SPATIAL ECOLOGY OF MOUNTAIN UNGULATES IN THE NORTHERN ROCKY MOUNTAINS: RANGE EXPANSION, HABITAT CHARACTERISTICS, NICHE OVERLAP, AND MIGRATORY DIVERSITY

by

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ABSTRACT

Mountain ungulates, although recognized as iconic and charismatic wildlife species, are the least studied and understood large mammals in western North America. The paucity of data, specifically concerning spatial ecology, presents a formidable challenge to regional wildlife managers tasked with the responsibility of managing populations with limited empirical studies on which to base decisions. We used GPS data collected from bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*) sampled from multiple populations throughout the northern Rocky Mountains to develop comparative studies characterizing seasonal habitats and potential range expansion of introduced mountain goats, niche overlap with native bighorn sheep, and migratory diversity of restored, augmented, and native bighorn sheep. Slope was the dominant predictor of mountain goat habitat use in both seasons, although mountain goats selected for steeper slopes in winter than in summer. Regional extrapolations depicted suitable mountain goat habitat in the Snake River, Teton, Gros Ventre, Wyoming and Salt Ranges centered around steep and rugged areas. Although bighorn sheep occurred on steeper slopes than mountain goats in summer and mountain goats occurred on steeper slopes in winter, we observed broad niche overlap according to season-species niche models and observed GPS locations where the two species were sympatric. In native bighorn sheep herds, we observed longer migrations on average and significantly more variation among individuals when compared to restored herds. The enhanced individual variation in native herds resulted in diverse portfolios of migratory behaviors and ranges, including newly documented high elevation long-distance migrants, increased switching rates between migratory behaviors, and sub-populations that were diffusely spread across both summer and winter ranges. In contrast, restored herds had limited individual variation, were largely non-migratory, had less switching between years, and were generally concentrated on both summer and winter ranges. In addition to increasing the abundance and distribution of bighorn sheep on the landscape, we suggest there may be value in simultaneously increasing the diversity of seasonal movement strategies, and in so doing, building resilience to future perturbations and disease, and mirroring the movement portfolios observed in native populations of bighorn sheep.

CHAPTER ONE

INTRODUCTION TO THE DISSERTATION

Mountain ungulates, although recognized as iconic and charismatic wildlife species, are the least studied and understood large mammals in western North America. The paucity of data, specifically concerning spatial ecology, presents a formidable challenge to regional wildlife managers tasked with the responsibility of managing populations with limited empirical studies on which to base decisions. While native, bighorn sheep (*Ovis canadensis*) have struggled to rebound to historic numbers since the early 1900's, and much of their historic range remains vacant or only partially inhabited after nearly a century of concerted restoration efforts (Buechner 1960, Singer et al. 2000). Although there are examples of robust native populations, many bighorn sheep in the western United States occur in small, isolated populations with fewer than 100 individuals and are hindered by respiratory pathogens and chronic lamb phenomena (Monello et al. 2001, Besser et al. 2012, Cassirer et al. 2013).

In contrast to bighorn sheep, the broad distribution of mountain goats (Oreamnos americanus) is largely characterized by range expansion. At the time of European settlement of North America, mountain goats were distributed from the mainland mountain ranges of southern Alaska, throughout the western Canadian Provinces and Territories, and into the northwestern United States including Washington, Oregon, and western Idaho and Montana (Côté and Festa-Bianchet 2003). While mountain goats did not experience the level of overexploitation and reduction typical of other North

American ungulates, wildlife management agencies included mountain goats in translocation programs during the early to mid-1900s and expanded their distribution beyond known historical ranges (Côté and Festa-Bianchet 2003). Translocation efforts have been largely considered a success with mountain goats broadly distributed across the western United States in a mosaic of native and restored populations throughout the northern Rocky Mountains and predominantly introduced populations to the south.

The northern Rocky Mountains, inclusive of the Greater Yellowstone Area (GYA) and western Montana (Figure 1.1), provides a rare opportunity to study many of the complex issues surrounding bighorn sheep and mountain goats, and provide descriptive characteristics of seasonal ranges and migration patterns. Mountain goats are considered non-native in the GYA according to reviews of archeological, paleontological, and historical records (Laundré 1990, Schullery and Whittlesey 2001) and have been steadily expanding their range since the introductions of 170 individuals from the 1940s to 1960s (Lemke 2004). Currently minimum population estimates are over 1,600 mountain goats within the GYA (Flesch et al. 2016). Information regarding continued range expansion and potential overlap with native bighorn sheep is a key issue for natural resource managers throughout the region (DeVoe et al. 2015).

Throughout the northern Rocky Mountains, bighorn sheep occur across a broad range of ecological and environmental conditions and represent a range of intrinsic factors with respect to demographic performance, migration strategies (Woolf et al. 1970, DeCesare and Pletscher 2006, Courtemanch et al. 2017), disease dynamics (Butler et al. In press), and genetic relatedness and diversity (Flesch et al. 2018). Consequently,

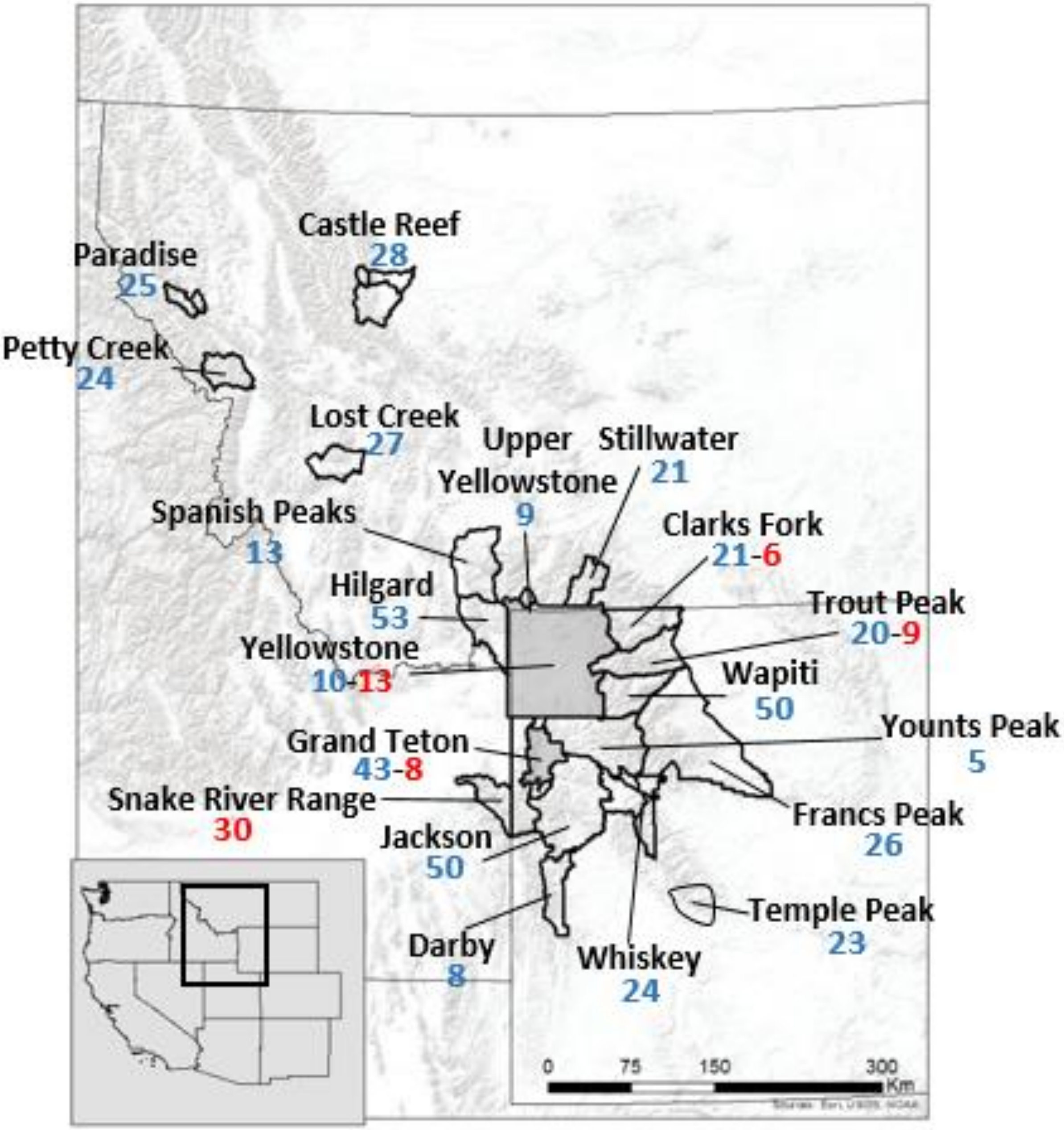

Figure 1.1 Bighorn sheep and mountain goat study herds throughout the northern Rocky Mountains, USA. The number of instrumented individuals is shown in blue for bighorn sheep and red for mountain goats.

traditional wildlife studies focused on a single population have limited ability to inform management over broader spatial scales. With respect to spatial ecology, while migratory movements clearly influence other large ungulates (e.g., White et al. 2007, Bolger et al. 2008, Sawyer et al. 2009, Tucker et al. 2018), our current understanding of bighorn sheep migration largely stems from management surveys or limited tracking of animals instrumented with VHF collars sampled from single populations. Given the diversity of bighorn sheep populations throughout the northern Rocky Mountains, a broad and comparative approach to studying spatial ecology will most effectively advance our understanding of the diversity of migration patterns and the relationship with demographic performance, disease dynamics, or genetics.

Recognizing the lack of empirical studies to address applied ecological questions, Montana State University and state and federal wildlife agencies initiated the Greater Yellowstone Area Mountain Ungulate Project and the State-wide Bighorn Sheep Research Initiative in 2009 and 2014, respectively (www.mtbighorninitiative.com). Broadly, the objectives of these two research efforts are to support management efforts by advancing our ecological knowledge of both species through developing and implementing comparative studies across broad spatial scales. Through collaborative efforts across multiple agencies and universities, the two projects have instrumented 525 bighorn sheep and 66 mountain goats throughout the study region (Figure 1.1) and greatly enhanced our ability to address ecological questions regarding spatial ecology.

Building from foundational ecological principles and theory, my dissertation addressed four applied research questions. In an effort to help predict the potential distribution of introduced mountain goats within the GYA, Chapter Two used resource selection models to characterize habitat relationships in the southwest GYA, and predicted suitable habitat in adjacent mountain ranges (Lowrey et al. 2017). Recognizing the concerns surrounding potential competition between native bighorn sheep and expanding mountain goats, Chapter Three employed a niche-based view of habitat and characterized niche similarities and overlap between sympatric bighorn sheep and mountain goats in the northeast GYA (Lowrey et al. 2018). In chapters four and five I transitioned from a habitat related questions and focused on migration patterns. More specifically, Chapter Four aggregated GPS relocation data across native, augmented, and restored bighorn sheep populations throughout the western United States, and characterized seasonal migration patterns with respect to elevational and geographic distances (Lowrey et al. In review). Using a similar approach, Chapter Five characterized the prevalence of multiple strategies across herds with different management histories, as well as behavioral fidelity to a strategy and spatial fidelity to seasonal ranges. Lastly, Chapter Six summarized general conclusions across the four research chapters of the dissertation and recommended areas for future research.

CHAPTER TWO

SEASONAL RESOURCE SELECTION BY INTRODUCED MOUNTAIN GOATS IN THE SOUTHWEST GREATER YELLOWSTONE AREA

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Abstract

Mountain goats (*Oreamnos americanus*) are among the least studied North American ungulates. Aided by successful translocations from the early to mid-1900's, introduced populations have greatly expanded within non-native ranges, yet there remains a paucity of empirical studies concerning their habitat requirements and potential distributions. The lack of studies presents a formidable challenge to managers tasked with monitoring mountain goat expansion and mitigating for any potential negative impacts posed to native species and communities. We constructed summer and winter resource selection models using GPS data collected during 2011–2014 from 18 (14 female, 4 male) mountain goats in the Snake River Range of the southwest Greater Yellowstone Area. We used generalized linear mixed-models and evaluated landscape and environmental covariates at multiple spatial grains (i.e. neighborhood analyses within 30, 100, 500, and 1,000 m buffers) within four related suites. The multi-grain resource selection function greatly improved model fit, indicating that mountain goat resource selection was grain dependent in both seasons. In summer, mountain goats largely selected rugged and steep areas at high elevations and avoided high solar radiation, canopy cover, and time-integrated NDVI. In winter, mountain goats selected lower elevations characterized by steep and rugged slopes on warm aspects and avoided areas with high canopy cover, NDVI amplitude, and snow water equivalent. Slope was the dominant predictor of habitat use in both seasons, although mountain goats selected for steeper slopes in winter than in summer. Regional extrapolations depicted suitable mountain goat habitat in the Snake River, Teton, Gros Ventre, Wyoming and Salt Ranges centered around steep and rugged areas. Winter range was generally characterized by the steepest slopes within a more broadly distributed and generally less steep summer range. Further research should examine the spatial and temporal overlap with native populations to further our understanding of resource selection dynamics and the potential for introduced mountain goats to alter intraguild behavioral processes of sympatric species, namely the Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*).

Key words

mountain goat; multi-grain analysis; *Oreamnos americanus*; resource selection function; RSF; Yellowstone.

Introduction

Mountain goats (*Oreamnos americanus*), because of their propensity to inhabit rugged and remote terrain, are among the least studied North American ungulates (Festa-Bianchet and Côté 2008). The paucity of empirical studies is most pronounced in the southern portions of their range where mountain goats are considered non-native according to reviews of archeological, paleontological, and historical records (Laundré 1990, Festa-Bianchet and Côté 2008, Schullery and Whittlesey 2001). Mountain goats are native to northwestern North America, primarily occurring within coastal and inland mountains west of the continental divide from southern Alaska, USA, through the Yukon Territories, Alberta, and British Columbia, Canada, and into the northwestern United States (Festa-Bianchet and Côté 2008). Successful translocations efforts during the early to mid-1900's have expanded the distribution of the species with introduced populations now established in Wyoming, Colorado, Utah, South Dakota, and Nevada as well as new areas of Alaska, Alberta, Washington, Idaho, and Montana (Festa-Bianchet and Côté 2008, Flesch et al. 2016). While the majority of mountain goats occur within their native range, the general range expansion within non-native regions has highlighted the need for empirical studies that investigate their ecological roles and management concerns. Studies of introduced mountain goats in Olympic National Park for example, documented negative impacts to fragile native alpine and subalpine communities including endemic and rare species, which prompted a large capture-relocation program in an attempt to reduce or eliminate mountain goats from the park (Houston et al. 1994). Moreover, the possibility that competition (Reed 2001) and disease transmission (Gross 2001) with native Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) is an important, but unevaluated concern throughout non-native ranges.

The Greater Yellowstone Area (GYA), one of the largest relatively intact temperate ecosystems in the world, represents a region where enhanced ecological knowledge of mountain goats within non-native ranges is needed. From an initial introduction of 170 animals to nine sites over 28 years (1942–1970), mountain goats have expanded their distribution and grown to an estimated 1648 individuals within the GYA (Flesch et al. 2016). The northeast GYA, where introductions were first initiated and most concentrated, is nearly completely colonized by mountain goats and contains roughly 632 individuals in and adjacent to Yellowstone National Park (Flesch et al. 2016). The most recent introductions occurred in the southwestern GYA in 1969 and

1970 with the translocation of 12 individuals into the Snake River Range. This population, currently estimated at 300 individuals (Fralick 2015, Idaho Department of Fish and Game 2015), is growing and expanding northward into the Teton Range including Grand Teton National Park where 40–60 animals were estimated in 2015. Despite the continuing increase in distribution and population numbers throughout the GYA, there remains a paucity of ecological data for mountain goats, specifically concerning their spatial ecology. The lack of ecological knowledge presents a formidable challenge to managers tasked with the responsibility of monitoring mountain goat expansion and mitigating for any potential negative impacts posed to native species and communities to maintain the ecological integrity within the region.

The summer occupancy surveys conducted in the northern GYA by DeVoe et al. (2015) provided the first assessment of the terrain and environmental characteristics associated with mountain goat occupancy and the first maps of their potential distribution throughout the GYA. DeVoe et al. (2015) predicted that mountain goats in the GYA could become 2.5–4.2 times more abundant than current population estimates if range expansion continues uninhibited. Data on mountain goat winter spatial ecology in the GYA is more limited and there are no regional habitat models that predict winter habitat use. Previous work on mountain goat wintering strategies in their native ranges generally indicate that they restrict movements to smaller geographic areas and move to lower elevations to avoid deep snow (Gross 2001, Poole and Heard 2003, White 2006, Poole et al. 2009). Wintering strategies are particularly important because of the harsh environments that mountain goats inhabit and the general restriction in suitable habitats which increases the possibility for intraguild competition if multiple species (e.g. bighorn sheep) are constrained to the same limited winter range (DeVoe et al. 2015).

Our objective was to broadly describe the seasonal spatial ecology of mountain goats in the southwest GYA. Using GPS data from 18 (14 female, 4 male) allopatric mountain goats, we built winter and summer resource selection models to: (1) further elucidate patterns in mountain goat resource selection within non-native ranges, including the terrain and environmental characteristics most strongly associated with seasonal ranges as well as the appropriate spatial grain, and (2) provide the first spatial predictions of seasonal habitat use by mountain goats in the southwest GYA and describe their potential distribution.

Methods

Study area

The Snake River Range spans the border between Wyoming and Idaho in the southwest GYA, with the Teton Range to the north and the Snake River and Palisades Reservoir to the south and west (Fig. 2.1). The rugged and steep Snake River canyon demarcates the range to the south and is frequently used by mountain goats. The Snake River Range is characterized by rugged, mountainous topography with elevations ranging from 1700–3000 m ASL. Mountain goats were first released into the Snake River Range in 1969 at Palisades Creek with an initial group of 5 individuals, and a secondary release of 7 individuals in 1970 at Black Canyon. While the animals at Black Canyon apparently did not survive (Hayden 1984), the release at Palisades Creek was successful with a population estimate of 300 individuals (adults = 253, kids = 47) in 2014 (Fralick 2015, Idaho Department of Fish and Game 2015). Although transient bighorn sheep are occasionally observed in the Snake River Range, the mountain goat population is considered allopatric. Mountain goats are now well distributed throughout the middle and southern portions of the Snake River Range and are presumed to be expanding northward.

Animal capture and handling

From 2011 to 2014 we used a combination of ground darting and helicopter net gunning to capture mountain goats, and primarily conducted capture efforts in summer and spring months. We targeted adult females, although due to the difficulty of capturing mountain goats, mature males were also included in the sample. All captured animals were fitted with a store-on-board GPS (Telonics TGW-4400-2 and TGW-4400-3) and VHF (Telonics MOD-401-1) radio collars. The dual collaring method enabled us to obtain fine spatial and temporal location information for 1.5–2 years before the GPS collar released from the animal, and an additional 5 years of monitoring with the VHF collar. The collars collected GPS locations at 4- or 6-hr intervals. All animals were processed at the capture location and handled according to the International Animal Care and Use Committee (IACUC) guidelines (Montana State University permit numbers 2011–17, 2014–32).

Data censoring

There are two dominant forms of error associated with GPS collars, spatial imprecision of acquired locations and habitat or behavior induced fix bias (Frair et al.

2004, Hebblewhite and Haydon 2010). We screened imprecise locations from the dataset by removing GPS locations with a horizontal dilution of precision (HDOP) >10. This follows the recommendation of D’Eon and Delparte (2005), but uses HDOP rather than position dilution of precision (PDOP), which does not include vertical error components and is no longer included in data files from the collar manufacturer. Measures of DOP are unitless and serve as an index of precision based on satellite configuration, but are not a measure of direct spatial imprecision (Telonics 2010). As a result we also screened locations based on the measurement of horizontal error included in Generation 4 Telonics collar data files and censored all locations with an estimated error > 60 m.

