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Research Article

Is Habitat Constraining Bighorn Sheep Restoration? A Case Study

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ABSTRACT Rocky Mountain bighorn sheep (*Ovis canadensis*) restoration continues to be a challenge throughout western North America despite nearly a century of efforts dedicated to the species' recovery. Though bighorn sheep restoration may be constrained by several environmental factors and behavioral tendencies, areas with unrealized restoration potential may exist if novel restoration strategies are considered. We used global positioning system (GPS) location data from 27 female bighorn sheep within the southern portion of the Madison Range in southwest Montana, USA, 2015–2017, to develop and validate winter and summer habitat models, which we extrapolated throughout the entire Madison Range to identify potential seasonal habitat. We estimated potential bighorn sheep minimum population estimates within the extrapolation area by linking our top-ranked winter habitat model to population count data. During summer, female bighorn sheep selected areas characterized by rugged and steep terrain, reduced canopy cover, southwestern aspects, and ridgelines. During winter, female bighorn sheep selected areas characterized by low elevations, southwestern aspects, steep slopes, reduced canopy cover, ridgelines, high normalized difference vegetation index amplitude, and areas close to steep terrain. Predicted summer habitat was concentrated along the high-elevation ridgelines associated with steep slopes and reduced canopy cover. Predicted winter habitat occurred in a non-contiguous distribution primarily along the low-elevation, southwest-facing aspects along the western slopes of the Madison Range. Our results suggest that the Madison Range may be capable of supporting 780–1,730 animals, which is 2–4 times the number of bighorn sheep currently observed within the range. Further, our findings provide managers with a quantification of female bighorn sheep habitat and suggests that a strategy focused on establishing a metapopulation through a series of within-range translocations may enhance bighorn sheep restoration. We suggest that similar restoration opportunities may be common in other unoccupied areas of bighorn sheep historical range. © 2020 The Wildlife Society.

KEY WORDS habitat, metapopulation, Montana, *Ovis canadensis*, resource selection function, restoration, RSF, translocation.

Rocky Mountain bighorn sheep (*Ovis canadensis*), like all ungulate species native to western North America, experienced population declines during the mid to late 1800s (Buechner 1960). Overharvest, habitat loss, resource competition with livestock, and disease all contributed to the species' decline and by the 1940s, bighorn sheep were considered a species of management concern throughout their range (Buechner 1960). Early efforts focused on translocation, harvest regulation, and habitat protection were successful in restoring elk (*Cervus canadensis*), mule deer (*Odocolieus hemionus*), and pronghorn (*Antilocapra americana*); however, bighorn sheep have not attained comparable levels of recovery (Singer et al. 2000*c*, Picton and Lonner 2008). Despite nearly a century of management and conservation efforts, current bighorn sheep abundance is estimated at <10% of historical levels (Buechner 1960) and the factors impeding successful restoration are still unknown.

Although capable of occupying a diversity of rugged landscapes (Shackleton et al. 1999), bighorn sheep generally exhibit a limited propensity to disperse and colonize unoccupied landscapes (Geist 1971, Bleich et al. 1996, Jesmer et al. 2018). Translocations have been instrumental in restoring bighorn sheep into historical habitat but have not

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always been successful in creating viable, self-sustaining populations (Gross et al. 2000, Singer et al. 2000*c*). For example, many native bighorn sheep populations occur within a metapopulation structure in which ≥2 populations occupy distinct ranges yet maintain some level of connectivity seasonally (Bleich et al. 1996, Singer et al. 2000*b*, Lowrey et al. 2019). Additionally, structuring within a population can result in the occurrence of subpopulations, spatially and demographically structured groups of animals within a population, with important implications for conservation and management (Festa-Bianchet 1986, Bleich et al. 1996, Demarchi et al. 2000). The metapopulation structure is hard to recreate in restored populations, and as a result, many restored populations of bighorn sheep remain small, isolated and densely concentrated near the reintroduction site (Singer et al. 2000*c*, 2001).

The long-term persistence, growth, and expansion of bighorn sheep populations may be limited by several factors. Given the successful restoration of most mid-sized to large carnivores (e.g., mountain lions [*Puma concolor*]) throughout western North America, predation may suppress small and isolated populations (Wehausen 1996, Rominger et al. 2004, Festa-Bianchet et al. 2006). Pathogens introduced by domestic livestock can cause all-age die-offs with mortality ranging from 10–90% (Enk et al. 2001, Sells et al. 2015). Depressed lamb recruitment is also commonly documented for years following a disease outbreak (Enk et al. 2001, Cassirer and Sinclair 2007, Plowright et al. 2013), creating a persistent problem. Finally, habitat availability and connectivity may influence population persistence. Bighorn sheep are habitat specialists that rely upon key resources for survival and reproduction and are highly associated with steep and rugged terrain (Geist 1971). This specialization often results in a fragmented distribution within geographically distinct areas (e.g., mountain ranges). Anthropogenic-induced habitat degradation may constrain bighorn sheep populations into increasingly small and isolated habitat patches (Bleich et al. 1996, Shackleton et al. 1999), discouraging natural exploration of surrounding areas (Smith et al. 1999) and potentially leading to seasonal deficiencies in forage quality (Festa-Bianchet 1988, Enk et al. 2001) and reduced gene flow (Epps et al. 2005).

Given the above factors that limit natural expansion of bighorn sheep, new management strategies may be needed to increase occupation of potential habitat and thereby create larger and more robust populations. Because moving animals into novel areas or between geographically separate populations increases the risk of pathogen transmission (Butler et al. 2017), an alternative restoration strategy to promote viable long-term populations of bighorn sheep may be short-distance translocations aimed at promoting a broader local distribution and spatially structured populations (Bleich et al. 1996, Singer et al. 2000*a*). Metapopulations are less vulnerable to extirpation by stochastic events than small, isolated populations (Quinn and Hastings 1987, Berger 1990, Festa-Bianchet et al. 2006). Translocations aimed at restoring metapopulation structure may increase overall abundance and distribution, promote natural recolonization of historical habitat (Bleich et al. 1996, Epps et al. 2010), increase genetic heterozygosity (Epps et al. 2005), and potentially lower the risk of disease events by reducing local population densities and pathogen transmission rates (Sells et al. 2015). Efforts focused in part on restoring a metapopulation structure are proving effective for endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierra*; U.S. Fish and Wildlife Service 2007) and desert bighorn sheep (*Ovis canadensis nelson*) where targeted translocations have resulted in recolonization of historical habitat (Epps et al. 2010).

The Madison Range, located on the northwestern edge of the Greater Yellowstone Ecosystem (GYE) in southwest Montana, USA, is an example of a mountain complex with suspected unrealized potential for restoring a bighorn sheep metapopulation. Although bighorn sheep were historically observed throughout the Madison Range, only 2 remnant populations, Taylor-Hilgard and Spanish Peaks, were recognized by management agencies at the time of our study (Fig. 1; Montana Fish, Wildlife and Parks [MFWP] 2010). The 2 populations occupied relatively small portions of the available landscape on opposite ends of the mountain range and despite increases in population size and established migratory behavior, demonstrated little expansion into adjacent areas during nearly 8 decades of management and conservation (MFWP 2013).

