of a modified habitat suitability model for bighorn sheep. Restoration Ecology 8:38–46.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3687/full