Fix bias can introduce error into resource selection studies by under representing habitat types or landscape characteristics that reduce the probability of a GPS unit acquiring a location (Johnson and Gillingham 2008, Frair et al. 2010). Previous work suggests that dense canopy cover and steep slopes reduce GPS collar performance by diminishing communication with orbiting satellites (D’Eon et al. 2002). Because mountain goats inhabiting inland areas predominantly occur within subalpine and alpine vegetation zones with little to no canopy cover in both summer (Gross et al. 2002, Poole and Heard 2003) and winter (Taylor and Brunt 2007, Poole et al. 2009), it is unlikely that canopy cover results in large reductions in fix success. For mountain goats, terrain (e.g., slope) is likely to have a greater impact on collar performance. However, because of the strong seasonal association with steep, alpine environments (Poole et al. 2009, DeVoe et al. 2015), it is unlikely that these habitats will be greatly underrepresented in the dataset. As a result, we did not censor individuals based on fix success, and assumed that any potential bias from steep slopes would not alter the fundamental conclusions regarding mountain goat seasonal resource selection.

Delineating mountain goat seasons

Mountain goat movements are difficult to delineate into seasons because of the large degree of individual variation in response to seasonal environmental conditions (Rice 2008). We applied nonlinear regression analyses of net-squared displacement (NSD; Bunnefeld et al. 2011) to delineate individuals into groups according to migration strategy and estimate migration parameters. Rather than calculate NSD from the capture location of each individual (i.e. Bunnefeld et al. 2011), we calculated NSD from a mean winter range centroid. For each individual we calculated the centroid of the GPS locations obtained between 1-December and 31-Janurary, which provided a location estimate of the 'mean winter range' from which we measured displacement (Euclidian distance) of each GPS relocation. This approach better accommodated our seasonally-staggered capture schedule and allowed us to calculate displacement from a mean winter range regardless of where or in what season an animal was captured. We then fit the equations from Bunnefeld et al. (2011) and averaged the individual start and end dates for migrants and mixed-migrants to obtain an estimate of the mid-point for spring and fall migratory periods for the population. We then buffered the migratory midpoints by +/-20 days, which approximated the 90th percent quantile of the observed maximum spring and fall migration durations. This process provided estimates of spring and fall migratory periods which were removed from the data set to build season-specific resource selection models without the associated 'noise' created by migratory movements.

Defining habitat availability

We evaluated population-level resource selection (i.e., second-order; Johnson 1980) and employed a used-available design where individuals were identified and contained a unique ‘used’ set, but ‘availability’ was measured at the population level (i.e. Design II; Manly et al. 2002). We defined the extent of availability using a buffered minimum convex polygon (MCP) and used the same extent for summer and winter seasons. The MCP encompassed the pooled GPS locations and was then buffered by the 95 percent step length between consecutively acquired locations (Laforge et al. 2015b). This approach allowed the extent of availability to be determined by the movement metrics of the study animals. Within the availability extent we generated a random sample of points at a ratio of 1:10 (used:available). The 1:10 ratio ensured a sufficient sample to avoid numerical integration error and convergence issues (Northrup et al. 2013), and adequately described the distribution of each covariate within the study area (Appendix S2.1).

Resource covariates and spatial grain

We hypothesized the effect (Table 1; positive or negative) of each covariate on mountain goat use and evaluated these hypotheses through the model selection process. We evaluated covariates within four suites including terrain, vegetation, heat load, and snow (Table 2.1; DeVoe et al. 2015). The terrain suite included elevation (ELEV), slope (SLP), and three measures of ruggedness – slope variance (SLPv), calculated as the standard deviation^2 of SLP (DeVoe at al. 2015), the standard deviation of landscape curvature (CurvSD; Poole et al. 2009), and Vector Ruggedness Measure (VRM), which measured the integrated variation in slope and aspect (Sappington et al. 2007). With the exception of ELEV in winter, we predicted that all of the terrain covariates would be positively correlated with mountain goat use (Table 2.1). We did not include measures of distance to escape terrain in the initial model building process following recent suggestions from DeVoe et al. (2015) who concluded that the combined use of SLP and SLPv provided a more biologically meaningful understanding of mountain goat habitat. Rather, we conducted post-hoc model comparisons with distance to escape terrain (*Post-hoc model comparisons* section below) to further evaluate the findings of DeVoe et al. (2015).

The vegetation suite contained canopy cover (CanCov) and two competing measures of normalized difference vegetation index (NDVI), NDVI amplitude ($NDVI_{Amp}$; USGS EROS Center 2016) and time-integrated NDVI ($NDVI_{Tin}$; USGS EROS Center 2016). We included NDVI covariates as a measure of forage in both summer and winter seasons and predicted that NDVI would be positively correlated with mountain goat use. While vegetation is mostly covered by snow during the winter months, including NDVI as a winter covariate allowed us to evaluate whether or not the areas in which mountain goats forage in winter were associated with summer NDVI. We calculated the mean $NDVI_{Amp}$ and $NDVI_{Tin}$ from 2011 to 2014 to create a single measure for the duration of the study. The heat load suite contained two covariates that captured the intensity of solar radiation on the landscape. We estimated the duration of solar radiation (RAD; Fu and Rich 1999) and aspect, which was transformed into a biologically interpretable index by taking the inverse cosine of the angle minus 35 degrees (AspectCos; Cushman and Wallin 2002). This transformation changed the axis from N - S to NNE - SSW and ranges from -1 to 1, respectively (Cushman and Wallin 2002). For both measures of heat load we predicted that mountain goats would select for relatively warm areas in winter and relatively cool areas in summer. Lastly, we included two measures of snow accumulation, snow depth (SnowDepth; NOHRSC 2004) and snow water equivalent (SWE; NOHRSC 2004), and created a single value for each covariate by averaging the daily values from 1-December to 31-January in 2011 to 2014. We predicted that both measures would be negatively associated with mountain goat use.

In addition to including a linear term for each covariate, we evaluated a pseudothreshold (natural log) form for the three ruggedness indices and a squared term for SLP and ELEV (Table 2.1). We hypothesized that the pseudothreshold form, whereby the relationship with resource selection was allowed to asymptote above a given ruggedness threshold, would provide a better fit to the data (DeVoe et al. 2015). Similarly, we hypothesized the squared terms for SLP and ELEV, which allowed the relationship to peak at an optimal covariate value, would also be ranked higher than the linear form (Gross et al. 2002, Poole et al. 2009). Evaluating additional functional forms provided more flexibility in determining the most explanatory covariates, and has been shown to improve model fit for previous mountain ungulate resource selection studies (Gross et al. 2002, Poole et al. 2009, Hoglander et al. 2015, DeVoe et al. 2015).

Recent work has highlighted the importance of evaluating covariates at multiple spatial grains, and suggests that a multi-grain approach provides a more informative predictive model by incorporating the ‘space of influence’ on animal decisions in regards to resource selection (Meyer and Thuiller 2006, Laforge et al. 2015b). 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. minimum resolution of the data) but may also be influenced by a broader region (e.g. the 'space of influence'; Laforge et al. 2015b). Within the context of a multi-grain analysis, grain is defined as the size of an area surrounding a point (or pixel) within which ecological data are measured (Meyer and Thuiller 2006, Laforge et al. 2015b), and does not specifically refer to the minimum resolution of the data (e.g. Hobbs 2003). We evaluated covariates at four grain sizes by performing neighborhood analyses at 30, 100, 500, and 1,000 m circular buffers using the raster package (Hijmans et al. 2015) in program R (R Core Team 2015). Multiple grains were not evaluated below the minimum resolution of the data for any given covariate and were restricted to covariates that could be visually perceived (Table 2.1). Following DeVoe et el. (2015), we hypothesized that terrain covariates would be best characterized by larger spatial grains and that forage covariates would be best characterized at relatively small spatial grains. These hypotheses reflect a possible hierarchical structuring to mountain goat habitat selection whereby animals first select broadly for terrain covariates and secondarily select for vegetation covariates at smaller spatial grains (DeVoe et al. 2015).

Statistical framework and model selection

We identified individual mountain goats as the sample unit and accounted for the autocorrelation within individuals and unbalanced sample size among individuals by specifying a random intercept for each mountain goat using a mixed model framework

(Gillies et al. 2006, Fieberg et al. 2010). We calculated the relative probability of use using the exponential resource selection function (RSF):

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

where $\hat{\beta}_0$ is the intercept, and $\beta's$ are the coefficients of the effects of the covariates, X_i, on $\widehat{w}(x)$, the relative probability of use. The exponential RSF is a relative probability function, not a true probability (i.e. RSPF; Lele and Keim 2006, Lele 2009). Following similar studies (e.g. Gillies et al. 2006, Hebblewhite and Merrill 2007, Laforge et al. 2015b), we retained the intercept term, $\hat{\beta}_0$, when generating regional predictions within the mixed-model framework. We then applied a linear stretch to rescale the predicted RSF values between 0 and 1 (Johnson et al. 2004):

$$\widehat{w} = \left(\frac{w(x) - \ w_{min}}{w_{max} - \ w_{min}}\right)$$

We employed a tiered approach in model selection that guided our progression from relatively simple univariate models focused on identifying the most explanatory functional form and spatial grain, to multivariate models that evaluated different covariate combinations within model suites (Franklin et al. 2000, DeVoe et al. 2015). More specifically, in tier one we fit univariate models for each covariate for which we evaluated multiple grains and functional forms (Table 2.1), and selected a single grain and form for each covariate using AIC_c (Burnham and Anderson 2002). Because we evaluated similar indices for some covariates (e.g., $NDVI_{Amp}$ and $NDVI_{Tin}$), we again used univariate models and AIC_c to select between similar indices in tier two. In tier three we began multivariate model building using the covariates and the respective grains and functional forms identified in tiers one and two. Because of the strong association with steep and rugged terrain throughout their range and the predominance of terrain covariates in previous mountain goat resource selection studies (Smith 1986, Poole and Heard 2003, White 2006, Poole et al. 2009, DeVoe et al. 2015), we began by building a base terrain model which evaluated all non-collinear combinations of SLP, ELEV, CurvSD, SLPv, and VRM. Lastly, we built upon the base terrain model with an all combinations approach using the remaining covariates from the vegetation, heat load, and snow (in winter) suites. Because we were predominantly interested in marginal (population) inferences, we used conventional AIC_c throughout the model selection process as recommended by Vaida and Blanchard (2005). In all multivariate models we excluded covariate parings with a Pearson's correlation coefficient of $r > |0.6|$. We followed the same sequential, step-wise approach for summer and winter and fit mixed-effects models using the lme4 R package (Bates et al. 2016) with scaled and centered covariates.

Post-hoc model comparisons

We performed a series of post-hoc model comparisons to evaluate distance to escape (i.e. steep) terrain as an additional covariate and also evaluated the multi-grain approach. Distance to escape terrain (DET) is often used as an explanatory covariate for mountain ungulate habitat models and resource selection studies (Gross et al. 2002, DeCesare and Pletscher 2006, Poole et al. 2009), but the choice of a threshold with which to define escape terrain is highly variable (ranging from 25° to 50°) and subjective (Gross et al. 2002, DeVoe et al. 2015). After evaluating a model set comparing measures of DET with slope and slope variance, DeVoe et al. (2015) recommend that slope and slope variance be used in place of DET as a more biologically informative interpretation of mountain goat habitat associations. While these efforts have helped to demonstrate the combined importance of slope and slope variance, their model comparisons did not allow for the combined influence of DET with slope and slope variance. Notwithstanding collinearity issues which can be problematic when characterizing landscape terrain (Fu and Rich 1999, Poole et al. 2009), we hypothesized that DET, in combination with slope and slope variance, would improve model performance and predicted that DET would have negative relationship with mountain goat resource selection. We evaluated this hypothesis with three measures of DET defined as slopes ≥ 40, 45, and 50 degrees (DET40, DET45, DET50, respectively), and added each to our top summer and winter model. We then evaluated the inclusion of the DET terms using AIC_c (Burnham and Anderson 2002). All DET covariates were characterized at the 30 spatial grain. DET measures with a Pearson's correlation coefficient of $r > |0.6|$ when combined with any covariate in our top a priori models were not evaluated.

We tested the multi-grain approach by fitting a new model with the same covariate structure as our top a priori model, including the potential addition of DET, but used the minimum resolution available for each covariate. For each season we ranked the multi-grain and minimum resolution models using AIC_c. Using the minimum resolution available for a given covariate is often the default approach for resource selection studies, but there is little biological justification for the practice (Hobbs 2003, Boyce 2006, Laforge et al. 2015b). Following Laforge et al. (2015b), the post-hoc model comparison served as an additional confirmatory test of the multi-grain approach.

Mountain goat RSF extrapolations

To meet our second research objective we generated regional extrapolations of the top seasonal models to delineate mountain goat habitat throughout the southwest GYA. We extrapolated from the Snake River Range study area to the broader Snake River Range, and also north to the Teton Range, east to the Gros Ventre Range, and south to the Wyoming and Salt Ranges. Collectively, the five mountain ranges of the southwest GYA represent a nearly contiguous expanse of mountainous terrain. In each region we generated predications of the relative probability of use and discretized the RSF value of each pixel into ten equal-area bins representing a relative habitat classification from poor to best. We also generated maps of 'suitable' habitat for each region and defined suitable areas as those with an RSF value ≥ the lower 5 percent of the RSF values from used locations and quantified the amount of suitable habitat in each region (DeVoe et al. 2015).

Model validation

We used a multifaceted approach to evaluate model predictive performance. First, within the study area we performed k-fold cross-validation where k indexed each individual rather than a random data fold (Boyce et al. 2002). Within an iterative process we withheld the locations for each individual, 1 through k, fit an exponential RSF with the individuals 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-rank correlation (Boyce et al.

2002). The adjusted frequencies should be highly correlated with the relative RSF if the model performs well (Boyce et al. 2002).

Secondly, we validated the Teton Range extrapolation with an independent sample of 800 winter and 2,405 summer mountain goat GPS locations that were collected from December 2014 to March 2016. We indexed the available distribution of RSF values within the Teton Range by generating 10,000 random locations which were used to define 10 equal-area bins for each seasonal extrapolation. Following the same *k*-fold methods employed within the study area, we summed the frequency of occurrence within each equal-area bin using the independent sample and evaluated the predictive performance with Spearman-rank correlation (Boyce et al. 2002).

Results

Data collection, censoring, and definitions

Capture efforts began in the summer of 2011 and continued to the spring of 2014, resulting in the instrumentation of 18 mountain goats (14 female, 4 male; Appendix S2.2) with GPS and VHF collar pairs. With the exception of one yearling male, all animals were classified as adults with a mean age of 4 years (Appendix S2.2). Animals were monitored for an average of 514 days (range 265–753), resulting in 38,040 GPS locations. We censored 28 locations with a HDOP > 10 and 140 locations with a horizontal error > 60 m. After censoring, the mean summer and winter fix success was 86 and 81 percent, respectively (Appendix S2.2). There were 15 animal-years that produced coefficient estimates for each of the Bunnefeld et al. (2011) movement equations.

Thirteen of the 15 animal-years were classified as migrant or mixed-migrant and two were classified as resident. Using the buffered midpoints from the population spring and fall migrations we defined the summer season as June 16th to October 13th and the winter season as November 22th to May 7th (Appendix S2.3). After removing locations associated with migratory periods we had 15,029 and 12,495 used locations for summer and winter respectively. The study area MCP was buffered by 642 m, representing the 95th percent quantile of sequential step lengths and encompassed 472 km^2 (Fig. 2.1).

Model selection and validation

Our tier one results highlighted the importance of evaluating multiple spatial grains and indicated that the relationship with a given covariate can be grain-dependent. For each covariate where multiple spatial grains were evaluated, there was a clear top-ranked spatial grain and substantial differences between AIC_c scores (Appendix S2.4: Table S2.1, Fig. S2.1, S2.2). With the exception of CanCov and VRM which had opposite grain sizes in each season, the top ranked spatial grain for a given covariate was similar for summer and winter (Appendix S2.4: Table S2.1). In contrast to our predictions, the covariates from the vegetation suite were best characterized at large spatial grains (i.e. 1000 m) in both seasons. There were mixed results within the terrain suite. In summer CurvSD and SLP were best characterized at 500 m, SLPv at 30 m, and VRM at 1000 m. In winter there was a general reduction in the spatial grain. Within the terrain suite CurvSD was best characterized at 500 m, SLP at 100 m and SLPv and VRM at 30 m. In support of our predictions we also observed striking differences in predictive power for different functional forms (Appendix S2.4: Table S2.1, Fig. S2.1, S2.2). Within the terrain suite the pseudothreshold form was top-ranked for all covariates while the quadratic form was top-ranked for all covariates within the forage suite (Appendix S2.4: Table S2.1).

In tier two, there were substantial differences in AIC_c rankings between related indices within a suite. In summer, $NDVI_{Tin}$ was ranked above $NDVI_{Amp}$ (ΔAIC 16,263), and RAD was ranked above AspectCos (ΔAIC_c 314; Appendix S2.4: Table S2.2). The results were opposite in winter where $NDVI_{Amp}$ was ranked above $NDVI_{Tin}$ (ΔAIC_c 11,335) and AspectCos was ranked above RAD (ΔAIC 1,964; Appendix S2.4: Table S2.2). In winter SWE was ranked above SnowDepth (ΔAIC 368; Appendix S2.4: Table S2.2).

The tier three base terrain model had the same covariates and functional forms across seasons, but there were slight differences in the spatial grains (Appendix S2.4). The multivariate combination of SLP, SLP^2, $SLPv^{ps}$, ELEV and $ELEV^2$ was the most supported, non-collinear terrain model for both seasons. When evaluated with the other top ranked covariates from tiers one and two, the top-ranked summer model contained SLP_{500}, SLP^2_{500}, $SLPv^{ps}_{30}$, $ELEV_{30}$, $ELEV^2_{30}$, $CanCov_{1000}$, $NDVI_{Tin1000}$, and RAD_{30}. The top ranked winter model contained SLP_{100}, SLP^2_{100}, $SLPv^{ps}_{30}$, $ELEV_{30}$, $ELEV^2_{30}$, $CanCov_{30}$, $NDVI_{Amp1000}$, $AspectCos_{30}$, and SWE_{1000} (Appendix S4: Table S3).

As predicted, the post-hoc evaluations indicated that measures of DET provide additional explanatory power above the paired combination of SLP and SLPv. When added to the previous models, DET50 and DET40 were ranked highest in summer and winter, respectively (Appendix S2.4: Table S2.4). Adding DET in winter had a greater impact on model performance than in summer (Fig. 2.2, Appendix S2.4: Table S2.4). The post-hoc test of multiple spatial grains further supported the multi-grain approach (Laforge et al. 2015b). When compared to our summer and winter multi-grain models (including the respective measures of DET), models with the same structure at the minimum resolution had substantially higher AIC_c sores (summer ΔAIC 5,179; winter ΔAIC 1,651; Appendix S2.4: Table S2.5).

As predicted, mountain goats generally selected for relatively high elevations in summer and lower elevations in winter (Fig. 2.2). The quadratic form of the covariate indicated optimal summer and winter elevations of 2630 and 1888 m, respectively. In both seasons there was a strong positive association with SLP, however the opposite signs for SLP^2 resulted in strikingly different relationships (Fig. 2.2; Appendix S2.4: Table S2.6). In summer, the negative coefficient for SLP^2 resulted in a convex function with an optimal slope angle of 35°. In contrast, the positive coefficients for both SLP and SLP^2 in winter indicated that the relationship with slope increased as a positive quadratic function and that relatively steeper slopes were selected in winter than in summer (Fig. 2.2). In both seasons, mountain goats selected for rugged areas with high SLPv values at the minimum spatial grain (30 m). The pseudothreshold form of SLPv was stronger in summer than in winter, yet in both seasons the relationship began to asymptote as SLPv increased (Fig. 2.2).