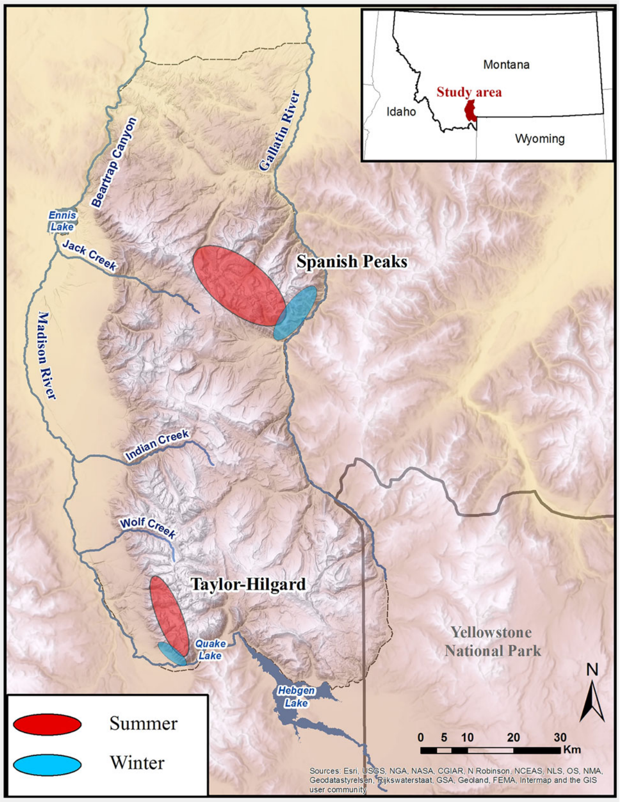

Figure 1. Madison Range study area located in southwestern Montana, USA, with generalized ranges for the Taylor-Hilgard and Spanish Peaks bighorn sheep populations, 2013–2016. The Wolf Creek translocation site is approximately 20 km north of the Taylor-Hilgard capture site on winter range.

In this observational study, we used global positioning system (GPS) data from female bighorn sheep in the Taylor-Hilgard population to address 2 objectives. First, we developed seasonal resource selection models, which we extrapolated throughout the broader Madison Range to identify areas of potential habitat beyond the currently occupied ranges of the Taylor Hilgard and Spanish Peaks populations. Given the broad historical distributions of bighorn sheep throughout the Madison Range, we hypothesized that habitat availability was not limiting current bighorn sheep distributions and that our habitat extrapolations would indicate a broad distribution of potential seasonal habitat. Second, we linked our winter habitat model to population count data to generate minimum population estimates throughout the Madison Range and predicted that potential habitat could support a larger metapopulation of bighorn sheep with higher abundance and expanded distributions.

STUDY AREA

The Madison Range (Fig. 1) consisted of approximately 3,420 km^2 within southwest Montana. Elevations ranged from 1,219–3,449 m, with a largely metamorphic bedrock (Turiano 2003). Approximately 2,019 km^2 (60%) of the study area consisted of publicly owned land primarily managed by the United States Forest Service (USFS) with the remainder consisting of privately owned agricultural lands and some residential and recreational development associated with a ski resort at the northern end of the range. Annual precipitation in the study area ranged from 30–50 cm, and average annual snow depth varied from 116–285 cm (Natural Resources Conservation Service 2019). Vegetation was dominated by mountain grassland and shrub communities in the low elevations, mixed spruce-fir forests at mid-elevations, and meadow graminoid-forb and krummholz communities in alpine areas (Patten 1963). The study area supported populations of elk, mule deer, and mountain goats (*Oreamnos americanus*), lower densities of white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*), and the full suite of native predators including wolves (*Canis lupus*), mountain lions, grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and coyotes (*C. latrans*).

Two isolated populations of bighorn sheep were recognized by management agencies within the Madison Range study area (Fig. 1; MFWP 2010). The Taylor-Hilgard population occurred in the southwestern portion of the Madison Range within the Madison River watershed (Fig. 1). The population numbered approximately 100 individuals when it experienced a respiratory disease epizootic in 1987, was subsequently augmented, and experienced a second disease die-off in 1997 that reduced the population to <20 animals. The population recovered without management intervention to a minimum of 185 animals counted on winter range at the start of the study in December 2013 (MFWP 2013). Over the period of population growth there was no perceived increase in the population distribution. As a result, between 2014 and 2018, MFWP translocated 97 bighorn sheep from the Taylor-Hilgard population to historical winter range in Wolf Creek, approximately 20 km north of the capture site in the Taylor-Hilgard population (Fig. 1; MFWP 2013).

The Spanish Peaks population occurred in the northeastern portion of the range, within the Gallatin River watershed, and was estimated to have approximately 165 animals. Although experiencing steady growth since the early 2000s, this native population had historically remained relatively small and experienced chronic low-level pneumonia-related mortalities during the winter (MFWP 2010). There are no major impediments to animal movement between the 2 populations.

METHODS

Animal Capture and Instrumentation

We conducted our primary capture efforts using a 24-m drop net in the Taylor-Hilgard population in December 2013. We baited the site with alfalfa and apple pulp for 2–3 weeks prior to capture. We instrumented 15 adult (>1.5 yr) female bighorn sheep with store-on-board GPS radio-collars (model TGW-4400-3, Telonics, Mesa, AZ, USA) programmed to record locations at 4-hour intervals for approximately 29 months before releasing from the animal. We handled all animals on site according to approved Montana State University Institutional Animal Care and Use Committee protocols (permit numbers 2011–17 and 2014–32). We used the dataset that we recovered from these individuals for model development.

Additionally, we obtained 3 independent datasets used for model validation. The first was from subsequent captures within the Taylor-Hilgard study area (using the same drop net methods) in the winters 2016 ($n = 10$), 2017 ($n = 1$), and 2018 ($n = 1$) in which we instrumented an additional 12 adult females with remote-download collars (model TGW-4570-4, Telonics) programmed to transmit a location every 12 hours with an expected battery life of approximately 5 years. We used the remaining 2 datasets to evaluate the extrapolations across the Madison Range and obtained them from 25 GPS-collared adult females translocated between 2014 and 2018 from the Taylor-Hilgard winter range to Wolf Creek (Fig. 1), and 13 GPS-collared adult females within the Spanish Peaks population in the northern Madison Range instrumented during the winter of 2017 and monitored until fall 2018.