Within the vegetation suite, the indices for NDVI varied among seasons. Contrary to our prediction we found a negative relationship with $NDVI_{Tin1000}$ in summer and $NDVI_{Amp1000}$ in winter (Fig. 2.2). As expected, there were negative relationships with

CanCov in both seasons. In summer mountain goats avoided CanCov at a larger spatial grain than in winter (Fig. 2.2). The top ranked covariates within the heat load suite varied between seasons, yet corroborated our predictions and indicated that mountain goats selected against heat in summer and for heat in winter. In summer, RAD_{30} was the top ranked index of heat load and showed a negative relationship. In winter head load was best indexed by AspectCos_{30} with which there was a positive relationship, indicating preference for southwest aspects (Fig. 2.2). Lastly, as expected there were negative relationships with SWE in the winter snow suite and DET in both seasons and (Fig. 2.2).

The *k*-fold evaluation methods for interpolations within the study area showed a strong correlation between area-adjusted frequencies and the relative RSF in summer $(r_s = 0.98, p < 0.0001)$ and winter $(r_s = 1, p < 0.0001$; Appendix S5: Fig. S2.1; Appendix S6). Moreover, the extrapolations within the Teton Range were also highly correlated with the relative RSF score in both seasons $(summer\colon r_s = 0.98, p < 0.0001; winter\colon\ r_s = 0.95, p < 0.0001$; Appendix S2.5: Fig. S2.1).

Mountain goat RSF extrapolations

Regional extrapolations highlighted the importance of high elevation rugged terrain in summer, which served as the core mountain goat habitat throughout the southwest GYA (Fig. 2.3; Appendix S2.7). Winter extrapolations depicted broad range contraction and preference for steep areas patchily distributed across mid-elevations (Fig. 2.3; Appendix S2.7). The cutpoints used to define suitable summer and winter habitat were 0.0023 and 0.0002 respectively. Although there were distinctive summer and winter ranges delineated by elevation, there was noticeable overlap in suitable habitat centered around steep and rugged slopes at mid-elevations (Fig. 2.3). In many areas, core winter habitat was defined by the steepest slopes within a more broadly distributed and generally less steep summer range (Fig. 2.3; Appendix S2.7).

In general the proportions of suitable habitat within each mountain range were low (Table 2.2). The Salt and Wyoming Ranges had the smallest proportion of suitable habitat in both summer and winter, 3.4 and 0.9 percent, respectively. In contrast, the Snake River Range (inclusive of the study area) had the highest proportions of suitable habitat, 9.3 and 5.6 percent for summer and winter, respectively. On average, suitable habitat in summer was more than double that of winter.

Discussion

Our results provide an empirical assessment of the landscape and environmental covariates influencing mountain goat resource selection within their non-native ranges and the first seasonal predictions of mountain goat habitat in the southwest GYA constructed from GPS collar data. Our findings broadly corroborate with similar studies throughout the mountain goat's native range and demonstrate a strong seasonal association with rugged and steep mountain environments (Gross et al. 2002, Poole and Heard 2003, White et al. 2012, DeVoe et al. 2015, White and Gregovich 2017), yet provide new insights for introduced mountain goats that highlight seasonal differences in resource selection and the importance of spatial grain in predicting habitat selection.

During the summer months, mountain goats largely inhabited rugged and steep areas at high elevations and avoided high solar radiation, canopy cover, and time-integrated NDVI. Slope was the most influential predictor of the relative probability of use and indicated an optimal slope angle of 35 degrees. The strong positive relationship with steep slopes was also evident in the inclusion of distance to escape terrain, which in summer was defined as slope angles ≥ 50 degrees. The transition to high, alpine areas in summer is commonly observed in mountain ungulates and coincides with the greening of vegetation and snow melt (Varley 1994, DeCesare and Pletscher 2006, Pettorelli et al. 2007). The results from our evaluation of NSD and seasonal habitat predictions indicate that mountain goats in the southwest GYA undergo seasonal movements to relevantly high elevations in summer as snow dissipates. However, the negative relationship with NDVI was a surprising result and counter to our hypothesized relationship with the relative probability of use.

The use of NDVI as an index of forage is ubiquitous in similar research with related taxa (Pettorelli et al. 2005, 2011), but has not been included as a habitat covariate for similar studies of mountain goats on native ranges. Within non-native ranges of the GYA, DeVoe et al. (2015) reported a positive relationship between summer occupancy and NDVI. The explanation for the apparent avoidance of NDVI by mountain goats in this study, is likely best interpreted through the differing sampling designs. Within an RSF context, we defined availability with random points generated within a buffered population MCP. These methods thoroughly indexed the entire study area, including high NDVI values associate with low elevation forests. In contrast, DeVoe et al. (2015) targeted alpine and subalpine ‘viewsheds,’ which were largely void of low elevation forests. Given the relatively broad characterization of available sites within the RSF context, the contrasting results with DeVoe et al. (2015) likely result from different characterizations of available (or unused) sites (Beyer et al. 2010) which resulted in a relatively broad characterization of NDVI within the RSF framework. Moreover, while we minimized the influence of canopy cover on NDVI by evaluating two indices which measure change in NDVI from the first day of the growing season (USGS EROS Center 2016), NDVI values within the study area were consistently lower in the rugged and steep terrain selected by mountain goats when compared to surrounding regions. While forage is obviously an important component of mountain goat habitat, the relationship was likely masked by the dominant selection for steep and rugged slopes at the home range level, which are characteristically rocky and have relatively low NDVI values. It is likely that a third order (i.e. within home range) analysis would show positive associations with NDVI.

Our top winter model indicates that mountain goats select lower elevations characterized by steep and rugged slopes and avoid areas with high canopy cover, NDVI amplitude, and SWE. In winter, mountain goats also selected for relatively warm southwest aspects and for areas close to slopes ≥ 40 degrees. As in summer, slope was the most influential covariate, but with a notably different relationship with the relative probability of use. Selection for slope in winter resulted in a positive quadratic function that was not maximized at an optimal slope angle and indicated that mountain goats select for steeper slopes in winter than in summer. The relative importance of steeper slopes in winter was also highlighted by the striking improvement in the top model with the post-hoc addition of distance to escape terrain. We suspect steeper slopes are selected in winter as a behavioral adaptation to avoid deep (or recently fallen; i.e., Richard et al. 2014) snow, which is more readily shed in steep environments, and in so doing reduces the metabolic costs associated with movement and increases access to forge. Moreover, mountains goats also selected southwest aspects in winter, which further reduces snow accumulation due to increased solar radiation.

Winter is an important season for mountain goats that can influence population dynamics through increased juvenile mortality (Côté and Festa-Bianchet 2003), reduced kid production (Adams and Bailey 1982), and possibly determine the ecological carrying capacity through decreased forage availability (Houston and Stevens 1988). Because of the critical importance of winter, there have been a number of targeted studies examining mountain goat wintering strategies and movements on native ranges which generally indicate that mountain goats inhabit timbered, low elevation slopes (White 2006, White et al. 2012) and show no differences in the optimal slope angle between seasons (White et al. 2012, White and Gregovich 2017). We speculate the difference in wintering strategies between native and non-native populations is largely influenced by regional snow climates. Much of previous work regarding mountain goat movement patterns and resource selection has been conducted within maritime environments (although see Poole and Heard 2003) which are characterized by a relatively stable and dense snowpack (McClung and Schaerer 2006). In contrast, the majority of introduced mountain goats, including those in the GYA, are within a continental snowpack with dry, low density snow that is more frequently shed from steep slopes (McClung and Schaerer 2006). Within the maritime environments winter snow can accumulate on relatively steep slopes and thereby nullify the effect of slope angle on snow depth that is observed in continental snow climates. In maritime snow climates low elevation timbered slopes likely offer a better refuge from winter snow than do steep slopes. The wintering strategy of mountain goats in the southwest GYA is akin other mountain ungulates in continental regions such as the alpine ibex (*Capra ibex*), which select for steep rocky environments in the presence of high snow cover (Grignolio et al. 2004).

DeVoe et al. (2015) suggested that distance to escape terrain be replaced by slope and slope variance, accurately arguing that measures of distance to escape terrain "constrain selection to an arbitrary threshold value and assume equal selection of slopes greater than that threshold." Nonetheless, their approach to evaluate the paired combination of slope and slope variance with distance to escape terrain assumed that all measures of distance to escape terrain were highly correlated with slope, and therefore were not appropriate for inclusion in the same model (e.g., Gross et al. 2002). While we recognize the limitations of distance to escape terrain in the absence of slope and slope variance, our results suggest that non-collinear measures of distance to escape terrain can be paired with slope and slope variance to produce a more informative and predictive model. Our results also support the notion that limiting the interpretation of distance to escape terrain to a predator avoidance strategy misses the larger ecological story. Mountain goats have evolved to occupy an ecological niche largely associated with steep and rugged terrain where they have access to a unique suite of environmental resources necessary for survival and reproduction. While steep terrain can certainly provide a refuge from predators, our work broadens the interpretation of escape terrain to include other fundamental components of the mountain goat niche, for example strongly associating with steep cliffs in winter as a snow avoidance strategy. We encourage future efforts to more broadly interpret the importance of escape terrain beyond simply predator avoidance in order to more realistically describe the mountain goats' ecological niche.

The striking differences in AIC_c ranking between multiple spatial grains of the same covariate (univariate tier one models), as well as the post-hoc comparison of our top models with the minimum resolution models provides additional support for the multi-grain RSF (MRSF; Laforge et al. 2015b) and demonstrates that mountain goat resource selection can be grain-dependent. Heterogeneity and fragmentation are important determinants when relating animal resource selection to scalar processes such as a multi-grain RSF (Laforge et al. 2015b, Boyce et al. 2003), which is therefore dependent on the conditions within the study area. While our top seasonal models were greatly improved by evaluating multiple spatial grains, there is likely a tradeoff in broad utility as models incorporate additional study area dependent covariates which may result in a predictive cost when extrapolated to new areas. While there was some corroboration with DeVoe et al. (2015), for example the importance of slope at 500 m, comparisons between studies in the southern and northern extremes of the GYA should be conducted with caution. DeVoe et al. (2015) suggested a hierarchical structuring to mountain goat habitat selection whereby animals first select for terrain covariates at broad grains and secondarily select for vegetation covariates at smaller spatial grains. In contrast to DeVoe et al. (2015), our results did not depict a clear distinction in the top ranked grain sizes among the covariate suites. Our results for winter indicate a general reduction in the spatial grain and suggest mountain goats perceive landscape attributes at smaller spatial grains in winter than in summer. The smaller grain sizes in winter likely reflect the observed range contraction and reduced mobility. Additional studies over broad distributions will help to highlight conclusions regarding the importance of spatial grain in predicting animal resource selection. Nonetheless, the multi-grain RSF is an important methodological step in resource selection studies that can significantly improve model fit and biological interpretation (Hobbs 2003, Boyce 2006, Laforge et al. 2015b, 2015a, Northrup et al. 2016), although we encourage additional work that explores the potential predictive cost when predicting to disjunct regions.

Although the expansion of mountain goats throughout the GYA has been relatively slow, their distribution has been steadily increasing since the initial introduction (Lemke 2004, Flesch et al. 2016). As mountain goats continue to expand throughout the GYA, so too does the concern that competition and disease transfer could negatively impact native bighorn sheep on sympatric ranges (Gross 2001). Moreover, it has been hypothesized that sympatric populations on shared winter ranges are particularly vulnerable to competition due to the general restriction in suitable habitats and observed range contractions of both species (Poole and Heard 2003, DeVoe et al. 2015, Poole et al. 2016).

Within the Teton Range our spatial predictions of suitable habitat were largely centered along the rugged and steep core of GTNP and comprised 4.9 and 2.8 percent of the study area in summer and winter, respectively. These areas have also been the first to be colonized by emigrating mountain goats (S. Dewey, unpublished data), and are generally sparsely inhabited by native bighorn sheep which largely occur in the northern and southern regions (Whitfield 1983, Courtemanch 2014, S. Dewey, unpublished data). While the seasonal ranges of mountain goats and bighorn sheep in GTNP are mostly non-overlapping at present (Courtemanch 2014, S. Dewey, unpublished data), it is unclear if the observed spatial separation results from behavioral differences in resource section influenced by intraguild competition, or because of the nascent stages of mountain goat colonization. If mountain goat numbers continue to increase within GTNP, it is reasonable to expect their distribution to expand into additional suitable areas throughout the Teton Range and increase their spatial overlap with native bighorn sheep. While sporadic sightings of single or small groups of mountain goats have been documented in GTNP since the late 1970's, 2008 marked the beginning of a steady population increase and year-round residence. Since 2008, mountain goat population estimates have increased to 20–40 individuals in 2014 and 40–60 individuals in 2015 (S. Dewey, unpublished data), prompting park managers to begin drafting a Mountain Goat Management Plan Environmental Assessment (http://parkplanning.nps.gov/mountaingoat). Within the Tetons specifically, DeVoe et al. (2015) suggested that mountain goat numbers could ultimately range from 248–411 individuals.

Our seasonal resource selection models indicate the Gros Ventre Range has ample suitable habitat for mountain goats, although they are currently not present. Summer range in the Gros Ventre largely consists of the high elevation steep slopes which generally trend from northwest to southeast, while winter range was restricted to the steepest slopes at mid-elevations as well as lower elevations in the western portion of the range. Given the nearly 40 years it has taken mountain goats to expand to the contiguous

Teton Range, it is unlikely that the potential colonization of the Gros Ventre will be a rapid event. Nonetheless, although the Gros Ventre Range is relatively isolated from current mountain goat populations in the Snake River and Teton Ranges, dispersing individuals have been documented crossing large swaths of unsuitable habitat when colonizing new areas that exceed the geographic distance between the Gros Ventre Range and current mountain goat populations (Côté and Festa-Bianchet 2008). Moreover, as population densities continue to grow, it is likely that dispersal rates will increase (Williams 1999), thus further increasing the likelihood of colonization of unoccupied ranges. Bighorn sheep in the Gros Ventre Range remain allopatric and are currently estimated at 425 individuals that are widely distributed throughout the range (Wyoming Game and Fish Department 2015).

Interestingly, the Wyoming and Salt Ranges currently do not have resident mountain goat populations, yet are immediately south of the Snake River Range. The absence of mountain goats in the Wyoming and Salt Ranges is surprising given the close proximity to a robust source population, and is possibly explained by the joint barrier posed by Hwy 89 and the Snake River, and/or the largely disconnected seasonal ranges (Fig 2.3). While our models indicate 173 km^2 of suitable summer habitat, winter habitat is noticeably sparse and relatively distant from summer ranges. Both the amount and lack of continuity between suitable summer and winter habitats may limit the southern expansion into the Wyoming and Salt Ranges, especially considering the relatively short seasonal migrations we observed (Appendix S2.3). Currently, the Wyoming and Salt Ranges are mostly void of bighorn sheep.

Using similar methods to define a ‘suitable’ habitat cutoff, our summer model produced smaller estimates of the amount of suitable habitat in each region when compared to DeVoe (2015). For example, DeVoe (2015) estimated 495 km^2 of suitable summer habitat in the Teton Range compared to an estimate of 70 km^2 in this study. In addition, DeVoe (2015) estimated 350 km^2 of suitable summer habitat in the Gros Ventre Range compared to our estimate of 95 km^2. It is likely that the variation in results stems from the interaction between regional differences between the two study areas and methodological differences in the modeling techniques. While we recognize the important contributions of DeVoe et al. (2015) in generating the first predictions of mountain goat habitat throughout the entire GYA, this study provides revised estimates for the southwest GYA from a local study area. We encourage additional local studies as data become available and the continued refinement and strengthening of mountain goat resource selection models and projected densities within the GYA.

While there are a number of theoretical and speculative hypothesis regarding the ecological relationships of sympatric mountain goats and bighorn sheep (Adams et al. 1982), there have been few empirical studies (although see Laundré 1994 and Varley 1994), and no study using GPS collared animals. Our seasonal resource selection models indicate that as mountain goats continue to expand, so too will their spatial overlap with native bighorn sheep. In the face of continued range expansion there is a pressing need to empirically examine the spatial and temporal overlap and develop comparative studies to further our understanding of resource selection dynamics and the potential for introduced mountain goats to alter bighorn sheep behavioral processes. Moreover, additional studies examining fine-scale temporal overlap are needed to understand the potential of mountain goats to serve as an additional vector of deleterious respiratory pathogens. The GYA presents a unique opportunity to examine the ecological relationships of sympatric and allopatric mountain ungulates and we encourage additional studies within the region.

Throughout the GYA, there are a diverse array of land and wildlife management agencies with varying objectives and mandates. The National Park Service, for example, is mandated to manage for native species and has taken steps to largely remove introduced mountain goats in other regions such as Olympic National Park (Houston et al. 1994, Schreiner 1993). In contrast, mountain goats have expanded their range in Yellowstone National Park without substantial documented impacts to native vegetation communities (Aho 2012). Grand Teton National Park is currently developing a mountain goat management plan which will evaluate and rank multiple management options (S. Dewey, personal communication). As mountain goats continue to expand, federal and state agencies will be faced with additional decisions regarding the expansion of this introduced species. Our work has provided novel results regarding the seasonal resource selection of introduced mountain goats and developed applicable tools to help predict and anticipate the continued range expansion of introduced populations throughout the region.

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Tables and figures

Table 2.1. Covariate descriptions and the hypothesized relationships (summer, winter) with the relative probability of use (Pr(use)) for introduced mountain goats in the Snake River Range, WY, ID, 2011 – 2015. For each covariate the functional forms and spatial grains that were evaluated are shown.

Abbreviation	Description	Form †	Spatial grain‡	Relationship with Pr(use)
Terrain suite				
CurvSD	Standard deviation of landscape curvature	Li, Ps	30, 100, 500, 1000	pos, pos
ELEV	Elevation (m)	Li	30	pos, neg
SLP	Slope (degrees)	Li, Sq	30, 100, 500, 1000	pos, pos
SLPv	Slope variance: standard deviation2 of SLP	Li, Ps	30, 100, 500, 1000	pos, pos
VRM	Vector ruggedness measure	Li, Ps	30, 100, 500, 1000	pos, pos
Vegetation Suite				
CanCov	Canopy cover	Li	30, 100, 500, 1000	neg, neg

NDVI_Amp	NDVI Amplitude: mean difference between max NDVI and baseline at beginning of growing season from 2011-2014.	Li	500, 1000	pos, pos
NDVI_Tin	Time integrated NDVI: mean daily (interpolated) integration of NDVI above the baseline for the duration of the growing season from 2011 - 2014.	Li	500, 1000	pos, pos
Heat load suite				
AspectCos	The inverse cosine of aspect minus 35 degrees	Li	30	pos, neg
Solar	Solar radiation (watt/m2)	Li	30	neg, pos
Snow suite				
SWE	Snow water equivalent: Mean Dec-Jan from 2011 -2014.	Li	1000	na, neg
Snow	Snow depth: Mean Dec-Jan from 2011 -2014 .	Li	1000	na, neg

† Li = Linear, Sq = Quadratic, Ps = Natural log/pseudothreshold

‡Circular buffer in meters

Table 2.2. Predicted estimates of suitable mountain goat habitat for four regional mountain ranges, southwest GYA. Area (km^2) and percentages (in parentheses) are shown for each mountain range. The cutpoints used to define suitable summer and winter habitat were 0.0023 and 0.0002, respectively.

Region	Total Area (km2)	Suitable Habitat (km2)	
		Summer	Winter
Wyoming and Salt Ranges	5100.24	173.71 (3.41)	45.84 (0.90)
Gros Ventre	2184.90	95.51 (4.37)	80.09 (3.67)
Teton Range	1444.41	70.47 (4.88)	40.98 (2.84)
Snake River Range	1804.77	167.62 (9.29)	100.33 (5.56)
Study Area (buffered MCP)	472.75	142.12 (30.06)	77.41 (16.37)

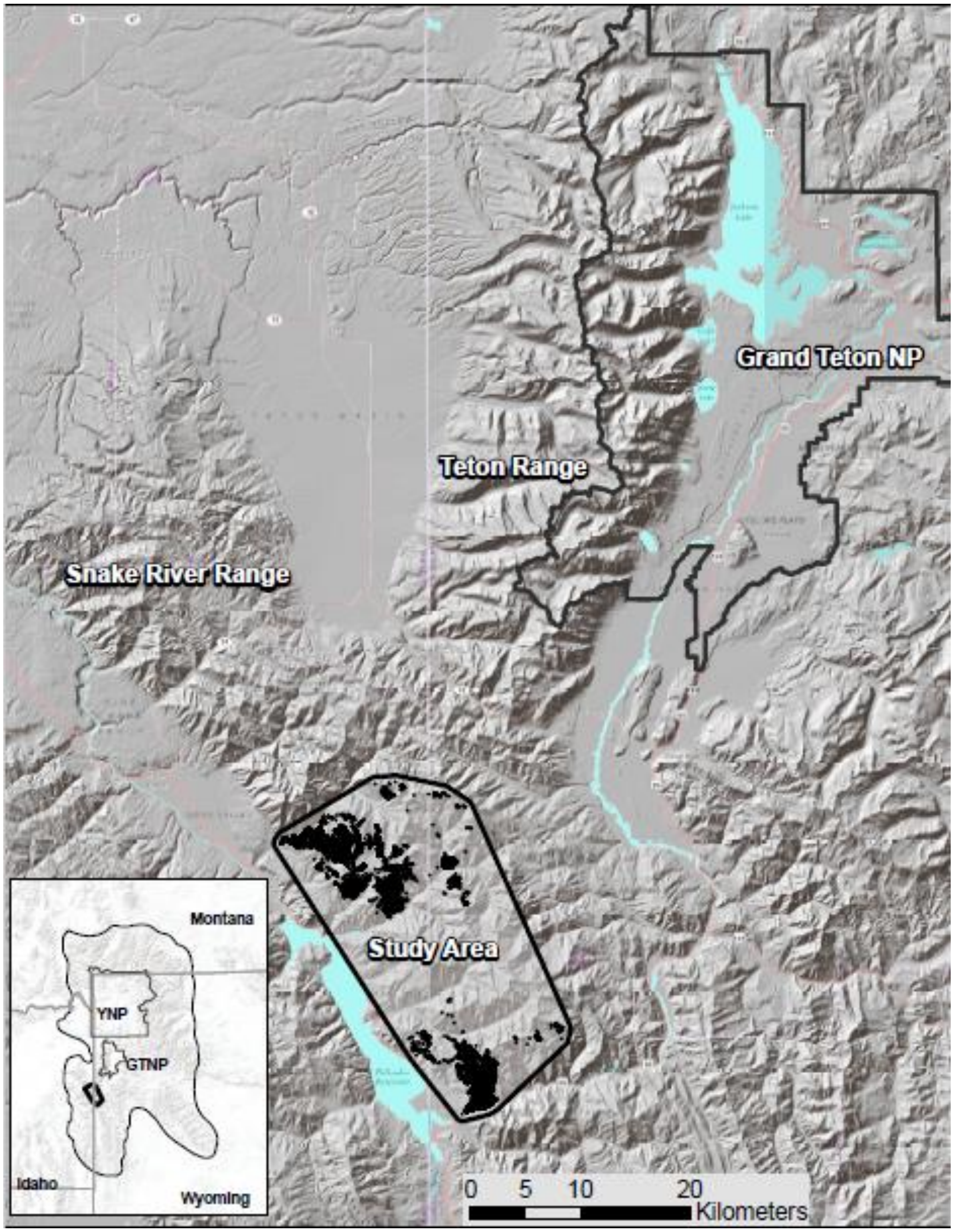


Fig. 2.1. GPS locations of 18 (14 female, 4 male) instrumented mountain goats within the Snake River Range study area spanning Idaho and Wyoming, USA, 2011 – 2015. The study area is contained within the Snake River Range (black polygon). The Teton Range stretches northward.

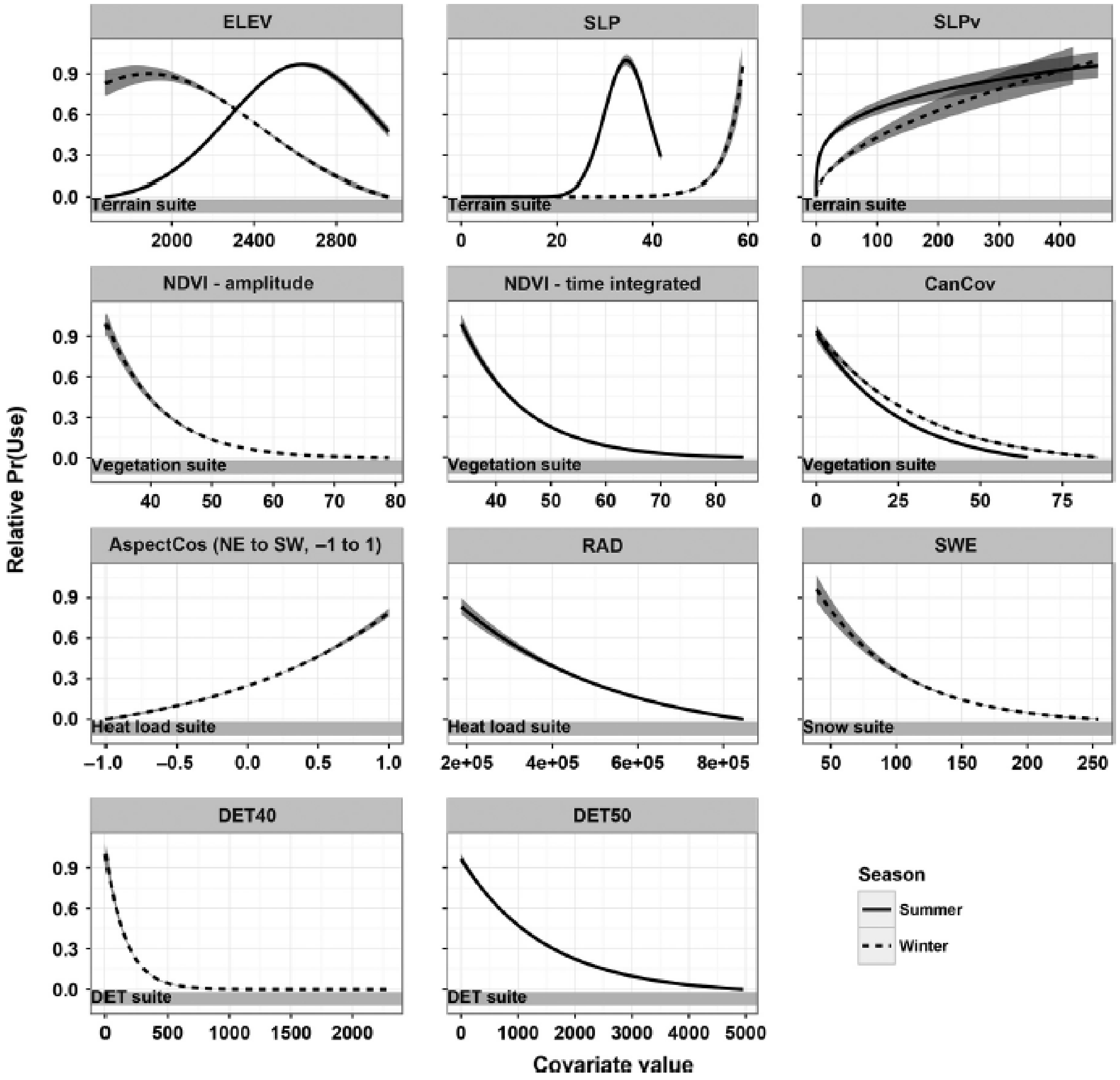


Fig 2.2. Predictions of the relative probability of use for the top covariates in the final summer and winter resource selection model. Covariates are presented within suites noted at the bottom of each graph. Ninety-five percent confidence bands were generated using bootstrap techniques within the merTools R package (Knowles and Frederick 2016) and do not account for the variation associated with the random effect. Predictions were generated across the covariate range with all other covariates held at their mean value.

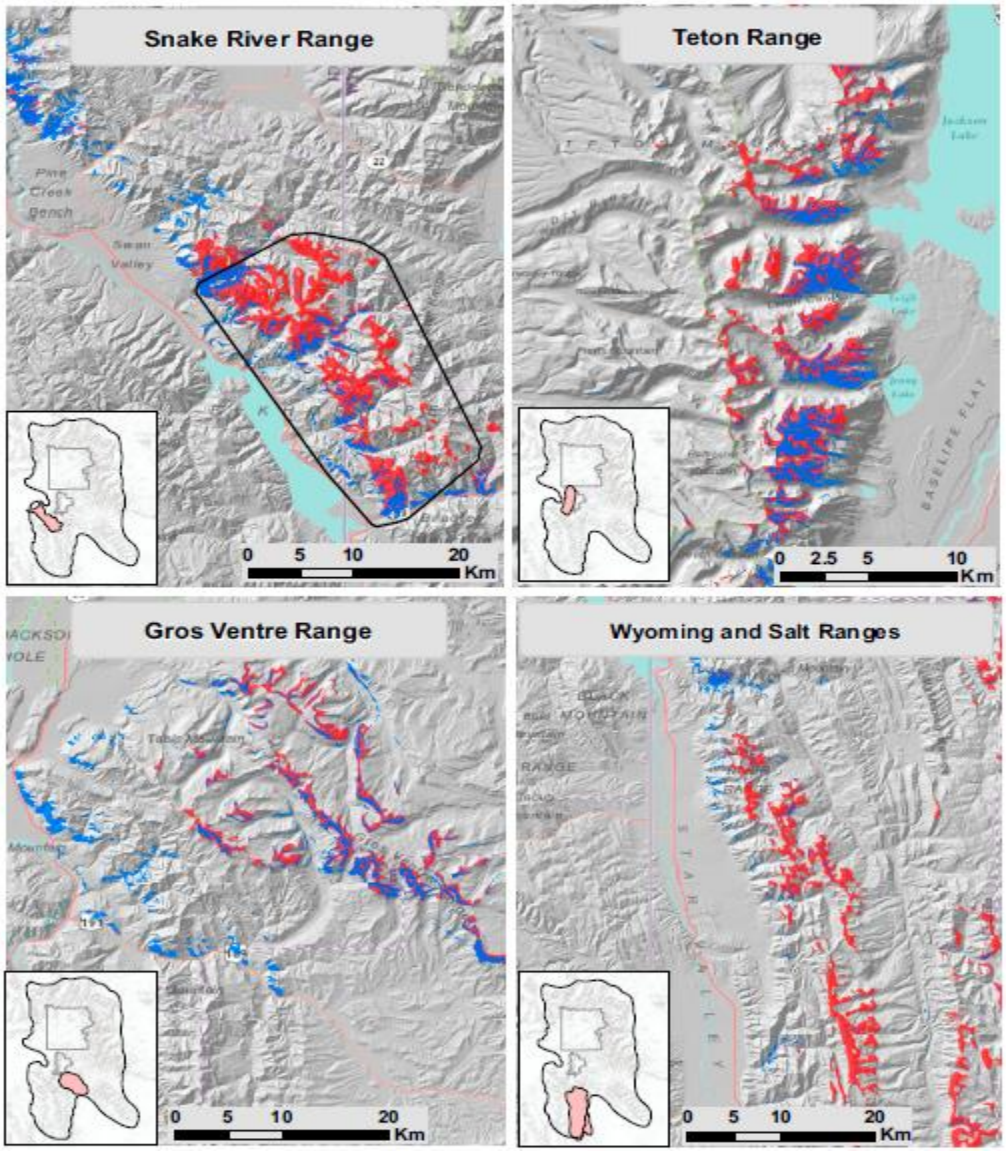


Fig. 2.3. Regional extrapolations of suitable mountain goat habitat within the southwest Greater Yellowstone Area. The cutpoints used to define suitable summer (red) and winter (blue) habitat were 0.0023 and 0.0002, respectively.

CHAPTER TWO APPENDICES

Appendix S2.1. Simulation methods to evaluate multiple sampling intensities when defining a used to available ratio for the study of resource selection by introduced mountain goats (*Oreamnos americanus*), southwest Greater Yellowstone Area, USA

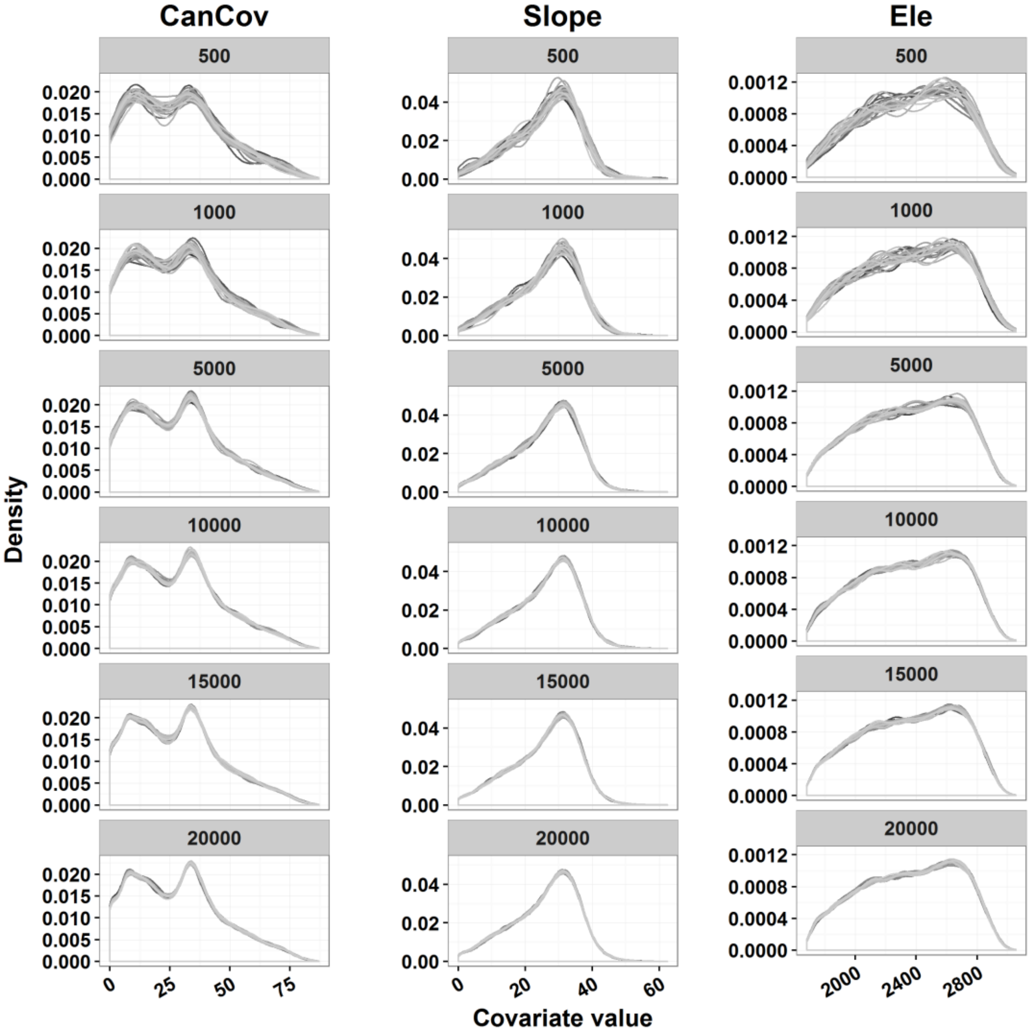
Resource selection functions (RSFs) are often used to study patterns in animal resource selection and are commonly fitted using a used-available study design (Manly et al. 2002, Boyce et al. 2002). Used locations are often collected from GPS collars while available locations are randomly distributed within an extent deemed 'available' given the scale of inquiry (Johnson 1980), and with a specified intensity (e.g. number or points). The number of available points is often defined in relation to the number of used points (e.g. used:available ratio) and needs to be large enough to allow for model convergence, and to accurately describe the distribution of the covariates of interest within the study area (Northrup et al. 2013). Both the extent and number of available locations can influence coefficient estimates and conclusions regarding animal resource selection (Beyer et al. 2010, Northrup et al. 2013).

For our work with introduced mountain goats in the southwest Greater Yellowstone Area (GYA) we defined the availability extent using a buffered minimum convex polygon (MCP) and used the distribution of the straight-line distance between sequential 4 or 6 hour GPS relocations to define the buffer distance (Laforge et al. 2015). These methods are documented within the manuscript and are not further described herein. To select the proper sampling intensity we conducted a simulation to identify the number of locations that best described the 'true' distribution of the covariates within the study area. We evaluated 6 sampling intensities, 500, 1,000, 5,000, 10,000, 15,000, and 20,000 randomly distributed locations. For each intensity level we ran 25 simulations in which a sample was generated and covariate values were extracted to the sample locations. In each simulation we extracted values from 13 covariates – AspectCos, CanCov, CurvSD, DET45, ELEV, NDVI_{Amp}, RAD, SLP, SLPv, Snow, and SWE - all of which are further detailed in the manuscript (Table 2.1). All raster processing and sampling was conducted using the raster package in program R (R Core Team 2015, Hijmans et al. 2015). We evaluated the influence of sampling intensity on the distribution of each sample by generating density plots for each simulation and covariate (Appendix S2.1: Fig. S2.1). Second, we used boxplots to summarize the mean covariate value for each of the 25 simulations as a function of sampling intensity (Appendix S2.1: Fig. S2.2).

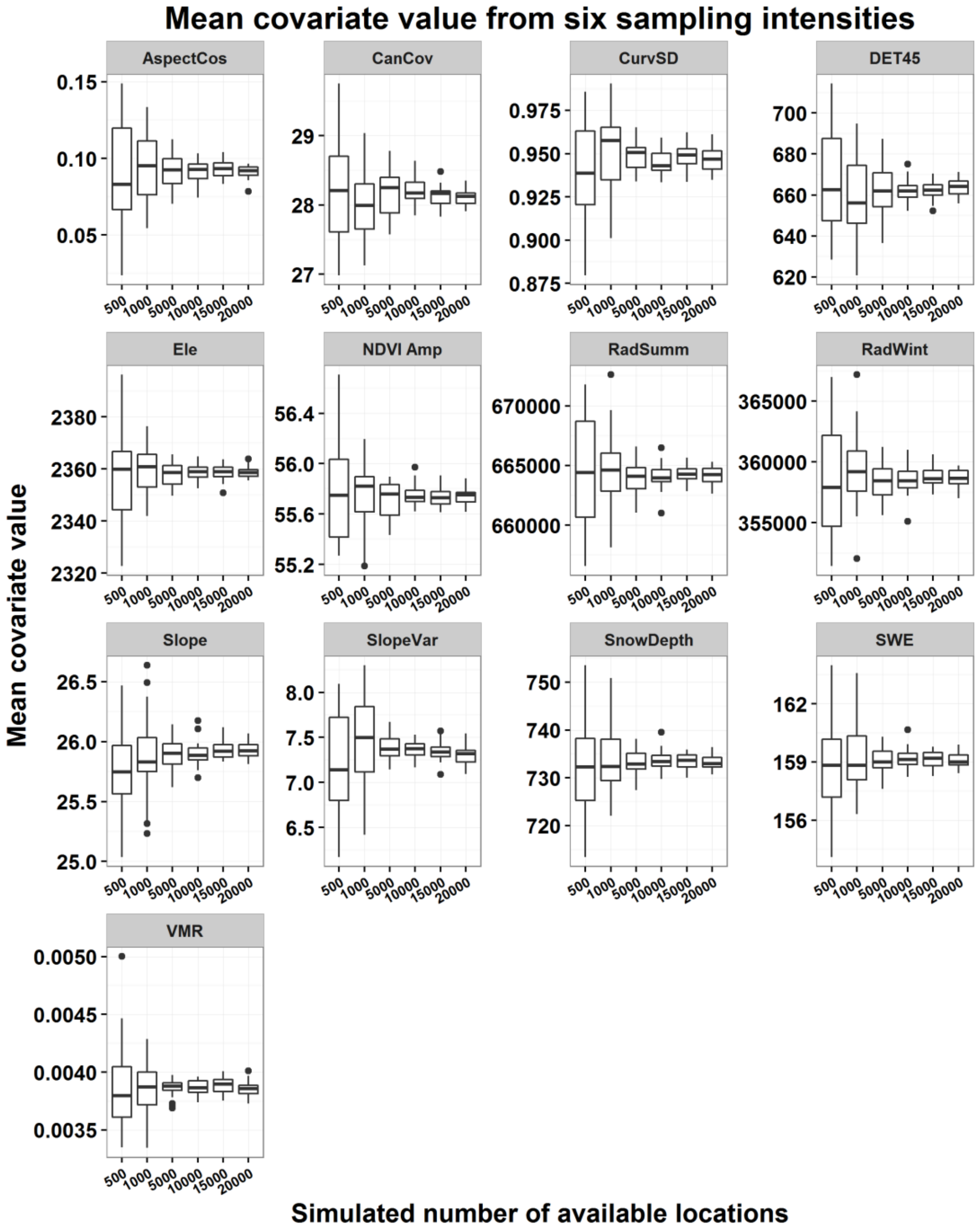
The variance among the 25 simulations begins to stabilize at 5,000 random locations (Appendix S2.1: Figs. S2.1, S2.2). In some instances, for example CanCov or DET45, 10,000 locations may provide slightly more consistent estimates, but when examined in context of the scale on the y-axis, the differences would likely have a negligible influence on the β coefficients of the fitted models. These results suggest that repeat samples of at least 5,000 random locations will provide a similar distribution and accurately describe availability within the study area.