We delineated biologically meaningful seasons based on the dates of spring and fall migrations of the Taylor-Hilgard population. We identified migration dates using nonlinear regression movement models developed by Bunnefeld et al. (2011) and modified by Spitz et al. (2017), which estimated migration parameters and classified individual migration behaviors based on elevation profiles through time (Fig. S1, available online in Supporting Information). We removed locations collected during the population-defined migratory period to minimize additional noise associated with transitional movements between summer and winter ranges (Lowrey et al. 2018) and used the remaining location data to build summer and winter resource selection models.

Resource Selection Model Covariates

We developed multiple suites of environmental covariates expected to influence bighorn sheep resource selection and hypothesized the direction of their effect during winter and summer (Table 1). Terrain covariates included elevation, slope, and landscape curvature (curve), which ranged from −1 to 1, with positive values indicating convex curvatures (i.e., ridgelines) and negative values indicating concave curvatures (i.e., valleys; Villepique et al. 2015). We also considered 2 measures of landscape ruggedeness: slope variance (slope SD), calculated as the standard deviation^2 of slope within a 90 × 90-m neighborhood (DeVoe et al. 2015), and vector ruggedness measure (VRM), which measured the integrated variation in slope and aspect (Sappington et al. 2007). We predicted that female bighorn sheep would select relatively steep and rugged terrain throughout the year and would select for lower elevations during the winter given the Taylor-Hilgard population's documented migratory behavior (MFWP 2013, Lowrey et al. 2019). We used a transformed form of aspect (Cushman and Wallin 2002) as a measure of solar exposure. The transformation generated a biologically interpretable index by taking the inverse cosine of the angle −35° (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 expected female bighorn sheep to select for cooler north-northeast slopes during the summer and warmer south-southwest slopes during winter. Distance to escape terrain is frequently supported when modeling bighorn sheep habitat (Gross et al. 2002, DeCesare and Pletscher 2006), although definitions for the threshold slope value are often subjective, variable, and difficult to interpret biologically (DeVoe et al. 2015). We included distance to steep terrain (Lowrey et al. 2018), which we defined as the distance to slopes ≥27°, 37°, and 45°, and predicted that female bighorn sheep would have a negative relationship with distance to steep terrain in both seasons (Smith et al. 1991, Zeigenfuss et al. 2000, Poole et al. 2016).

Vegetation covariates included an estimate of percent canopy cover and 2 measures of normalized difference vegetation index (NDVI), time-integrated NDVI (NDVItin) and NDVI amplitude (NDVIamp; Table 1). The NDVI is a remotely sensed measure of vegetative greenness often used to characterize relative primary production of forage (Pettorelli et al. 2007, 2011; U.S. Geological Survey 2016). Time-integrated NDVI represents the daily integrated NDVI above baseline for duration of growing season (Meier and Brown 2014), whereas NDVI amplitude represents the difference between the maximum and baseline NDVI at the beginning of growing season (Meier and Brown 2014). For both NDVI indices we calculated mean values for each pixel over the duration of the study from 2014–2016. Although vegetation is largely covered with snow in the winter, we included the NDVI metrics to evaluate the potential that residual senescent vegetation influenced selection by bighorn sheep the following winter. We predicted that female bighorn sheep

Table 1. Covariate descriptions and hypothesized seasonal relationships with the relative probability of use for adult female bighorn sheep in the Taylor-Hilgard population in the Madison Range, southwestern Montana, USA, 2013–2016.

Covariate	Functional form[a]	Spatial resolution (m)	Predicted relationship (summer/winter)	Reference
Elevation (m)	Ln, Sq	30	+/−	Courtemanch et al. (2017)
Slope (°)	Ln, Sq	30, 100, 500, 1,000	+/+	DeCesare and Pletscher (2006)
Distance to steep terrain: 3 separate covariates defined as the distance (m) from slopes ≥27°, 37°, and 45°	Ln, Ps	30	−/−	Smith et al. (1991), Poole et al. (2016)
Landscape curvature	Ln, Sq	30	+/+	Villepique et al. (2015)
Slope variance: SD^2 of slope	Ln, Ps	30, 100, 500, 1,000	+/+	DeVoe et al. (2015)
Vector ruggedness measure	Ln, Ps	30, 100, 500, 1,000	+/+	Sappington et al. (2007)
Aspect: the inverse cosine of aspect −35°	Ln	30	−/+	DeCesare and Pletscher (2006)
Canopy cover (%)	Ln	30, 100, 500, 1,000	−/−	Smith et al. (1991)
Time-integrated NDVI[b]: mean daily integrated NDVI above baseline for duration of growing season (2014–2016)	Ln	30, 100, 500, 1,000	+/+	Lowrey et al. (2018)
NDVI[b] amplitude: the mean difference between max. and baseline NDVI at beginning of growing season (2014−2016)	Ln	250, 500, 1,000	+/+	Lowrey et al. (2018)
Snow: average proportion of winter covered in snow (2013–2015)	Ln, Ps	500	na/−	Tilton and Willard (1982), Smith et al. (1991)

[a] Ln = linear, Sq = quadratic, Ps = Psuedothroeshold (natural log).

[b] Normalized difference vegetation index.

would avoid canopy cover and positively select for NDVItin and NDVIamp in both seasons (Wakelyn 1987). Finally, we used Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery (MOD10A1; Hall and Riggs 2016) to create a snow severity index (snow) as the mean proportion of days each pixel was snow covered during the 2013–2015 winter seasons, and hypothesized that winter selection would be negatively associated with increased snow severity (Tilton and Willard 1982, Smith et al. 1991).

Although we largely assumed covariate functional forms to be linear, we also evaluated quadratic forms of elevation and slope, allowing selection for these resources to peak at optimal intermediate values (Gross et al. 2002, Walker et al. 2007, Poole et al. 2016). Similarly, we evaluated a pseudothreshold (natural log) form for our 2 measures of landscape ruggedness (slope SD and VRM), allowing selection for rugged terrain to asymptote at a threshold value (DeVoe et al. 2015, Lowrey et al. 2017). Recent work has highlighted the importance of evaluating covariates at multiple spatial grains to create more predictive and process-driven models (Meyer and Thuiller 2006, Laforge et al. 2015). The multi-grain approach formalizes the concept that an animal's choice to select a given spatial location may not result solely from the attributes in the immediate vicinity (e.g., min. resolution of data) but may also be influenced by a broader region (e.g., the space of influence; Laforge et al. 2015). We performed neighborhood analyses at 30-, 100-, 500-, 1,000-m circular buffers to evaluate the space of influence of bighorn sheep resource selection for covariates that are visually perceived (Lowrey et al. 2017). We did not attempt to evaluate spatial grains below the minimum resolution of the data for any given covariate (Table 1) and hypothesized that female bighorn sheep would select terrain covariates at larger spatial grains, and vegetation covariates at smaller grains (DeVoe et al. 2015).