After censoring imprecise GPS locations, the number of used locations for each individual ranged from 319–1406 in summer and from 189–16,64 in winter (Appendix S2.1: Table S2.1). Given the number of used locations, a used to available ratio of 1:10 nearly ensured that all individuals approximated 5,000 available locations (Appendix S1:

Table S1). While there were a few notable individuals with fewer locations (MTG_012_A in summer; MTG_023_A and MTG_005_A in winter), we did not want to over inflate the available sample larger than necessary, nor did we want to unnecessarily remove individuals from the analysis. Given the relatively small study area (473 km^2), even a modest number of available locations (e.g. 1,000) did not dramatically influence the variance among simulations (Appendix S2.1: Figs S2.1, S2.2). A 1:10 ratio represents an effective balance between accurately describing availability within the study area and not over inflating the available sample.



Appendix S2.1: Fig. S2.1. Sample density plots of canopy cover (CanCov), slope, and elevation (Ele) obtained from 25 simulations using 6 sampling intensities. Each line represents the distribution of a single sample from the respective sampling intensity and covariate.



Appendix S2.1: Fig. S2.2. Boxplots of the mean value for 12 covariates obtained from 25 simulations using six different sampling intensities.

Appendix S2.1: Table S2.1. Use and available sample with a 1:10 used to available ratio for the study of introduced mountain goats in the southwest greater Yellowstone area, USA, 2011 – 2014.

IndID	Summer Used	Summer Avail	Winter Used	Winter Avail
MTG_001_A	955	9550	1089	10890
MTG_002_A	999	9990	923	9230
MTG_003_A	962	9620	1027	10270
MTG_005_A	491	4910	189	1890
MTG_006_A	618	6180	488	4880
MTG_007_A	613	6130	434	4340
MTG_008_A	661	6610	496	4960
MTG_009_A	679	6790	423	4230
MTG_010_A	708	7080	566	5660
MTG_011_A	517	5170	514	5140
MTG_012_A	319	3190	489	4890
MTG_018_A	1306	13060	1038	10380
MTG_019_A	708	7080	431	4310
MTG_020_A	1406	14060	1264	12640
MTG_023_A	685	6850	198	1980
MTG_024_A	1307	13070	861	8610
MTG_025_A	714	7140	401	4010
MTG_026_A	1381	13810	1660	16640
Mean	**771**	**7713**	**623**	**6231**

Appendix S2.2. Details of individual mountain goats

Appendix S2.2: Table S2.1. Details of study mountain goats, Snake River Range, USA, 2011 – 2014.

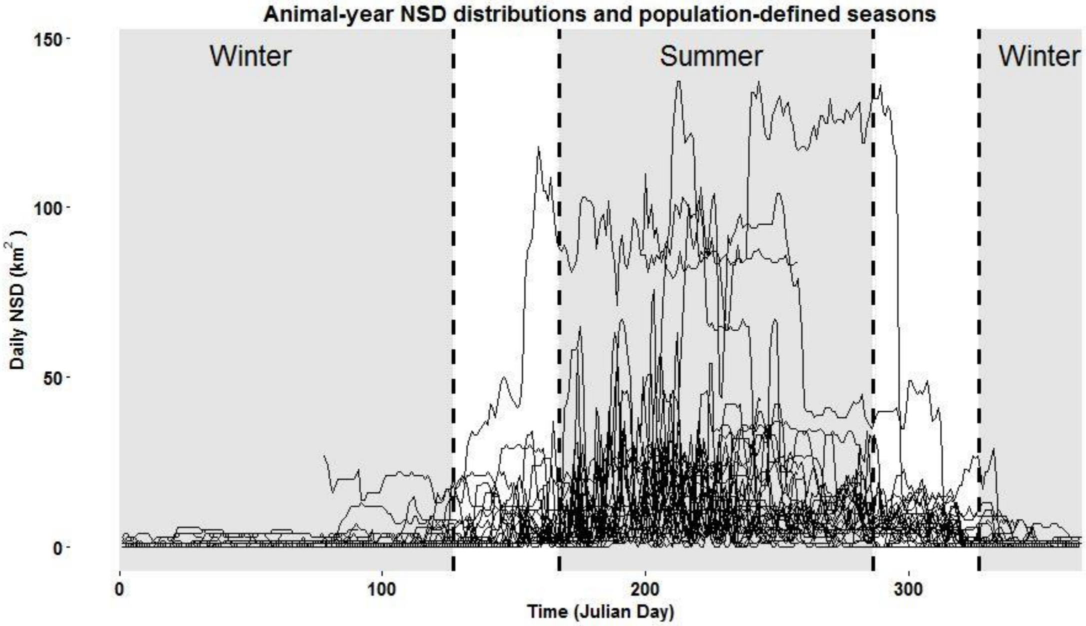
IndID	**Start date**	**End date**	**Number of locations**		**Fix success rate**	
			Summer	**Winter**	**Summer**	**Winter**
MTG_001	11-Aug-11	31-Aug-13	955	1089	0.83	0.88
MTG_002	10-Aug-11	1-Sep-13	999	923	0.87	0.74
MTG_003	17-Aug-11	1-Sep-13	962	1027	0.86	0.82
MTG_005	19-Mar-13	9-Dec-13	491	189	0.92	0.86
MTG_006	17-Jul-13	15-Sep-14	618	488	0.80	0.79
MTG_007	17-Jul-13	15-Sep-14	613	434	0.79	0.70
MTG_008	17-Jul-13	15-Sep-14	661	496	0.86	0.81
MTG_009	17-Jul-13	14-Sep-14	679	423	0.88	0.68
MTG_010	17-Jul-13	15-Sep-14	708	566	0.92	0.92
MTG_011	17-Jul-13	2-Aug-14	517	514	0.87	0.83
MTG_012	17-Jul-13	6-May-14	319	489	0.85	0.79
MTG_018	13-Apr-13	1-Apr-15	1306	1038	0.82	0.94
MTG_019	14-Apr-13	11-Mar-14	708	431	0.89	0.77
MTG_020	17-Apr-13	5-Apr-15	1406	1264	0.88	0.89
MTG_023	25-Mar-14	3-Apr-15	685	198	0.88	0.93
MTG_024	24-Mar-14	15-Apr-16	1307	861	0.82	0.58
MTG_025	26-Mar-14	11-Jan-15	714	401	0.90	0.84
MTG_026	24-Mar-14	15-Apr-16	1381	1664	0.87	0.90
Mean			**835**	**694**	**0.86**	**0.81**
Totals			**15029**	**12495**		

Appendix S2.3. Detailed results from the delineation of mountain goat seasons according to migration parameters estimated from nonlinear regression modeling of net-squared displacement

There were 15 animal-years that produced coefficients for each of the Bunnefeld et al. (2011) movement equations (Appendix S2.3: Table S2.1). Thirteen of the 15 animal-years were classified as migrant or mixed-migrant and had estimated starting and ending dates for the spring and fall migration periods (Appendix S2.3: Table S2.1). From the individual dates we calculated a population midpoint by taking the average of the Julian start and end dates for each season. We then buffered the midpoints by +/-20 days, which approximated the 90th percent quantile of the spring and fall migration durations (36 days). We censored the migratory periods from the data and modeled mountain goat resource selection for summer, June 16th to October 13th, and winter, November 22th to May 7th (Appendix S2.3: Fig. S2.1). The summer season was characterized by relatively high net-squared displacement (NSD) values and greater variation. In contrast, the winter season was characterized by relatively low NSD values that were more constant throughout the season (Appendix S2.3: Fig. S2.1). Our quantitative analysis of NSD to delineate summer and winter modeling periods accurately captured the behavioral differences associated with each season and minimized the additional 'noise' associated with transitional movements between summer and winter ranges (Appendix S2.3: Fig. S2.1).

Appendix S2.3: Table S2.2. Spring and fall migration periods for the 15 animal-years for which all of Bunnefeld et al. (2011) movement models were estimated. Mountain goat captures occurred from 2011 to 2014, Snake River Range, Wyoming and Idaho, USA.

Animal.Year	**Spring start**	**Spring end**	**Fall start**	**Fall end**	**Top model**
MTG_001.2012	5-Jun-12	25-Jun-12	14-Nov-12	14-Nov-12	Mixed migrant
MTG_002.2012	5-Jun-12	25-Jun-12	5-Oct-12	25-Oct-12	Mixed migrant
MTG_003.2012	12-May-12	14-May-12	29-Oct-12	18-Nov-12	Mixed migrant
MTG_005.2013	-	-	-	-	Resident
MTG_018.2013	6-Jun-13	26-Jun-13	22-Oct-13	11-Nov-13	Mixed migrant
MTG_018.2014	19-Apr-14	9-May-14	3-Nov-14	3-Nov-14	Mixed migrant
MTG_019.2013	6-Jun-13	26-Jun-13	6-Oct-13	26-Oct-13	Mixed migrant
MTG_020.2013	6-Jun-13	26-Jun-13	6-Oct-13	26-Oct-13	Mixed migrant
MTG_020.2014	6-Jun-14	26-Jun-14	6-Oct-14	26-Oct-14	Migrant
MTG_023.2014	6-Jun-14	26-Jun-14	26-Nov-14	14-Dec-14	Migrant
MTG_024.2014	11-May-14	31-May-14	6-Oct-14	26-Oct-14	Mixed migrant
MTG_024.2015	27-May-15	16-Jun-15	9-Oct-15	29-Oct-15	Migrant
MTG_025.2014	-	-	-	-	Resident
MTG_026.2014	6-Jun-14	26-Jun-14	6-Oct-14	26-Oct-14	Mixed migrant
MTG_026.2015	3-Jun-15	23-Jun-15	8-Oct-15	23-Oct-15	Mixed migrant



Appendix S2.3: Fig. S2.1. Net-squared displacement distributions for all study individuals and the population-defined summer and winter seasons, Snake River Range, Wyoming and Idaho, USA, 2011 – 2014.

Appendix S2.4. Complete results from the tiered model selection process and post-hoc model evaluation

Tier one results

Within tier one we fit univariate models for each covariate for which we evaluated multiple grains and functional forms (Table 2.1). We fit a total of 88 models (Summer: 44; Winter: 44) (Appendix S2.4: Table S2.1), and selected the top-ranked form and/or grain for each covariate using AIC$_c$. For each covariate there was a clear top-ranked form and/or grain that was carried forward to tiers two and three (Appendix S2.4: Table S2.1, Figs S2.1 and S2.2).

Appendix S2.4: Table S2.1. Tier one univariate model results for summer and winter seasons. Models are ranked by ΔAIC$_c$ within each covariate.

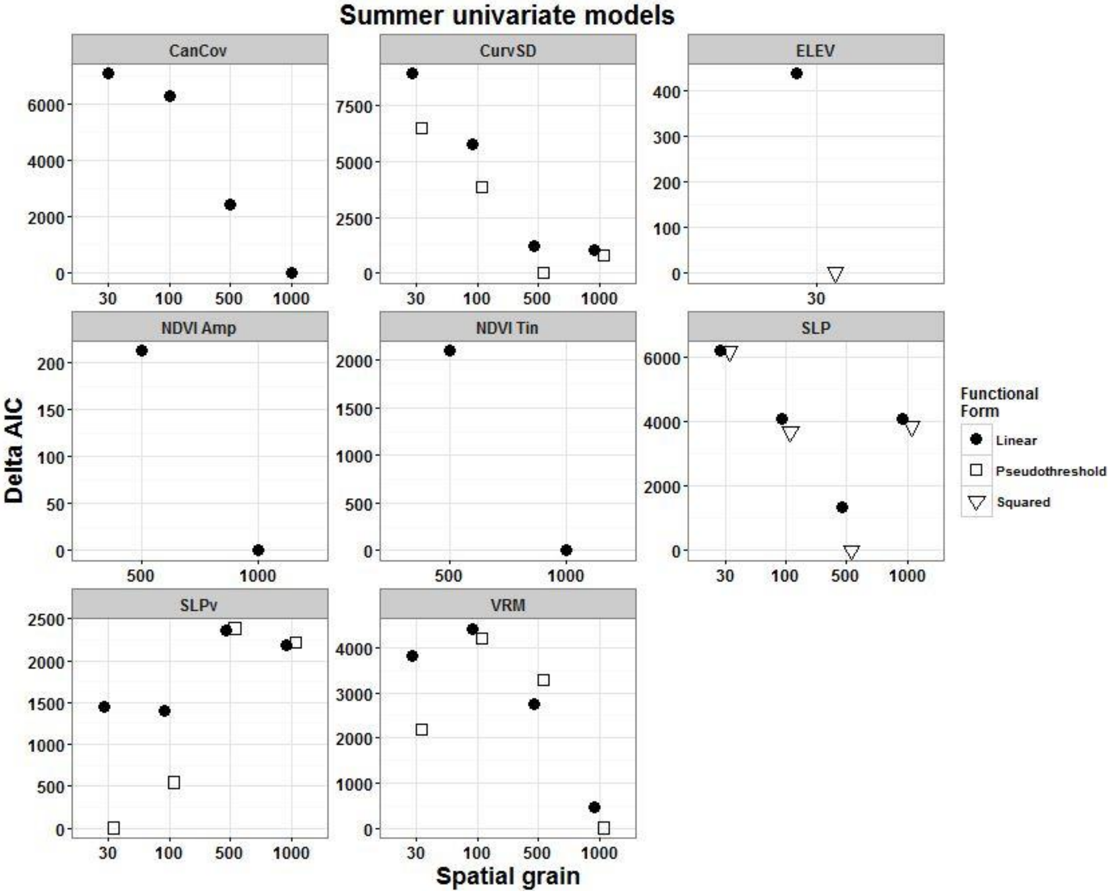
Summer tier one univariate models					
Covariate	**Grain**	**Form**	**AIC$_c$**	**Beta**	**ΔAIC$_c$**
CanCov	1000	Li	75838	-1.491	0
CanCov	500	Li	78265	-1.355	2427
CanCov	100	Li	82111	-1.121	6273
CanCov	30	Li	82936	-1.063	7098
CurvSD	500	Ps	76181	1.548	0
CurvSD	1000	Ps	76961	1.314	781
CurvSD	1000	Li	77235	1.014	1054
CurvSD	500	Li	77375	1.001	1194
CurvSD	100	Ps	80055	1.386	3874
CurvSD	100	Li	81986	0.757	5805
CurvSD	30	Ps	82689	1.092	6508
CurvSD	30	Li	85145	0.600	8964
ELEV	30	Sq	83086	-0.285	0
ELEV	30	Li	83526	0.959	439
NDVI$_{Amp}$	1000	Li	86230	-0.718	0
NDVI$_{Amp}$	500	Li	86442	-0.690	212
NDVI$_{Amp}$	250	Li	87224	-0.619	995
NDVI$_{Tin}$	1000	Li	70984	-1.316	0
NDVI$_{Tin}$	500	Li	73084	-1.213	2101

NDVI_{Tin}	250	Li	75998	-1.083	5015
SLP	500	Sq	75027	-1.030	0
SLP	500	Li	76382	1.724	1355
SLP	100	Sq	78706	-0.279	3679
SLP	1000	Sq	78864	-0.324	3837
SLP	1000	Li	79102	1.518	4076
SLP	100	Li	79105	1.326	4079
SLP	30	Sq	81175	-0.057	6148
SLP	30	Li	81202	1.145	6176
SLPv	30	Ps	89420	0.481	0
SLPv	100	Ps	89965	0.453	545
SLPv	100	Li	90814	0.234	1394
SLPv	30	Li	90876	0.210	1456
SLPv	1000	Li	91605	-0.134	2184
SLPv	1000	Ps	91643	-0.115	2223
SLPv	500	Li	91775	-0.054	2355
SLPv	500	Ps	91806	0.018	2385
VRM	1000	Ps	85891	1.001	0
VRM	1000	Li	86361	0.684	470
VRM	30	Ps	88072	0.491	2181
VRM	500	Li	88653	0.470	2762
VRM	500	Ps	89170	0.538	3279
VRM	30	Li	89702	0.303	3811
VRM	100	Ps	90101	0.361	4210
VRM	100	Li	90320	0.280	4429

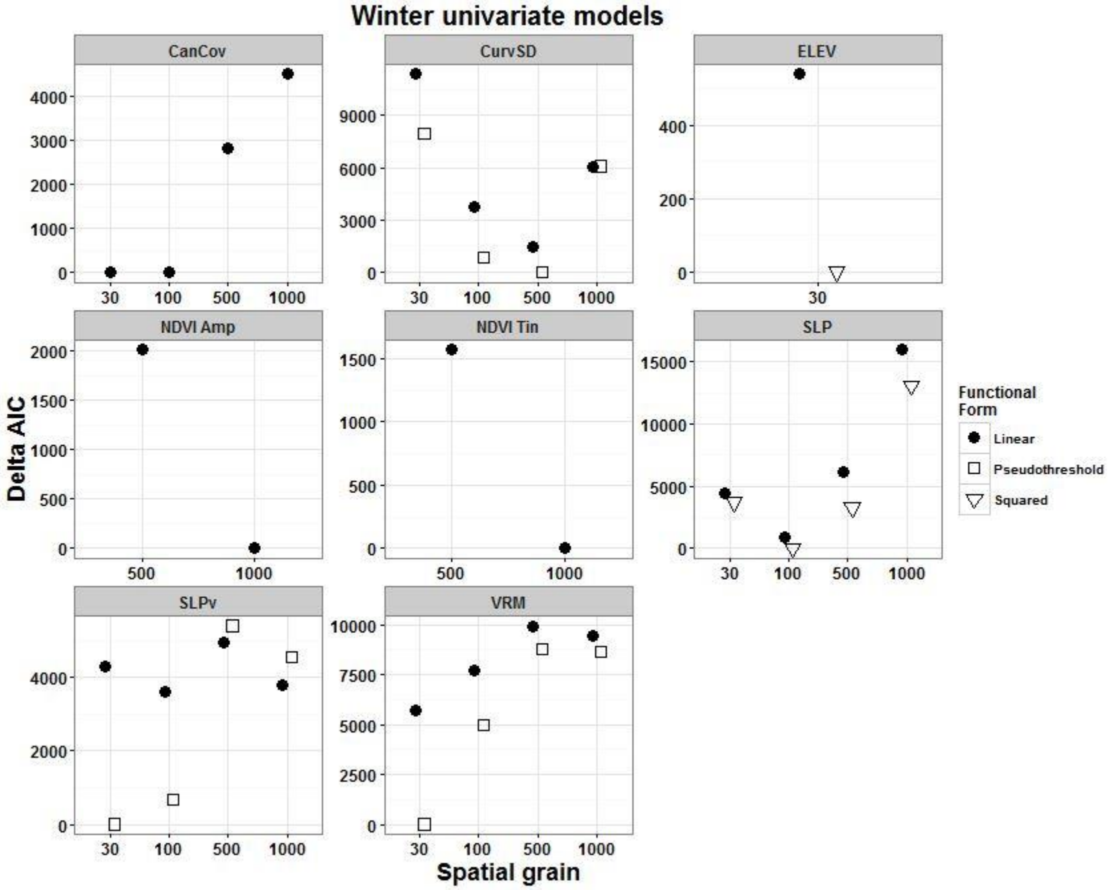
Winter tier one univariate models

Covariate	**Grain**	**Form**	**AIC_c**	**Beta**	**ΔAIC_c**
CanCov	30	Li	102616	-0.682	0
CanCov	100	Li	102622	-0.679	6
CanCov	500	Li	105449	-0.424	2833
CanCov	1000	Li	107140	-0.215	4523
CurvSD	500	Ps	75871	2.200	0
CurvSD	100	Ps	76722	2.351	852
CurvSD	500	Li	77334	1.426	1464
CurvSD	100	Li	79645	1.272	3774
CurvSD	1000	Li	81908	1.290	6037
CurvSD	1000	Ps	81943	1.680	6073
CurvSD	30	Ps	83825	1.813	7954