Statistical Framework and Model Selection

We used a used-available study design (Manly et al. 2002) in which the used set consisted of GPS locations collected from collared bighorn sheep, and availability was characterized with randomly generated locations within the population annual range. We defined the annual range using a minimum convex polygon (MCP) that encompassed the pooled winter and summer locations buffered by the 95th percentile distance between consecutive 4-hour fix locations (Walker et al. 2007, Laforge et al. 2015). We generated available points with a 1:5 (used:available) ratio, which adequately described the distribution of each covariate within the study area and avoided numerical integration and convergence issues (Northrup et al. 2013, Lula 2019). We used the exponential resource selection function (RSF):

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

to calculate a relative probability of selection $\hat{w}$, where β_0 is the intercept and $\hat{\beta}_1 \cdots \hat{\beta}_n$ are the coefficients derived as a function of the covariates x_i. Using a generalized linear mixed-model framework, we considered the individual female bighorn sheep as the sample unit (White and Garrott 1990) and specified a random intercept to account for autocorrelation within individuals and unbalanced sample size among individuals (Gillies et al. 2006). We rescaled the predicted values between 0 and 1 using a linear stretch transformation (Johnson et al. 2004).

We used a tiered approach to evaluate covariates and develop competing models for each season (Franklin et al. 2000, DeVoe et al. 2015), and used corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson 2003) to select the most supported model in all tiers. In the first tier, we fit univariate models for each covariate for which we evaluated multiple grains and functional forms (Table 1) and selected a single grain and form for each covariate. In tier 2, we again used univariate models to select a single index for covariates where we considered multiple indices (e.g., NDVIamp and NDVItin). Because bighorn sheep strongly associate with terrain characteristics (Geist 1971), we began tier 3 of model selection by building a multivariate base terrain model using non-collinear (e.g., Pearson's correlation coefficient of $|r| < 0.6$) combinations of terrain covariates (Lowrey et al. 2017). We then combined covariates selected from the base terrain model with all combinations of covariates that were selected as part of the tier 1 and the tier 2 processes to develop candidate models for each season. We performed model fitting and selection with scaled and centered covariates using the mean and 1 standard deviation.

Using our top seasonal models, we estimated seasonal relative probabilities within the study area and extrapolated the predictions across the Madison Range. A key assumption of the RSF extrapolation is that the range of covariates used in model development is the same as the range of covariate values across the extrapolated extent (Hirzel and Le Lay 2008). We evaluated this assumption by comparing distributions of model covariates within the population range and extrapolated extent and removed areas from our extrapolation that fell outside of the covariate range used for model development (Lula 2019). Lastly, we defined habitat as the range of RSF values that include 95% of the RSF values associated with used locations (DeVoe et al. 2015, Lowrey et al. 2017) and quantified the amount of habitat within the Madison Range.

RSF Validation

We conducted 2 model validations of the interpolation within the Taylor-Hilgard study area and 2 validations of the extrapolations within the Madison Range. First, with the data used in model construction within the Taylor-Hilgard study area, we performed an iterative *k*-fold cross validation in which we withheld the locations for each individual, 1 through *k*, fit an exponential RSF with the individuals that were retained, and predicted the fitted values for the observations that were withheld (Boyce et al. 2002). 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 (r_s; Boyce et al. 2002). Although the use of 10 bins is arbitrary, it is a commonly used standard that correctly fit our data distribution. For the remaining validations we used data from the subsequent captures in the Taylor-Hilgard population from 2016–2018, the animals translated from Taylor-Hilgard to Wolf Creek between 2014 and 2018, and the animals in the Spanish Peaks population captured in 2017. We used the data collected from within the Taylor-Hilgard population to perform an additional independent validation of our interpolation, whereas we used the datasets from the translocated animals and the animals in the Spanish Peaks to validate the extrapolation throughout the Madison Range. For each independent dataset we censored individual-seasons with <20 locations, summed the occurrence of used locations within each of the 10 equal-area RSF bins defined by the distribution of RSF values within the Taylor-Hilgard annual range, and used the Spearman-rank correlation to evaluate model performance (Boyce et al. 2002). In all validations, the adjusted frequencies should be highly correlated with the relative RSF if the model performs well (Boyce et al. 2002).

Minimum Population Estimation

To explore the potential for restoration within the Madison Range, we linked our winter RSF model to the Taylor-Hilgard population management objective ($N_{min} = 120$), and the 11-year maximum observed population count (2008–2018, $N_{max} = 266$; Table S1, available online in Supporting Information; Boyce and McDonald 1999). We used the winter RSF, in contrast to our summer RSF, to align our minimum population estimates to the period when the count data were collected (i.e., during the winter months when bighorn sheep were concentrated and visible at low elevations), and because the scarce resources and taxing weather conditions during winter more strongly limit population abundance relative to summer. Although we generated our winter habitat model from the female segment of the population, the management objective and population counts were in reference to the population and not separated by sex. For the purposes of generating minimum population estimates, we assumed males and females had similar winter habitat characteristics. This assumption was supported by local knowledge and consistent observations of both females and males of all age classes sharing the same highly visible winter range in the Taylor-Hilgard population over the duration of the historical counts (2008–2018; J. A. Cunningham, MFWP, unpublished data). For each of our selected count metrics (e.g., the population objective and maximum observed population count), we defined equal-area RSF bins based on the distribution of winter RSF values within the Taylor-Hilgard annual range. We explored multiple bin sizes (i.e., 5, 10, and 20 bins) all of which produced similar results, and selected 10 bins because this is most commonly used (Boyce et al. 2016). We then used the bin median to distribute bighorn sheep use and estimate a density of bighorn sheep for each bin. Using the bins defined within the annual range, we reclassified the full RSF and generated minimum population estimates ($\hat{N}$) as:

$$\hat{N} = \Sigma_j D(x_j) A'(x_j), \tag{2}$$

where $D(x_j)$ is the density of bighorn sheep within each bin and $A'(x_j)$ is the area (km^2) of defined habitat for each bin (Boyce and Waller 2003, Boyce et al. 2016). Our population estimates assume that all available habitat is occupied. To validate our minimum population estimates, we compared the estimate for the Spanish Peaks winter range by defining an MCP around winter locations of instrumented animals in the Spanish Peaks population, then generated minimum population estimates of bighorn sheep within this area using the winter model and density estimates from the Taylor-Hilgard population, and compared the model-derived estimate to observed population counts of animals on that winter range between 2008 and 2018. We conducted all analyses in the R environment for statistical computing (R Core Team 2015) in combination with the raster (Hijmans et al. 2016) package for spatial analysis, the lme4 package (Bates et al. 2015) for model fitting, and the tidyverse (Wickham 2017) suite for data wrangling and visualization.

RESULTS

We monitored female bighorn sheep captured in the Taylor-Hilgard population used for model development ($n = 15$) for an average of 842 (range = 516–865) days for 29 animal-years. Fourteen of the 15 animals retained their collars until the programmed release date and 1 animal died 516 days after capture from an unknown cause. We classified all animals as elevational migrants (Fig. S1). We defined summer as 20 June to 8 October and winter as 8 December to 10 May. After censoring imprecise fixes, the mean fix success rate was 94% (range = 91–96%) and 97% (range = 96–98%) for summer and winter, respectively. The resulting datasets used to construct resource selection models included 14,471 locations for summer and 30,302 locations for winter.

Seasonal Model Development and Selection

Within tiers 1 and 2, differences in AIC$_c$ scores clearly identified a top-ranked spatial grain and functional form and a single index for covariates where we considered multiple indices (Figs. S2–S3; Tables S2–S5, available online in Supporting Information). Our top-ranked summer model included pseudothreshold VRM, slope, slope^2, curve, and canopy at the 500-m scale and aspect at the 30-m scale. The top-ranked winter model included elevation, elevation^2, and aspect at the 30-m scale, slope, slope^2, and curve at the 1,000-m scale, canopy at the 100-m scale, NDVIamp at the 250-m scale, and pseudothreshold distance to steep terrain ≥45° (Table 2). As predicted, female bighorn sheep selected for relatively steep terrain throughout the year. A quadratic form of slope was included in summer and winter models and indicated that selection peaked at 38° and 36°, respectively (Fig. 2). Distance to steep terrain was also

Table 2. Tier 3 resource selection model results for resource selection of 15 adult female bighorn sheep from the Taylor-Hilgard population in the Madison Range, southwestern Montana, USA, 2013–2016. Models are arranged by difference in corrected Akaike's Information Criterion ($\Delta\mathrm{AIC}_c$). We also present the number of parameters (K) and model weight (w_i).

Model[a]	K	$\Delta\mathrm{AIC}_c$	w_i
Summer			
$\mathrm{VRM}^{\mathrm{Ps}}_{500} + \mathrm{SLP}_{500} + \mathrm{SLP}^2_{500} + \mathrm{CRV}_{500} + \mathrm{CANCO}_{500} + \mathrm{ASPC}_{30}$	8	0	1
$\mathrm{VRM}^{\mathrm{Ps}}_{500} + \mathrm{SLP}_{500} + \mathrm{SLP}^2_{500} + \mathrm{CRV}_{500} + \mathrm{CANCO}_{500}$	7	1,342	0
$\mathrm{VRM}^{\mathrm{Ps}}_{500} + \mathrm{SLP}_{500} + \mathrm{SLP}^2_{500} + \mathrm{CRV}_{500} + \mathrm{NDVIamp}_{1000} + \mathrm{ASPC}_{30}$	8	2,121	0
$\mathrm{VRM}^{\mathrm{Ps}}_{500} + \mathrm{SLP}_{500} + \mathrm{SLP}^2_{500} + \mathrm{CRV}_{500} + \mathrm{ASPC}_{30}$	7	2,874	0
$\mathrm{VRM}^{\mathrm{Ps}}_{500} + \mathrm{SLP}_{500} + \mathrm{SLP}^2_{500} + \mathrm{CRV}_{500} + \mathrm{NDVIamp}_{1000}$	7	3,382	0
$\mathrm{VRM}^{\mathrm{Ps}}_{500} + \mathrm{SLP}_{500} + \mathrm{SLP}^2_{500} + \mathrm{CRV}_{500}$	6	4,032	0
Winter			
$\mathrm{ELV}_{30} + \mathrm{ELV}^2_{30} + \mathrm{SLP}_{1000} + \mathrm{SLP}^2_{1000} + \mathrm{CRV}_{1000} + \mathrm{DST45}^{\mathrm{Ps}} + \mathrm{CANCO}_{100} + \mathrm{NDVIamp}_{250} + \mathrm{ASPC}_{30}$	10	0	1
$\mathrm{ELV}_{30} + \mathrm{ELV}^2_{30} + \mathrm{SLP}_{1000} + \mathrm{SLP}^2_{1000} + \mathrm{CRV}_{1000} + \mathrm{DST45}^{\mathrm{Ps}} + \mathrm{CANCO}_{100} + \mathrm{ASPC}_{30}$	9	636	0
$\mathrm{ELV}_{30} + \mathrm{ELV}^2_{30} + \mathrm{SLP}_{1000} + \mathrm{SLP}^2_{1000} + \mathrm{CRV}_{1000} + \mathrm{DST45}^{\mathrm{Ps}} + \mathrm{NDVIamp}_{250} + \mathrm{ASPC}_{30}$	9	2,924	0
$\mathrm{ELV}_{30} + \mathrm{ELV}^2_{30} + \mathrm{SLP}_{1000} + \mathrm{SLP}^2_{1000} + \mathrm{CRV}_{1000} + \mathrm{DST45}^{\mathrm{Ps}} + \mathrm{ASPC}_{30}$	8	4,319	0
$\mathrm{ELV}_{30} + \mathrm{ELV}^2_{30} + \mathrm{SLP}_{1000} + \mathrm{SLP}^2_{1000} + \mathrm{CRV}_{1000} + \mathrm{DST45}^{\mathrm{Ps}} + \mathrm{CANCO}_{100} + \mathrm{NDVIamp}_{250}$	9	5,467	0
$\mathrm{ELV}_{30} + \mathrm{ELV}^2_{30} + \mathrm{SLP}_{1000} + \mathrm{SLP}^2_{1000} + \mathrm{CRV}_{1000} + \mathrm{DST45}^{\mathrm{Ps}} + \mathrm{CANCO}_{100}$	8	6,958	0
$\mathrm{ELV}_{30} + \mathrm{ELV}^2_{30} + \mathrm{SLP}_{1000} + \mathrm{SLP}^2_{1000} + \mathrm{CRV}_{1000} + \mathrm{DST45}^{\mathrm{Ps}} + \mathrm{NDVIamp}_{250}$	8	10,804	0
$\mathrm{ELV}_{30} + \mathrm{ELV}^2_{30} + \mathrm{SLP}_{1000} + \mathrm{SLP}^2_{1000} + \mathrm{CRV}_{1000} + \mathrm{DST45}^{\mathrm{Ps}}$	7	13,732	0

[a] ASPC = aspect, ELV = elevation, CANCO = canopy cover, CRV = landscape curvature, DST45 = distance to slopes ≥45°, NDVIamp = normalized difference vegetation index amplitude, SLP = slope, VRM = vector ruggedness. Subscripts identify covariate spatial grain (m) and superscripts identify functional form, where x^2 = quadratic and x^{Ps} = pseudothreshold.

included in our winter model and indicated that bighorn sheep selected areas closer to slopes ≥45°. During winter, elevation was the most influential covariate with selection approaching 0 when elevation was >2,000 m (Table 3; Fig. 2). A pseudothreshold functional form of VRM was most influential on summer selection, indicating that bighorn sheep selected for more rugged areas, but that the relationship was not linear (Fig. 2). Consistent with our predictions, bighorn sheep avoided canopy cover >35% during summer and winter and selected for positive values of landscape curvature (i.e., ridgelines), though our results indicated a stronger positive relationship during winter than in summer (Fig. 2). Contrary to our predictions, bighorn sheep did not select for the cooler northwestern aspects during the summer but did select for warmer southwest slopes in winter.