CurvSD	30	Li	87254	1.001	11384
ELEV	30	Sq	97005	-0.252	0
ELEV	30	Li	97546	-0.901	540
NDVI_{Amp}	1000	Li	65728	-2.073	0
NDVI_{Amp}	500	Li	67744	-1.875	2016
NDVI_{Amp}	250	Li	70657	-1.631	4929
NDVI_{Tin}	1000	Li	77679	-1.104	0
NDVI_{Tin}	500	Li	79249	-1.020	1571
NDVI_{Tin}	250	Li	80410	-0.949	2731
SLP	100	Sq	78461	0.370	0
SLP	100	Li	79353	2.056	891
SLP	500	Sq	81708	0.512	3247
SLP	30	Sq	82175	0.290	3713
SLP	30	Li	82888	1.794	4426
SLP	500	Li	84603	1.980	6142
SLP	1000	Sq	91537	0.374	13075
SLP	1000	Li	94414	1.356	15953
SLPv	30	Ps	100332	0.826	0
SLPv	100	Ps	101007	0.852	675
SLPv	100	Li	103945	0.400	3613
SLPv	1000	Li	104117	0.450	3785
SLPv	30	Li	104644	0.339	4312
SLPv	1000	Ps	104882	0.462	4550
SLPv	500	Li	105276	0.360	4945
SLPv	500	Ps	105736	0.422	5405
VRM	30	Ps	95327	0.820	0
VRM	100	Ps	100288	0.707	4960
VRM	30	Li	101053	0.496	5725
VRM	100	Li	103033	0.439	7706
VRM	1000	Ps	103997	0.676	8670
VRM	500	Ps	104091	0.602	8764
VRM	1000	Li	104758	0.460	9431
VRM	500	Li	105274	0.391	9946



Appendix S2.4: Fig. S2.1. Summer tier one univariate model results. Delta AIC$_c$ is plotted on the y-axis and the spatial grain is on the x-axis.



Appendix S2.4: Fig. S2.2. Winter tier one univariate model results. Delta AIC$_c$ is plotted on the y-axis and the spatial grain is on the x-axis

Tier two results

Within tier two we evaluated similar indices within a suite using univariate models and AIC$_c$. For each covariate we used the top-ranked grain and/or form from tier one (Appendix S2.4: Tables S2.1, S2.2). The top-ranked covariates from tier two were carried forward to tier three.

Appendix S2.4: Table S2.2. Tier two univariate model results for summer and winter seasons. Models are ranked by AICc within each covariate and season.

Summer

Covariate	Grain	Functional Form	Beta	AIC_c	ΔAIC_c
Vegetation suite					
$NDVI_{Tin}$	1000	Li	-1.31	77904	0
$NDVI_{Amp}$	1000	Li	-0.75	94167	16263
Heat load suite					
RAD	30	Li	-0.1599	100359	0
AspectCos	30	Li	-0.06444	100673	314

Winter

Covariate	Grain	Functional Form	Beta	AIC_c	ΔAIC_c
Vegetation suite					
$NDVI_{Amp}$	1000	Li	-2.109	58688	0
$NDVI_{Tin}$	1000	Li	-1.104	70023	11335
Heat load suite					
AspectCos	30	Li	0.4423	81766	0
RAD	30	Li	0.03817	83731	1965
Snow suite					
SWE	1000	Li	-0.9246	75388	0
SnowDepth	1000	Li	-0.8807	75757	368

Tier three results

In tier three we began multivariate model building. Because of the strong association with steep and rugged terrain throughout their range and the predominance of terrain covariates in previous mountain goat resource selection studies (Smith 1986, Poole and Heard 2003, White 2006, Poole et al. 2009, DeVoe et al. 2015), we began tier three by building a base terrain model from covariates within the terrain suite. In both seasons, VMR^{ps} and $CurvSD^{ps}$ were highly correlated with SLP (Pearson's correlation coefficient $> |0.6|$), and were therefore excluded from model building. The base terrain model in both seasons contained SLP, SLP^2, ELEV, $ELEV^2$, and $SLPv^{ps}$ described at similar spatial grains (Appendix S4: Table S3). We then used an all combinations approach to evaluate the top-ranked covariates from tiers one and two in combination with the terrain model for each season (Appendix S2.4: Table S2.3).

Appendix S2.4: Table S2.3. Tier three univariate model results for summer and winter seasons. Models are ranked by ΔAIC_c.

Summer

Model	**K**	**Log Likelihood**	**AIC_c**	**ΔAIC_c**
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + CanCov_{1000} + NDVI_{Tin1000} + RAD_{30}$	10	-31776	63572	0
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + NDVI_{Tin1000} + RAD_{30}$	9	-32064	64147	575
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + CanCov_{1000} + NDVI_{Tin1000}$	9	-32313	64644	1072
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + NDVI_{Tin1000}$	8	-32437	64891	1319
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + CanCov_{1000} + RAD_{30}$	9	-33666	67349	3777
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + CanCov_{1000}$	8	-34330	68676	5104
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + RAD_{30}$	8	-37064	74144	10572
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps}$	7	-37100	74213	10641

Winter

Model	**K**	**Log Likelihood**	**AIC_c**	**ΔAIC_c**
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp1000} + AspectCos_{30} + SWE_{1000}$	11	-17653.36	35328.71	0.00
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp1000} + AspectCos_{30}$	10	-17846.54	35713.09	384.37

$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp1000} + SWE_{1000}$	10	-18011.29	36042.59	713.87
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + NDVI_{Amp1000} + AspectCos_{30} + SWE_{1000}$	10	-18049.69	36119.38	790.66
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp1000}$	9	-18221.49	36460.98	1132.26
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + NDVI_{Amp1000} + AspectCos_{30}$	9	-18223.44	36464.88	1136.17
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + AspectCos_{30} + SWE_{1000}$	9	-20046.56	40111.12	4782.41
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + CanCov_{30} + AspectCos_{30} + SWE_{1000}$	10	-18987.80	37995.60	2666.88
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + NDVI_{Amp1000} + SWE_{1000}$	9	-18812.88	37643.77	2315.06
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + CanCov_{30} + SWE_{1000}$	9	-19406.62	38831.25	3502.53
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + SWE_{1000}$	8	-21217.91	42451.81	7123.10
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + AspectCos_{30}$	8	-21282.03	42580.06	7251.35
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + CanCov_{30} + AspectCos_{30}$	9	-19968.77	39955.54	4626.83
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + NDVI_{Amp1000}$	8	-18990.76	37997.52	2668.81
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps} + CanCov_{30}$	8	-20500.67	41017.34	5688.62
$ELEV_{30} + ELEV_{30}^2 + SLP_{100} + SLP_{100}^2 + SLPv_{30}^{ps}$	7	-22722.47	45458.94	10130.22

In both seasons, the additional covariates from the vegetation, heat load, and snow suites greatly improved model fit (Appendix S2.4: Table S2.3). The top ranked summer model contained $ELEV_{30}$, $ELEV_{30}^2$, SLP_{500}, SLP_{500}^2, $SLPv_{30}^{ps}$, $CanCov_{1000,}$ $NDVI_{Tin1000}$, and $RAD_{30,}$ and had an AIC_c score 574 units below the 2nd ranked model (Appendix S2.4:

Table S2.3). The top ranked winter model contained $ELEV_{30}$, $ELEV_{30}^2$, SLP_{100}, SLP_{100}^2, $SLPv_{30}^{ps}$, $CanCov_{30,}$ $NDVI_{Amp1000}$, $AspectCos_{30}$ and SWE_{1000}, and had an AIC_c score 384 units below the 2nd ranked model.

Post-hoc model comparisons

Our first post-hoc model comparison evaluated the hypothesis that measures of DET could improve model fit by adding non-collinear measures of DET to the top ranked model for each season and evaluating the model set with AIC_c. In summer DET40 and SLP had a Pearson's correlation coefficient of 0.67. As a result, only DET45 and DET50 were evaluated further. In winter there were no correlation coefficients $> |0.6|$.

In both seasons including DET improved model fit, although the improvement was more striking in winter than in summer (Appendix S2.4: Table S2.4). In summer $DET50_{30}$ decreased the AIC_c score by 51 units and in winter $DET40_{30}$ decreased the AIC_c score by 516 units.

Appendix S2.4: Table S2.4. Post-hoc model evaluations of DET. Models are ranked by ΔAIC_c.

Model	K	Log Likelihood	AIC_c	ΔAIC_c
Summer				
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + CanCov_{1000} + NDVI_{Tin1000} + RAD_{30} + DET50_{30}$	11	-31387	62796	0
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + CanCov_{1000} + NDVI_{Tin1000} + RAD_{30} + DET45_{30}$	11	-31413	62847	52
$ELEV_{30} + ELEV_{30}^2 + SLP_{500} + SLP_{500}^2 + SLPv_{30}^{ps} + CanCov_{1000} + NDVI_{Tin1000} + RAD_{30}$	10	-31776	63572	777
Winter				

$ELEV_{30} + ELEV_{30}^{2} + SLP_{100} + SLP_{100}^{2} + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp1000} + AspectCos_{30} + SWE_{1000} + DET40_{30}$	12	-16972	33968	0
$ELEV_{30} + ELEV_{30}^{2} + SLP_{100} + SLP_{100}^{2} + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp1000} + AspectCos_{30} + SWE_{1000} + DET45_{30}$	12	-17230	34485	516
$ELEV_{30} + ELEV_{30}^{2} + SLP_{100} + SLP_{100}^{2} + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp1000} + AspectCos_{30} + SWE_{1000} + DET50_{30}$	12	-17233	34491	522
$ELEV_{30} + ELEV_{30}^{2} + SLP_{100} + SLP_{100}^{2} + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp1000} + AspectCos_{30} + SWE_{1000}$	11	-17653	35329	1360

Lastly, we conducted a confirmatory analysis that compared our top model (including the respective measures of DET) from each season with a second model with the same covariates, but specified at the minimum resolution of the data (Appendix S2.4: Table S2.5). In both seasons the multi-grain RSF was ranked over the model with the minimum resolution of each covariate (Appendix S2.4: Table S2.5).

Appendix S2.4: Table D2.5. Post-hoc model evaluations of the multi-grain resource selection function. Models are ranked by ΔAIC_c.

Model	K	Log Likelihood	AIC_c	ΔAIC_c
Summer				
$ELEV_{30} + ELEV_{30}^{2} + SLP_{500} + SLP_{500}^{2} + SLPv_{30}^{ps} + CanCov_{1000} + NDVI_{Tin1000} + RAD_{30} + DET50_{30}$	11	-31387	62796	0
$ELEV_{30} + ELEV_{30}^{2} + SLP_{30} + SLP_{30}^{2} + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Tin250} + RAD_{30} + DET50_{30}$	11	-33977	67975	5180
Winter				
$ELEV_{30} + ELEV_{30}^{2} + SLP_{100} + SLP_{100}^{2} + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp1000} + AspectCos_{30} + SWE_{1000} + DET40_{30}$	12	-16972	33968	0
$ELEV_{30} + ELEV_{30}^{2} + SLP_{30} + SLP_{30}^{2} + SLPv_{30}^{ps} + CanCov_{30} + NDVI_{Amp250} + AspectCos_{30} + SWE_{1000} + DET40_{30}$	12	-17798	35619	1651

The coefficients tables for the final multi-grain models for each season are included in Appendix S2.4: Table S2.6.

Appendix S2.4: Table D2.6. Coefficients table for the top-ranked seasonal RSF. Estimates and standard errors (SE) were unscaled using the mean and standard deviation of the observed data for each season and can be applied to landscape covariates in their respective units. The 95% confidence intervals were calculated naively (i.e. estimate ± 1.96 * SE).

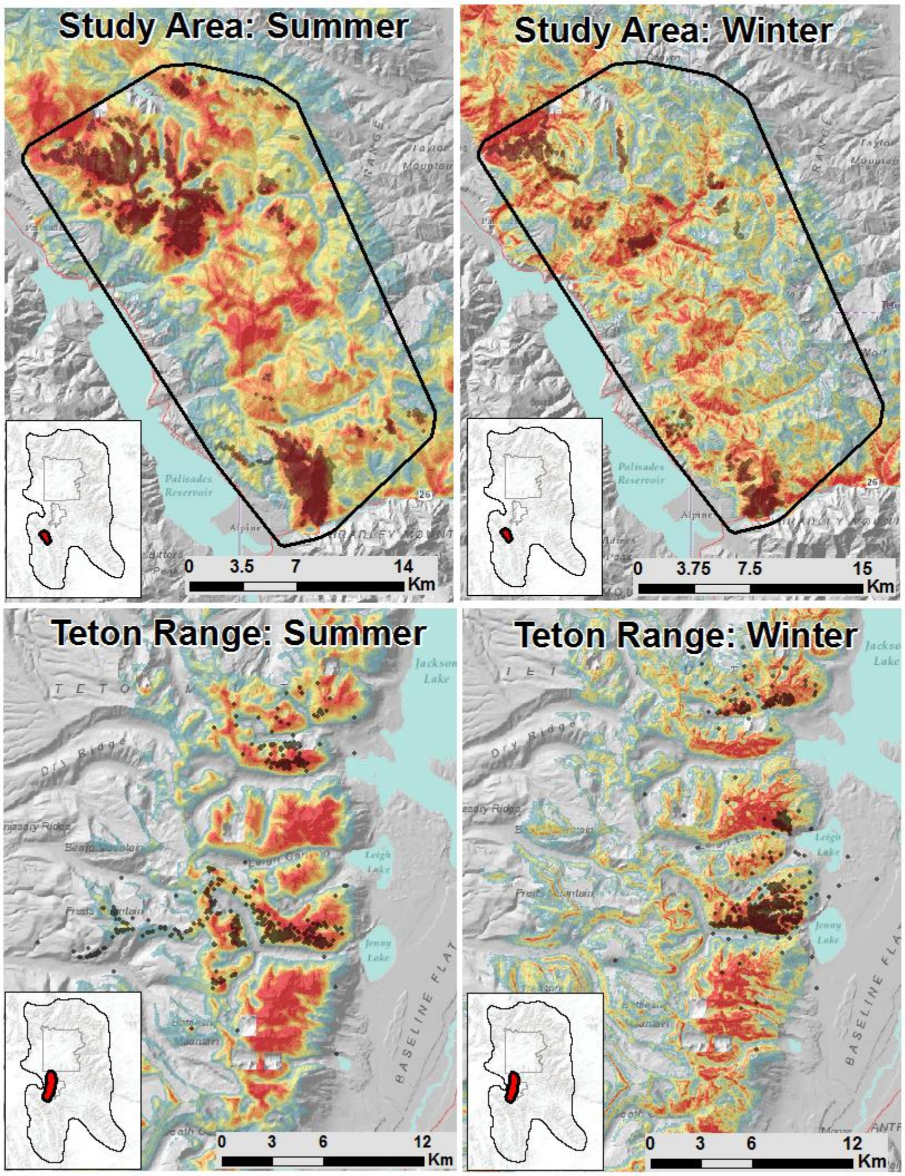
Summer

Covariate	Estimate	SE	95% CI		z-score	p-value
			Upper	Lower		
Intercept	-5.59955686	-0.72072849	-7.01218470	-4.18692902	-72.80	<0.0001
SLPv_{30}^{ps}	0.17379205	0.00839451	0.19024529	0.15733881	20.70	<0.0001
ELEV_{30}	0.00189231	0.00006776	0.00202512	0.00175950	27.93	<0.0001
ELEV_{30}^2	-0.00000026	0.00000001	-0.00000024	-0.00000028	-23.70	<0.0001
SLP_{500}	0.37488847	0.00809090	0.39074663	0.35903031	46.33	<0.0001
SLP_{500}^2	-0.00312689	0.00010427	-0.00292252	-0.00333126	-29.99	<0.0001
CanCov_{1000}	-0.03916369	0.00176081	-0.03571250	-0.04261488	-22.24	<0.0001
$\text{NDVI}_{\text{Tin1000}}$	-0.08891407	0.00162251	-0.08573395	-0.09209419	-54.80	<0.0001
RAD_{30}	-0.00000272	0.00000010	-0.00000252	-0.00000292	-26.96	<0.0001
DET50_{30}	-0.00067818	0.00002582	-0.00062757	-0.00072879	-26.26	<0.0001

Winter

Covariate	Estimate	SE	95% CI		z-score	p-value
			Upper	Lower		
Intercept	5.31987589	-0.65229512	4.0414	6.5984	-44.49	<0.0001
SLPv_{30}^{ps}	0.38217449	0.01247882	0.4066	0.3577	30.63	<0.0001
ELEV_{30}	-0.00158409	0.00008030	-0.0014	-0.0017	-19.73	<0.0001
ELEV_{30}^2	-0.00000011	0.00000001	0.0000	0.0000	-8.69	<0.0001
SLP_{100}	0.13377565	0.00446974	0.1425	0.1250	29.93	<0.0001
SLP_{100}^2	0.00048548	0.00004096	0.0006	0.0004	11.85	<0.0001
CanCov_{30}	-0.03222043	0.00118581	-0.0299	-0.0345	-27.17	<0.0001
$\text{NDVI}_{\text{Amp1000}}$	-0.11430309	0.00283022	-0.1088	-0.1199	-40.39	<0.0001
AspectCos_{30}	0.77693236	0.02644256	0.8288	0.7251	29.38	<0.0001
SWE_{1000}	-0.01542783	0.00063671	-0.0142	-0.0167	-24.23	<0.0001
DET40_{30}	-0.00623949	0.00021150	-0.0058	-0.0067	-29.50	<0.0001

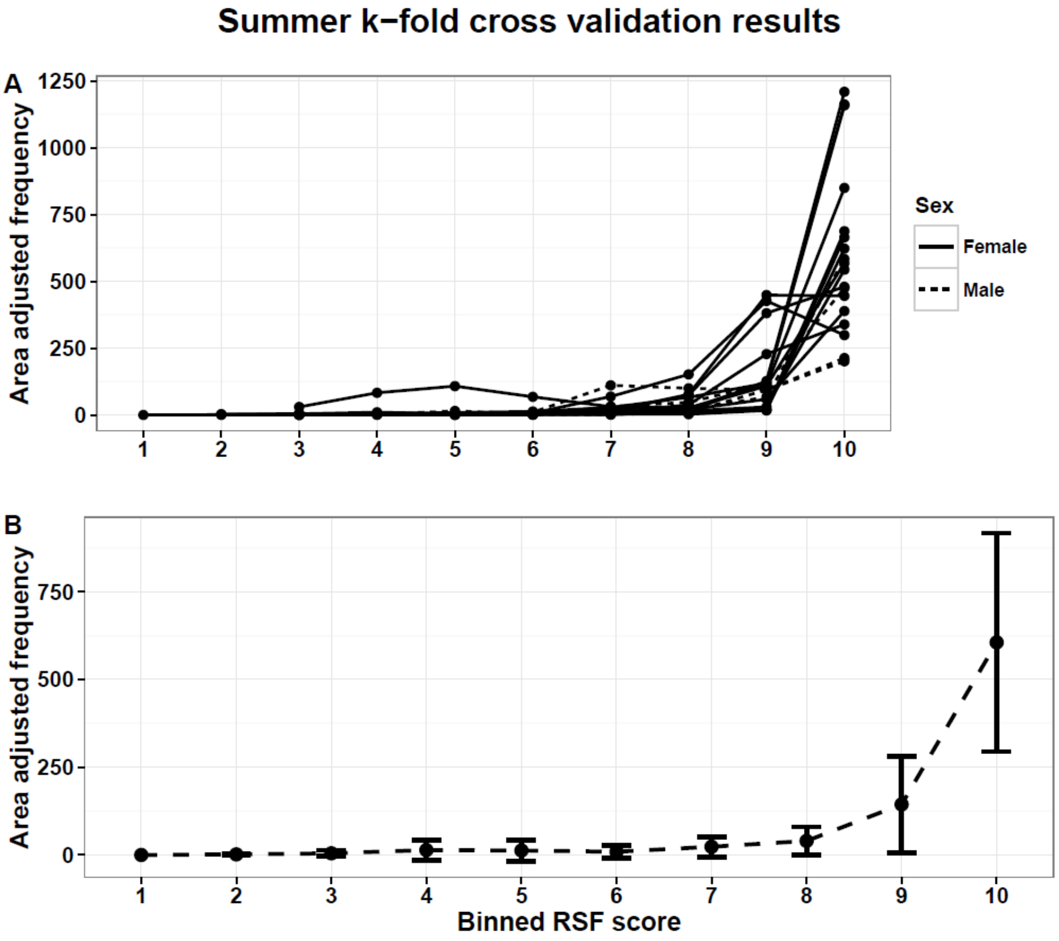
Appendix S2.5. Mountain goat GPS locations in relation to interpolated and extrapolated RSF predictions



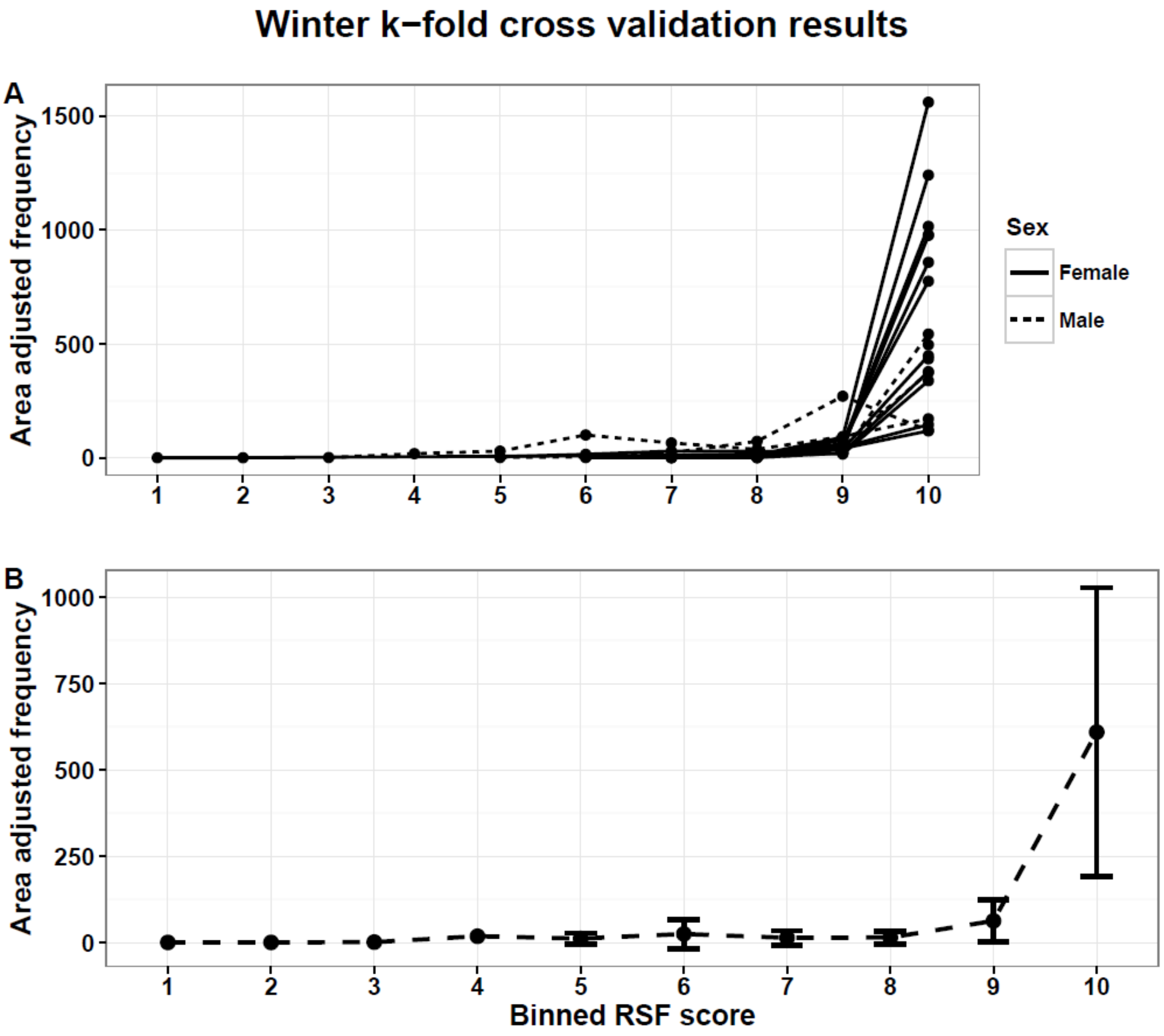
Appendix S2.5: Figure S2.1. Mountain goat GPS locations (black dots) in relation to seasonal RSF predictions in the Snake River Range study area and the Teton Range.

Appendix S2.6. Seasonal k-fold cross-validation results for the Snake River Range study area, ID and WY, USA

Area-adjusted frequency of RSF scores from withheld locations from individual mountain goat summer (Appendix S2.6: Fig. S2.1) and winter (Appendix S2.6: Fig. S2.2) RSF models, Snake River Range, WY and ID, USA. In each figure, panel (A) shows the frequency values for each individual, 1 through k, for males (dashed) and females (solid). Panel (B) shows the frequency values for the population (± S.D.).



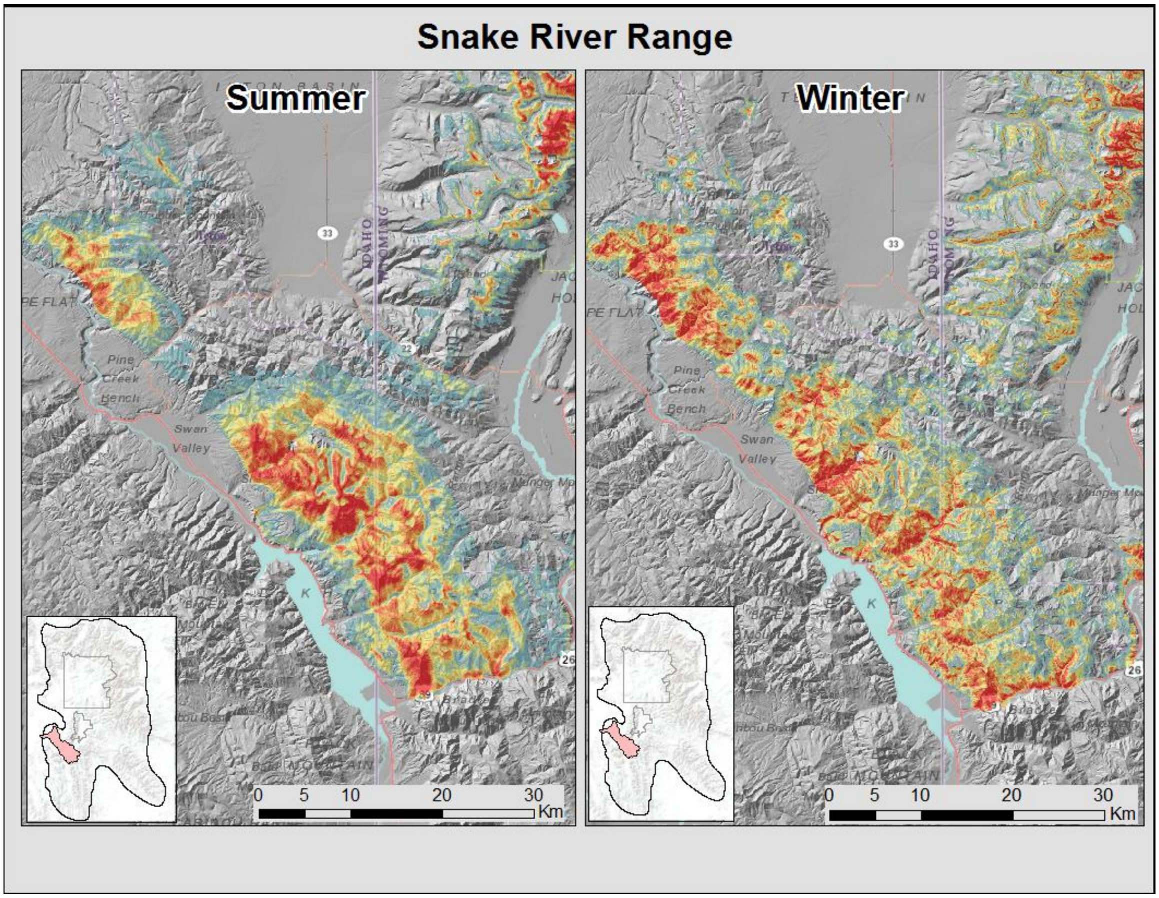
Appendix S2.6: Fig S2.1. Summer k-fold cross-validation results.



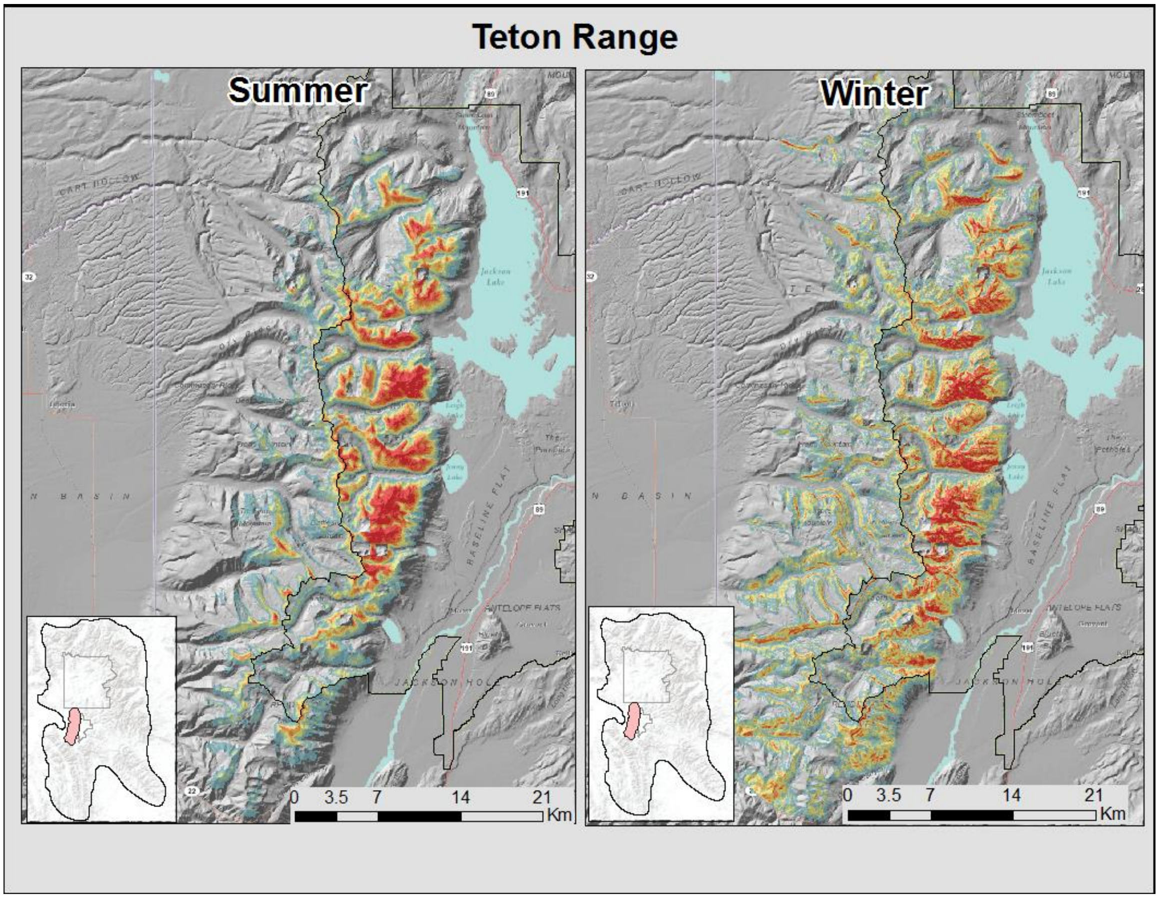
Appendix S2.6: Fig F2.2. Winter k-fold cross-validation results.

Appendix S2.7. Mountain goat RSF extrapolations to the southwest Greater Yellowstone Area

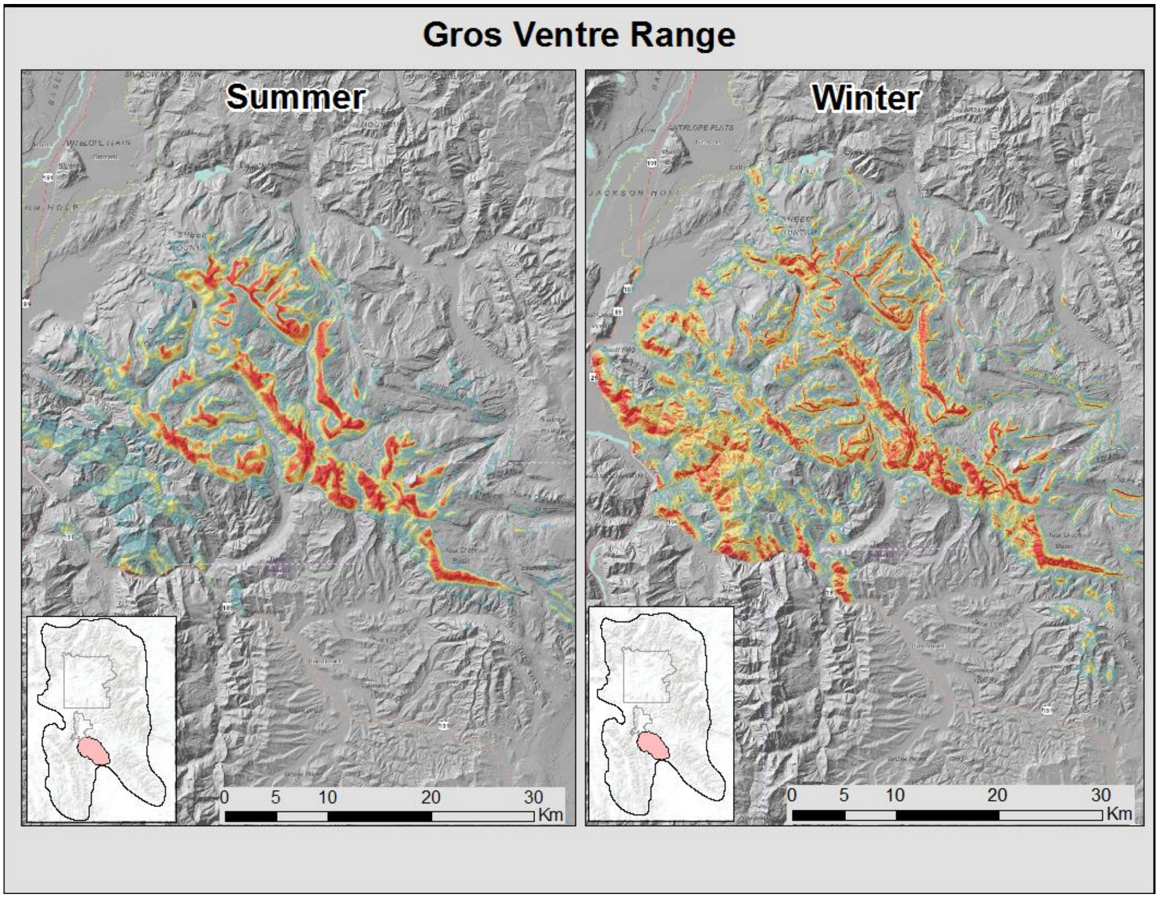
Seasonal extrapolations from the Snake River Range study area to the broader Snake River Range (Appendix S2.7: Fig. S2.1), Teton Range (Appendix S2.7: Fig. S2.2), Gros Ventre Range (Appendix S2.7: Fig. S2.3), and the Wyoming and Salt Ranges (Appendix S2.7: Fig. S2.4). Predicted RSF scores were classified into 10 equal-area bins based on the seasonal predictions within the Snake River Range study area. Grey and cool colors represent low relative RSF, while red and warm colors depict relatively high RSF values. Models were constructed separately for each season and all extrapolations were created with the raster R package (R Core Team 2015, Hijmans 2015).