Model Extrapolation and Validation

Our extrapolation identified unoccupied summer and winter habitat throughout the Madison Range (Fig. 3). We estimated approximately 85 km^2 of winter habitat and 208 km^2 of summer habitat existed within the Madison Range. The majority of predicted summer habitat occurred within the western half of the Madison Range, with the highest predicted RSF values occurring on high elevation, southwest facing slopes in a relatively continuous distribution between Quake Lake and Jack Creek (Fig. 3). Although not as abundant along the eastern half of the Madison Range, our model did identify substantial amounts of potential summer habitat within the Spanish Peaks area. Similar to our summer model extrapolation, the majority of predicted winter habitat occurred within the western half of the Madison Range. Compared to the summer habitat predictions, winter habitat occurred in a less uniform distribution along the entirety of the western front of the Madison Range on low-elevation, southwest-facing foothills. We also identified additional potential winter habitat on the northern end of the Madison Range, within the Taylor Creek drainage, and along the north shore of Hebgen Lake at the southern end of the Range (Fig. 3).

Validations of our interpolation within the Taylor-Hilgard seasonal ranges and extrapolations throughout the Madison Range indicated good model predictive performance. Our internal k-fold validations (summer $r_s = 1$, $P < 0.001$, winter $r_s = 0.957$, $P < 0.001$), and the validation using temporally independent data from within the study area (summer $r_s = 1$, $P < 0.001$, winter $r_s = 0.985$, $P < 0.001$) indicated strong relationships between use and the predicted RSF. The validation using data from the translocated animals provided further support for temporal robustness of our seasonal models and strong validation of our extrapolations outside of the Taylor-Hilgard study area. Winter locations were as highly correlated ($r_s = 0.988$, $P < 0.001$), although with notably more individual variation that is perhaps indicative of habitat exploration post-translocation (Lula 2019). Summer locations from the translocated animals produced a strong but slightly lower Spearman-rank correlation ($r_s = 0.877$, $P = 0.009$), although the number of individual locations available for external validation was limited because some translocated bighorn sheep either returned to the Taylor-Hilgard population or occupied the same summer range as the Taylor-Hilgard population. The external validation using the Spanish Peaks population range produced strong correlations during summer ($r_s = 0.887$, $P = 0.006$) and winter ($r_s = 0.988$, $P < 0.001$), clearly demonstrating the robustness of our extrapolation to areas beyond the model development area.

Minimum Population Estimation

Using the Taylor-Hilgard population management objective ($n = 120$) and the 11-year maximum count ($n = 266$), we estimated that the Madison Range is capable of supporting

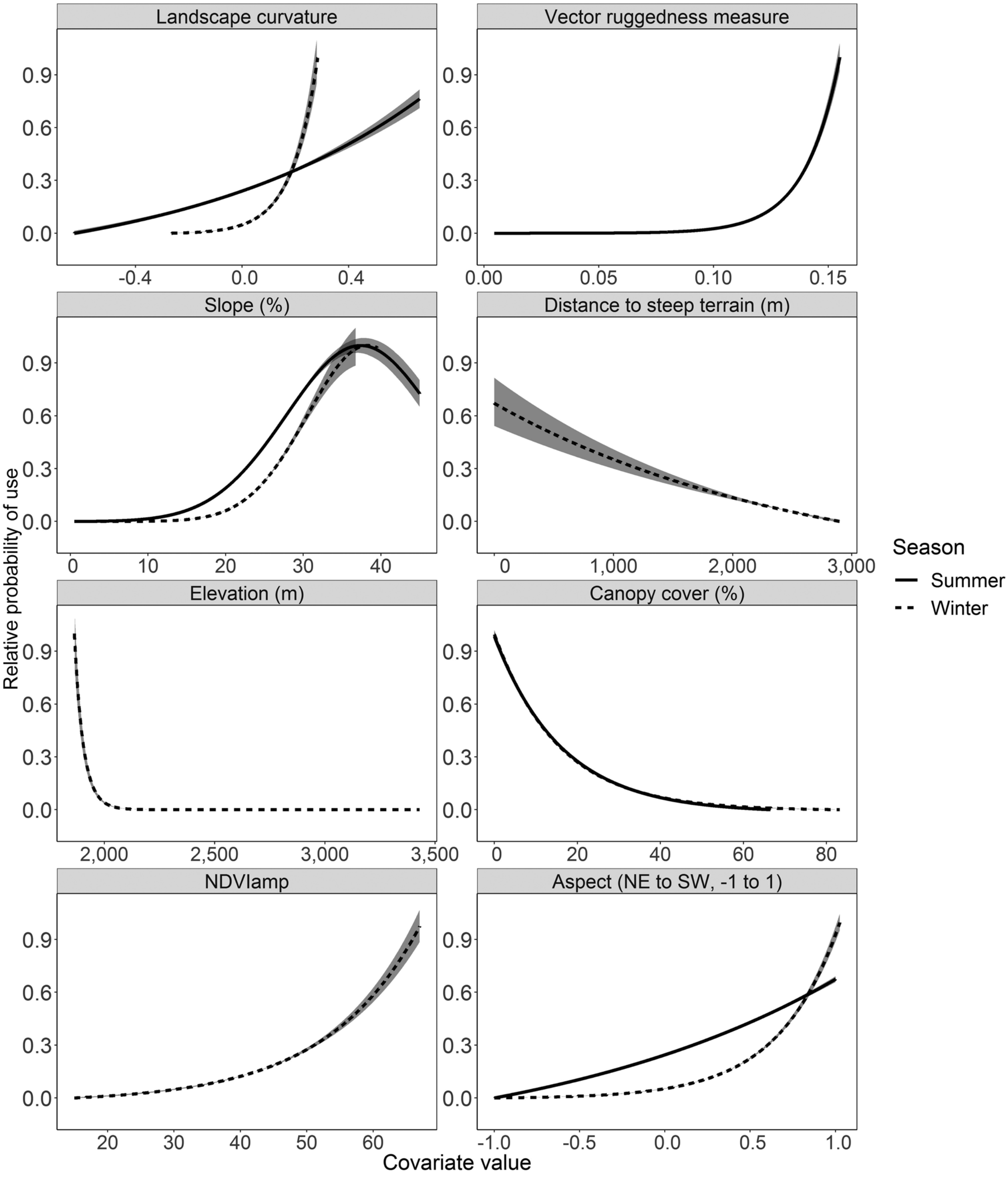

Figure 2. Predictions of the relative probability of use for the top covariates in the winter and summer resource selection models for adult female bighorn sheep in the Taylor-Hilgard population occupying the Madison Range, southwestern Montana, USA, 2013–2016. We generated predictions across the observed covariate range with all other covariates held at their mean value. We generated 95% confidence bands using bootstrap techniques within the merTools R package (Knowles and Frederick 2016); they do not account for any variation associated with the random effect. NDVIamp = normalized difference vegetation index amplitude.

minimum population estimates between 780–1,730 bighorn sheep if all predicted habitat was occupied. Our validation within the Spanish Peaks predicted minimum population estimates between 57–126 animals to occur on winter range, which was lower than observed counts (150–212 bighorn sheep). Although our validation may provide evidence for low bias within the Madison Range, potential minimum population estimates as predicted by our winter model indicated that the Madison Range was capable of supporting at least twice as many bighorn sheep as is currently observed.

DISCUSSION

Our study builds upon the established knowledge of bighorn sheep resource selection and explores the potential for broader restoration within a mountain range containing 2 established but non-expanding bighorn sheep populations. By evaluating the relationship between GPS data from

Table 3. Coefficients table displaying unscaled estimates for the top-ranked seasonal resource selection functions developed using global positioning system data from 15 adult female bighorn sheep from the Taylor-Hilgard population in the Madison Range, southwestern Montana, USA, 2013–2016. We unscaled estimates and standard errors (SE) using the mean and standard deviation of the observed data for each season; standardized estimates can be applied to landscape covariates in their respective units. We calculated the 95% confidence intervals as the estimate ±1.96 × SE.

Covariate[a]	Estimate	SE	95% CI	
			Upper	Lower
Summer				
Intercept	4.9847	0.0937	5.1683	4.8011
$\text{VRM}_{500}^{\text{Ps}}$	4.5154	0.0920	4.6958	4.3350
SLP_{500}	0.1344	0.0034	0.1410	0.1279
SLP^2_{500}	−0.0011	0.0001	−0.0010	−0.0012
CRV_{500}	0.0137	0.0008	0.0153	0.0122
CANCO_{500}	−1.2039	0.0247	−1.1555	−1.2522
ASPC_{30}	2.3173	0.0649	2.4445	2.1900
Winter				
Intercept	1.6696	−0.6334	0.4281	2.9110
ELV_{30}	−0.0090	0.0001	−0.0088	−0.0092
ELV^2_{30}	0.0000	0.0000	0.0000	0.0000
SLP_{1000}	0.2529	0.0044	0.2616	0.2243
SLP^2_{1000}	−0.0015	0.0000	−0.0015	−0.0016
CRV_{1000}	10.5180	0.3600	11.2235	9.8124
DST45^{Ps}	−0.7424	0.0087	−0.0573	−0.0912
CANCO_{100}	−0.0645	0.0013	−0.0619	−0.0670
NDVIamp_{250}	0.0707	0.0028	0.0763	0.0652
ASPC_{30}	2.8111	0.0490	2.9072	2.7149

[a] ASPC = aspect, ELV = elevation, CANCO = canopy cover, CRV = landscape curvature, DST45 = distance to slopes ≥45°, NDVIamp = normalized difference vegetation index amplitude, SLP = slope, VRM = vector ruggedness. Subscripts identify covariate spatial grain (m) and superscripts identify functional form, where x^2 = quadratic and x^{Ps} = pseudothreshold.

bighorn sheep within the Taylor-Hilgard population and a suite of landscape covariates expected to influence habitat selection, we developed and validated predictive summer and winter RSF models and identified potential habitat throughout the Madison Range. Our results indicate that approximately 82% and 42% of predicted winter and summer habitat within the Madison Range was unoccupied, respectively. Our case study suggested there are ample opportunities for bighorn sheep restoration within the Madison Range, and that habitat is not limiting the potential growth of bighorn populations in this area. Additionally, our approach used to quantify and identify suitable habitat provides detailed spatial information to guide future restoration efforts.

The distribution of predicted habitat has important implications for bighorn sheep restoration within the Madison Range. Although summer habitat generally occurred as essentially 3 large expanses within the high-elevation, mountainous regions of the Madison Range, winter habitat occurred on low-elevation foothills primarily within the Madison River watershed in a non-contiguous distribution of discrete habitat patches. Considering the migratory behavior and strong fidelity exhibited by instrumented animals in our study, we hypothesize that a metapopulation of bighorn sheep historically existed within the Madison Range as a collection of populations, in which distinct wintering subpopulations migrated to shared summer ranges to exploit seasonally variable resources such as the emergence of nutritious forage (Merkle et al. 2016). Our hypothesized structure is consistent with other wild sheep metapopulations composed of discrete populations with further sub-structuring on distinct seasonal ranges, with varying degrees of interaction through established seasonal migrations (Festa-Bianchet 1986, Bleich et al. 1996, Shackleton et al. 1999, Demarchi et al. 2000, Lowrey et al. 2019).

Recent work has demonstrated that bighorn sheep may establish and maintain knowledge of seasonal ranges via cultural transmission, the process by which knowledge of an area beyond the animal's perceptual range is passed down from generation to generation through social interaction (Jesmer et al. 2018). In the context of our hypothesized metapopulation, we speculate that cultural transmission may have been important in maintaining localized wintering subpopulations of bighorn sheep, and that their historical extirpation resulted in an overall reduction of the broader geographic landscape known to the remaining population. Once extirpated, wintering subpopulations are unlikely to be naturally reestablished by neighboring subpopulations given the high fidelity that female bighorn sheep exhibit to their natal home range (Bleich et al. 1996). We speculate that this behavioral tendency, in combination with subsequent disease related die-offs and factors such as increased predator densities, may have effectively suppressed the remnant populations of bighorn sheep within the Madison Range (i.e., Taylor-Hilgard and Spanish Peaks) from expanding into adjacent landscapes. This implies that further restoration success could be achieved through the mitigation of constraining factors and the encouragement of exploratory behavior via short-range translocations.

Our predictive models performed well using multiple spatially and temporally independent datasets, and when linked with count data, suggest that the Madison Range may support at least twice the number of bighorn sheep observed at the time of this study. Although model performance may be influenced by the number of bins used in the *k*-fold validation methods (Boyce et al. 2002), the strong performance across all validation datasets lends credence to our model's ability to predict bighorn sheep seasonal habitat throughout the Madison Range. Nonetheless, because our minimum population estimate was based on a management objective of 120 bighorn sheep on Taylor-Hilgard winter range and the population had consistently been observed above this objective in recent years without experiencing the negative effects associated with higher densities, true potential abundance likely falls above our minimum estimate of 780 animals. Our upper minimum population estimate (1,730 bighorn sheep) is based on the 11-year maximum count observed for the Taylor-Hilgard population and may more closely reflect the potential for bighorn sheep restoration within the Madison Range, provided that all patches of predicted winter habitat would be used similarly to the Taylor-Hilgard winter range. This assumption may

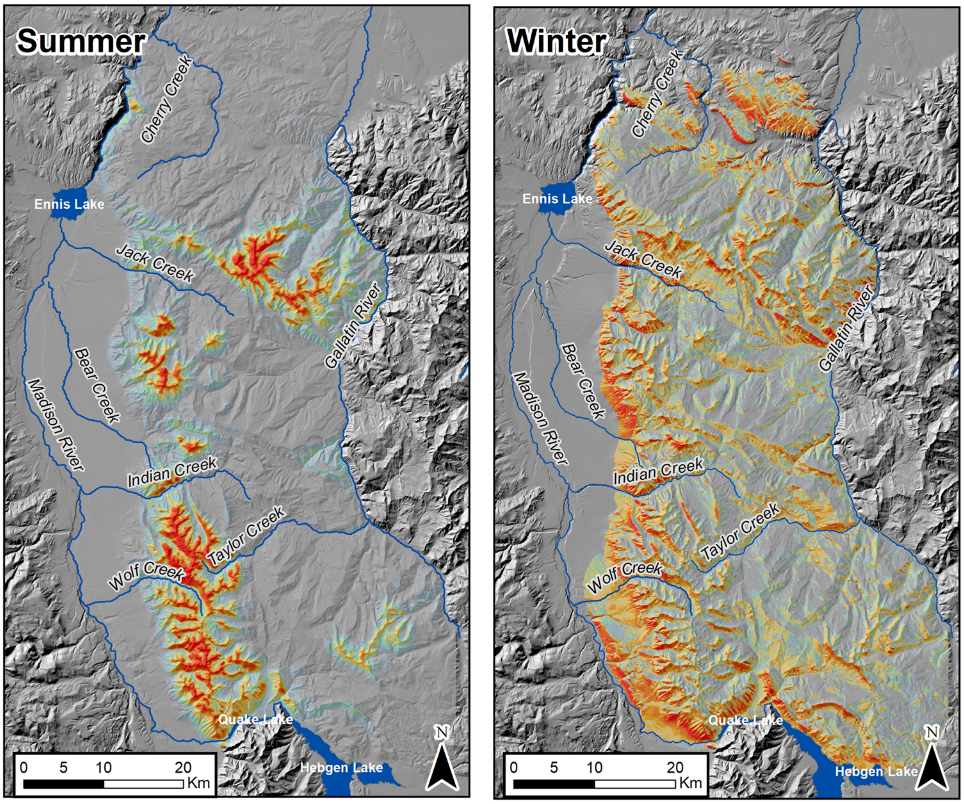

Figure 3. Seasonal resource selection model results extrapolated to the Madison Range, southwestern Montana, USA, using global positioning system data collected from 2013–2016 from 15 adult female bighorn sheep. We classified predicted values into 10 equal-area bins based on the seasonal predictions within the Taylor-Hilgard bighorn sheep population annual range. Cool colors represent low relative resource selection function (RSF) values and warm colors depict higher RSF values.

not apply to all predicted habitat and some habitat patches may be too small or lacking important small-scale resources (e.g., mineral licks) to support persistent subpopulations (Singer et al. 2000*c*, 2001). Small patches of habitat, or those with lower RSF values, should not be undervalued because they may promote exploration, provide access to rare but ephemerally important resources, and provide crucial linkages between habitat patches (Bleich et al. 1990).

Furthermore, predicted abundances for the Spanish Peaks population (57–126 bighorn sheep) were lower than counts observed during the past 10 years (150–212 bighorn sheep). This suggests that our minimum population estimate may be biased low. This bias could be the result of our reclassification of winter habitat, instrumented animals within the Spanish Peaks population failing to fully delineate the winter range of bighorn sheep observed during surveys, or observed densities of bighorn sheep on Taylor-Hilgard winter range being lower than what the habitat can actually support. Density equilibrium is an important assumption for abundance estimation (Johnson and Seip 2008, Boyce et al. 2016) and the 11-year maximum observed population count on Taylor-Hilgard winter range ($N_{max} = 266$) may not represent true equilibrium, given that the population has consistently been growing and was actively managed towards a lower objective via harvest and translocation. Given our lower than observed minimum population estimate within the Spanish Peaks and the relatively stable number of animals managed on the Taylor-Hilgard winter range, however, we contend that our upper minimum population estimate for the Madison Range is reasonable and demonstrates that there is unrealized restoration potential for bighorn sheep, perhaps upwards of 4 times the number currently estimated to occupy the Madison Range. Although our model validations using GPS data from the Spanish Peaks and the translocated animals strongly support the notion that bighorn sheep translocated to winter range would be able to access summer range, we did not directly evaluate connectivity between seasonal ranges. However, the amount of overlap between predicted summer and winter range (Fig. 3) suggests that bighorn sheep restored on low-elevation winter range should readily be able to access areas of high RSF-value summer habitat as elevational migrations are generally maintained through translocation (Lowrey et al. 2019).

A concern in the translocation of bighorn sheep into suitable but unoccupied habitat is the potential for commingling with domestic sheep and goats and the subsequent risk of transmission of bacterial pathogens associated with respiratory disease (Cassirer et al. 2017). Consequently, management agencies have established minimum separation distance policies when evaluating potential areas to establish new bighorn sheep populations to minimize risk of commingling (Western Association of Fish and Wildlife Agencies 2015). Almost all predicted bighorn sheep summer habitat in the Madison Range is in high-elevation National Forest lands, largely protected by wilderness designations with no permitted domestic sheep grazing allotments. Although livestock production is minimal in predicted low-elevation bighorn sheep winter range on the east side of the Madison Range, the Madison Valley on the west side of the range, where the majority of predicted bighorn sheep winter range occurs, is dominated by privately owned cattle ranches. Domestic sheep presence in the valley is primarily limited to short-term, intensively managed and localized grazing for weed control during the summer when bighorn sheep are on high elevation summer ranges. There is only 1 known flock of domestic sheep associated with a university agricultural research station at the northern end of our habitat extrapolation extent; thus, the majority of the unoccupied predicted bighorn sheep winter habitat has minimal commingling risk based on current management policies.

MANAGEMENT IMPLICATIONS

Our results indicate significant potential for bighorn sheep restoration within the Madison Range and describe a potential population structure that may maximize the possibility of higher abundances and broader distributions. Our results provide managers with a tool for identifying future translocation sites that maximize the probability of population establishment and provide an example framework for future restoration efforts. Given our predicted distributions of seasonal habitat, the strong behavioral fidelity that bighorn sheep exhibit towards seasonal ranges, and the slow generational process by which populations of animals accumulate geographic knowledge, it may be useful to consider short-range translocations into adjacent potential habitats as a means for restoring a metapopulation within the Madison Range. By moving animals within the same geographic region, short-range translocations may also reduce the risk of novel pathogen introduction. As managers face increasingly complex biological and social constraints to restoring and maintaining bighorn sheep populations, the implication that mountain ranges with established bighorn sheep populations may contain greater restoration potential than previously realized may provide new opportunities for creating and enhancing extant populations of bighorn sheep. Furthermore, by moving animals with an established knowledge of the broader landscape, rather than introducing naïve animals to a novel landscape, short-range translocations may promote exploration and decrease the number of generations needed to naturally recolonize unoccupied habitat.

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