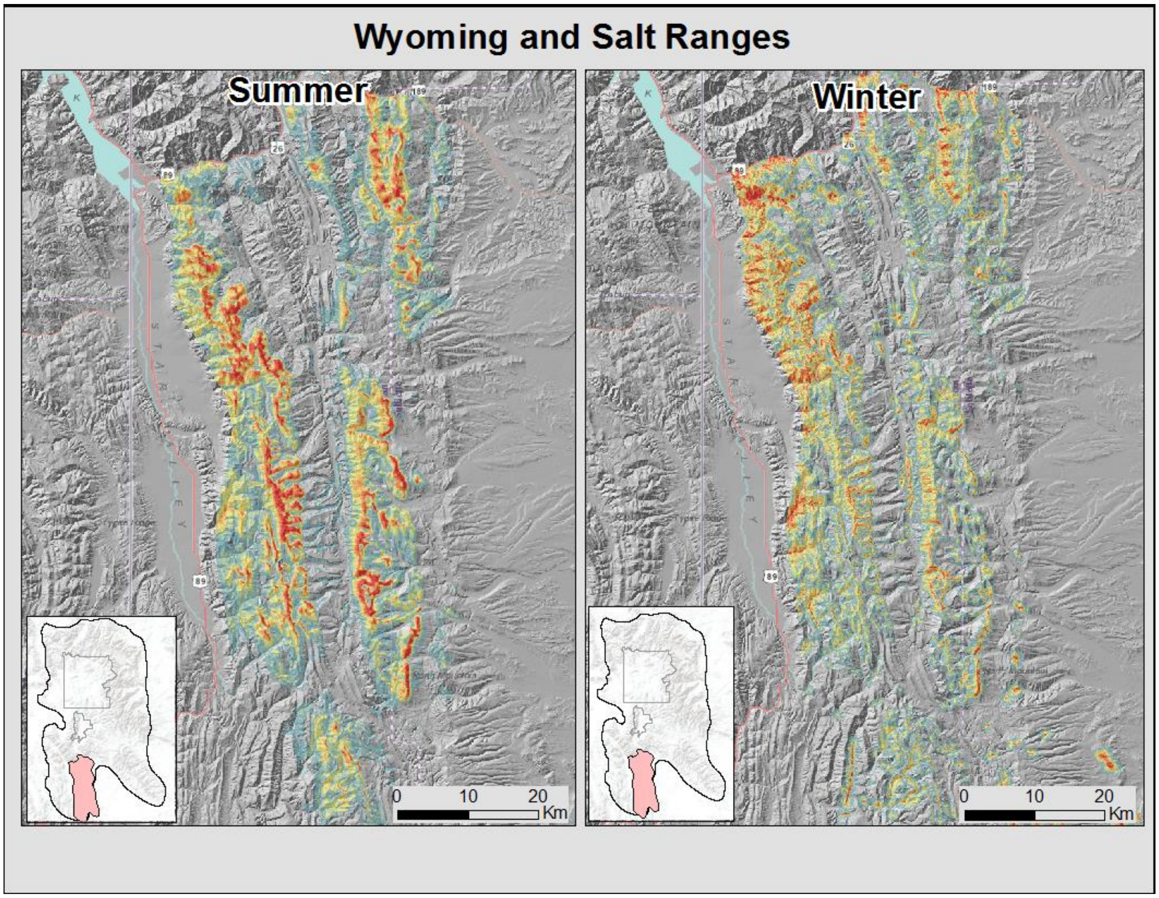
Appendix S2.7: Fig. S2.1. Snake River Range seasonal RSF extrapolations. Predictions for the southern terminus of the Teton Range are also shown.



Appendix S2.7: Fig. S2.2. Teton Range seasonal RSF extrapolations.



Appendix S2.7: Fig. S2.3. Gros Ventre Range seasonal RSF extrapolations.



Appendix S2.7: Fig. S2.4. Wyoming and Salt Ranges seasonal RSF extrapolations.

CHAPTER THREE

NICHE SIMILARITIES AMONG INTRODUCED AND NATIVE MOUNTAIN UNGULATES

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Blake Lowrey

Contributions: Conceived the study, performed the analyses, interpreted results, and wrote the manuscript.

Co-Author: Robert A. Garrott

Contributions: Conceived the study, interpreted results, and edited and commented on the manuscript.

Co-Author: Doug E. McWhirter

Contributions: Provided funding and data, and edited and commented on the manuscript.

Co-Author: P.J. White

Contributions: Provided funding and data, and edited and commented on the manuscript.

Co-Author: Nicholas J. DeCesare

Contributions: Provided technical and analytical expertise, and edited and commented on the manuscript.

Co-Author: Shawn T. Stewart

Contributions: Provided funding and data, and edited and commented on the manuscript.

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Abstract

The niche concept provides a strong foundation for theoretical and applied research among a broad range of disciplines. When two ecologically similar species are sympatric, theory predicts they will occupy distinct ecological niches to reduce competition. Capitalizing on the increasing availability of spatial data, we built from single species habitat suitability models to a multispecies evaluation of the niche partitioning hypothesis with sympatric mountain ungulates – native bighorn sheep (BHS; *Ovis canadensis*) and introduced mountain goats (MTG; *Oreamnos americanus*) in the northeast Greater Yellowstone Area. We characterized seasonal niches using two-stage resource selection functions with a used-available design and descriptive summaries of the niche attributes associated with used GPS locations. We evaluated seasonal similarity in niche space according to confidence interval overlap of model coefficients and similarity in geographic space by comparing model predicted values with Schoener's D metric. Our sample contained 37,962 summer locations from 53 individuals (BHS = 31, MTG = 22), and 79,984 winter locations from 57 individuals (BHS = 35, MTG = 22). Slope was the most influential niche component for both species and seasons, and showed the strongest evidence of niche partitioning. Bighorn sheep occurred on steeper slopes than mountain goats in summer and mountain goats occurred on steeper slopes in winter. The pattern of differential selection among species was less prevalent for the remaining covariates, indicating similarity in niche space. Model predictions in geographic space showed broad seasonal similarity (summer D = 0.88, winter D = 0.87), as did niche characterizations from used GPS locations. The striking similarities in seasonal niches suggest that introduced mountain goats will continue to increase their spatial overlap with native bighorn. Our results suggest that reducing densities of mountain goats in hunted areas where they are sympatric with bighorn sheep and impeding their expansion may reduce the possibility of competition and disease transfer. Additional studies that specifically investigate partitioning at finer scales and along dietary or temporal niche axes will help to inform an adaptive management approach.

Key words: bighorn sheep; mountain goat; niche; *Oreamnos americanus*; *Ovis canadensis*; resource selection function; RSF; Yellowstone

Introduction

First described by Joseph Grinnell (1917), the niche concept links environmental variables and conditions to the distribution and fitness of species, and continues to provide a strong foundation for theoretical and applied research among a broad range of disciplines (Chase and Leibold 2003). Hutchinson (1957) later formalized the ecological niche as a multi-dimensional hypervolume that completely defines a species' ecological properties required for positive growth, that is, the fundamental niche. While conceptually appealing, fundamental niches contain a virtually infinite number of axes and may be a purely theoretical construct (Panzacchi et al. 2014). The realized niche accounts for changes in a species' fundamental niche attributed to interspecific interactions and provides a more interpretable subset of the all-encompassing hypervolume (Hutchinson 1957). The striking increase in animal location data and environmental variables characterized in Geographic Information Systems (GIS) has strengthened ecologists' ability to estimate realized niches in both environmental and geographic space (Elith et al. 2006, Hirzel and Le Lay 2008, Soberón and Nakamura 2009). Largely reliant on abiotic niche components, habitat suitability models [e.g., resource selection functions (Manly et al. 2002); ecological niche factor analyses (Hirzel et al. 2002); and species distribution models (Phillips and Dudík 2008), among others] are being increasingly used to describe the characteristics, interactions, and evolution of realized niches with relevance to theoretical and applied contexts, and represent a novel approach to examine the niche characteristics of sympatric species (Hirzel and Le Lay 2008).

The long and varied history of the niche concept has resulted in a multitude of definitions within the field of ecology (Chase and Leibold 2003). Most notably, the term 'niche' has been confusingly used to address two distinct concepts, Grinnellian (i.e., habitat requirements of a species) and Eltonian (i.e., a species ecological role) niches (Hirzel and Le Lay 2008). Moreover, while Hutchinson's fundamental and realized niches provided a unifying and quantifiable framework, the measures added an additional interpretation to the niche concept (Chase and Leibold 2003). Herein we defined niche according to Hutchinson (1957), and quantified realized niches largely reliant on Grinnellian (i.e., abiotic) habitat components (Hirzel and Le Lay 2008).

While the advances in GPS technology have resulted in dramatic increases in species-specific habitat suitability models, far fewer studies have used GPS data to quantify niche similarity among sympatric species. When two ecologically similar species are sympatric, the niche partitioning hypothesis predicts they will occupy distinct niches to reduce interference (direct) and exploitive (indirect) competition (Pianka 1981). For example, MacArthur's warblers, five species of insectivorous wood warblers, were observed to alter foraging times and behavior in the presence of one another to exploit different food types and reduce interspecific competition and potential competitive exclusion (MacArthur 1958). Niche partitioning is realized through the behavioral process of resource selection which results in spatiotemporal separation in environmental, and in turn, geographic space (Schoener 1974). As the use of GPS technology continues to increase across a broad range of taxa with overlapping distributions (Hebblewhite and Haydon 2010), ecologists have an opportunity to expand from single species habitat suitability models to applied and theoretical research among relevant taxonomic groups (Hirzel and Le Lay 2008). For example, habitat suitability models of native and introduced species can be used to characterize their niche dynamics and evaluate the possibility for competition when the two species are sympatric. Moreover, in systems with introduced species, there is an opportunity to study interspecific competition and the extent to which natural selection has partitioned niches of related taxa. Herein, we integrate tools from the habitat suitability and niche literatures and develop a novel framework to evaluate the niche partitioning hypothesis with native and introduce mountain ungulates in the Greater Yellowstone Area (GYA).

Mountain goats (*Oreamnos americanus*) are an iconic species with strong associations with steep and rugged terrain (Chadwick 2002). Beginning in the mid-1900s state wildlife agencies used translocation programs to expand the distribution of mountain goats and increase hunting opportunities throughout western North America (Côté and Festa-Bianchet 2003). These efforts have largely been successful and greatly expanded the distribution of mountain goats both within and beyond their native ranges (Côté and Festa-Bianchet 2003, Flesch et al. 2016). Although the expanding mountain goat population in non-native areas has been embraced by some natural resource agencies, there is concern that encroachment into areas occupied by native bighorn sheep (*Ovis canadensis*) may be detrimental to regional restoration efforts (Adams et al. 1982, Lowrey et al. 2017). Bighorn sheep have struggled to rebound to historic numbers since the early 1900s and much of their historic range remains unoccupied (Buechner 1960). Moreover, bighorn sheep are negatively impacted by respiratory pathogens and habitat loss, particularly on low elevation winter ranges, and largely occur within restored populations numbering fewer than 100 individuals (Buechner 1960, Cassirer et al. 2017). Because of the general propensity of both species to inhabit rugged, mountainous terrain, there is potential for increased spatial overlap as mountain goats continue to expand their non-native range (Lowrey et al. 2017) and the possibility that competition (Reed 2001) and disease transfer (Gross 2001) will be detrimental to native bighorn sheep.

Because bighorn sheep and mountain goats have long occurred on sympatric native ranges within portions of western North America one would expect to observe niche partitioning as a likely consequence of their history on sympatric ranges (MacArthur 1958, Pianka 1981), although this prediction has not been directly evaluated. A conceptual model generalized across allopatric study areas suggested that mountain goats occur within the extreme end of some niche components (i.e., terrain steepness, ruggedness, snow cover, etc.) when compared to bighorn sheep (Adams et al. 1982). As mountain goats continue to expand their non-native ranges, there is a need to understand their niche dynamics and evaluate the possibility for introduced mountain goats to alter behavioral processes of native bighorn sheep.

The GYA represents one of the largest relatively intact temperate ecosystems in the world (Keiter and Boyce 1994), and provides a rare opportunity to describe the niche characteristics of native bighorn sheep and sympatric introduced mountain goats (Lowrey et al. 2017). From an initial introduction of 170 animals to nine sites over 28 yrs (1942–1970), mountain goats have expanded their distribution and grown to an minimum population estimate of 1,648 individuals within the GYA (Flesch et al. 2016). The northeast portion of the GYA, where introductions were first initiated and most concentrated, is nearly completely colonized by mountain goats with minimum counts of 632 individuals (Flesch et al. 2016). Herds of native bighorn sheep occur within and adjacent to the expanding mountain goat population throughout the GYA. Although the demographic performance of bighorn sheep within the GYA is varied, the northeastern portion represents an intact and robust population that was never extirpated, has no documented widespread disease related die-offs, and continues to show relatively stable demographic performance (Buechner 1960, Butler et al. 2017).

We tested the niche partitioning hypothesis through characterizing the realized niches of native bighorn sheep and introduced mountain goats within sympatric ranges of the GYA, and in so doing, built from single species habitat suitability models to interspecific research that broadens the ecological understanding of both species within an applied context. We hypothesized there would be broad similarity between summer niches as both species generally transition from relatively low-elevation winter ranges to high-elevation mountain environments following regional phenological patterns (Varley 1994, DeCesare and Pletscher 2006, Lowrey et al. 2017). In winter, we hypothesized that differing strategies among species would result in dissimilar niches. Although recent work suggests that wintering strategies can be varied with some individuals overwintering at high elevations (e.g., Courtemanch et al. 2017), bighorn sheep tend to occupy broad, low-elevation winter ranges (Festa-Bianchet 1988). Mountain goats, in contrast, select for steep cliffs at intermediate elevations which more consistently shed snow and are patchily distributed on the landscape (Chadwick 2002, Lowrey et al. 2017).

Methods

Study area

The study area was located within the northeast GYA of southwest Montana and northwest Wyoming, and was characterized by rugged, mountainous topography with elevations ranging from 1,200–3,800 m ASL and average annual precipitation of 130 cm. The region experiences harsh, cold winters with snow persisting into the summer months at higher elevations. Land ownership is dominated by federally managed lands within designated Wilderness areas, apart from valley bottoms, many of which were privately owned. The region has a strong predator population and hosts all native large carnivore species, including grizzly (*Ursus arctos horribilis*) and black bears (*Ursus americanus*), wolves (*Canis lupus*), coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcat

(*Lynx rufus*), wolverines (*Gulo gulo*) and Golden eagles (*Aquila chrysaetos*). While there are only scant records of regional predation on mountain goats, bighorn sheep comprise a relatively small proportion of mountain lion and wolf diets regionally (Stahler et al. 2006, Elbroch et al. 2013). Included in the study area were sympatric bighorn sheep and mountain goat populations (Fig. 3.1). Ninety-six mountain goats were introduced within and adjacent to the study area from the early 1940s to the mid-1950s. Mountain goats have continued to increase in abundance and distribution since their initial introductions (Laundré 1990, Flesch et al. 2016) and have been sympatric with bighorn sheep for approximately 50 yrs (Lemke 2004). Bighorn sheep and mountain goat minimum counts were 1,500 and 632 individuals in 2016, respectively (Flesch et al. 2016, McWhirter 2016, MFWP 2016). Within the study area, bighorn sheep were never extirpated or augmented, and have maintained relatively stable population demographics with modest harvest rates and nearly ubiquitous presence of respiratory pathogens in sampled animals (Butler et al. 2017).

Data collection and censoring

From 2012 to 2016 we used ground darting and helicopter net gunning to capture bighorn sheep and mountain goats, primarily during winter. We targeted adult females of both species though some mature male mountain goats were also included. All captured animals were fitted with both a store-on-board GPS (Telonics TGW-4400-2 or TGW-4400-3) and VHF (Telonics MOD-401-1) radio collar, enabling the acquisition of fine scale spatiotemporal data as well as additional survival monitoring once the GPS collar released from the animal (Lowrey et al. 2017). The collars collected GPS locations at 4-, 5-, or 6-hr 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).

We defined summer (3-July to 4-October) and winter (18-November to 15-May) periods using migration parameters estimated from nonlinear regression modeling of net-squared displacement (Bunnefeld et al. 2011, Spitz et al. 2017) and censored location data collected during the population-mean migratory periods to minimize the additional ‘noise’ associated with transitional movements between summer and winter ranges (Appendix S3.1). We censored imprecise locations from the dataset by removing GPS locations with a horizontal dilution of precision (HDOP) >10 (D’eon and Delparte 2005) and/or an estimate of horizontal error (included in Generation 4 Telonics data files) > 60 m (Lowrey et al. 2017). After censoring, the mean species-season fix success rates were ≥ 87% (Appendix S3.2).

Realized niche components

We used covariates (Table 1) supported by previous habitat studies of allopatric populations to characterize the realized niches of bighorn sheep and mountain goats. Terrain attributes included elevation (ELEV), slope, slope variance (SlopeVar), calculated as the variance of slope values within the 8-cell neighborhood surrounding each grid cell of a 10 m DEM (DeVoe et al. 2015, USGS 2009), and three measures of distance to steep terrain [DST, akin to distance to escape terrain (DeCesare and Pletscher 2006)], defined as slopes ≥ 30, 40, and 50 degrees. Indices of vegetation and forage abundance included canopy cover (CanCov; Homer et al. 2011) and time integrated normalized difference vegetation index (NDVI; USGS EROS Center 2016), respectively. To characterize heat-load, we transformed aspect into a biologically interpretable covariate by taking the inverse cosine of the angle - 35° (AspectCos; Cushman and Wallin 2002). This transformation changed the axis from N-S to NNE-SSW and ranged from -1 to 1, respectively. Lastly, snow water equivalent (SWE; NOHRSC 2004) indexed winter snow.

We included multiple spatial grains and functional forms for selected covariates to allow for differences in interspecific behavioral processes characteristic of niche partitioning and generated hypotheses regarding the strength, direction, and form of each covariate based on previous studies (Table 3.1). In addition, we incorporated the ‘space of influence’ on animal decisions regarding resource selection (i.e., the multi-grain resource selection function; 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., minimum resolution of the data), but may also be influenced by a broader region (e.g., the ‘space of influence’; Laforge et al. 2015). In addition to the minimal resolution of the data (i.e., 30 and 250 m; Table 3.1), we performed neighborhood analyses within 500-, and 1000-m circular buffers to evaluate alternative areas of influence and their relevance to mountain ungulate niches. We restricted our analysis of multiple grains to covariates that could be visually perceived to capture the behavioral processes driving resource selection. Covariates that are not directly perceived by animals (e.g., elevation), and therefore do not elicit a response, were not evaluated at multiple grains (Table 3.1; Lowrey et al. 2017).

Seasonal niche characterizations

We employed a variety of techniques to characterize the seasonal realized niches of sympatric mountain ungulates in niche and geographic space. First, we characterized seasonal niches employing a used-available design (i.e., Design II; Manly et al. 2002) where individual GPS locations represented the 'used' set and 'availability' was sampled within a shared study area-level minimum convex polygon (MCP; Fig. 3.1) buffered by the 95 percent step length between consecutively acquired locations (Laforge et al. 2015). We used the same availability extent for each species and season, and employed a two-stage approach to move from individual-based models to a single mean population resource selection function (RSF) for each season, which approximated the seasonal realized niches (Marzluff et al. 2004, Fieberg et al. 2010). We treated individual as the experimental unit (White and Garrott 1990) and fit separate models for each individual-season combination with separate random samples of available points at a 1:10 (used:available) ratio (Appendix S3.3).

Beginning with individual univariate models, we used a tiered approach to identify the most explanatory functional form and/or spatial grain for covariates where multiple forms and/or grains were evaluated (Table 3.1). For each individual, we identified the top-ranked forms and grains using AIC_c (Burnham and Anderson 2002). To generate a single model structure at the population-level for each species-season, we selected the form and grain for each covariate with the highest number of top-ranked occurrences when summed within the species-season groupings. We retained all covariates from the individual models, but allowed the form, grain-size, and DST definition (30, 40, or 50 degree slopes) to vary between species and seasons (Marzluff et al. 2004, Sawyer et al. 2009). When there was a tie in the top-ranked grain-size, we subjectively defaulted to the smaller unit. We then combined covariates from the univariate models with those not evaluated with multiple forms and/or grains to evaluate collinearly. We maintained a Pearson’s correlation coefficient of r < |0.6| by selecting the least collinear form and/or grain size rather than using the top-ranked form and/or grain size from the univariate results. In addition, we removed covariates if the correlation coefficient could not be reduced below the |0.6| threshold for any covariate combination. With a final list of covariates that balanced the univariate results with collinearity, we fit a single multivariate model for each individual and generated a single population-averaged model for each species-season group to estimate inverse variance weighted mean coefficients (β’s; Murtaugh 2007, DeCesare et al. 2012) across individuals *i* for each species *j*, season *s*, and covariate *k*:

$$\hat{\beta}_{jsk} = \sum_{i=1}^{N} w_{ijsk}\,\hat{\beta}_{ijsk}$$

where $w_{ijsk}{}'s$ represented the seasonal individual parameter weights estimated as

$$w_{ijsk} = \frac{1/[SE(\hat{\beta}_{ijsk})]^2}{\sum_{i=1}^{N}(1/[SE(\hat{\beta}_{ijsk})]^2)}$$

and standard errors are estimated as

$$SE(\hat{\beta}_{jsk}) = \sqrt{\frac{\sum_{i=1}^{N} w_{ij}\,(\hat{\beta}_{ijsk} - \hat{\beta}_{jks})^2}{N-1}}.$$

Second, we characterized the seasonal realized niches in geographic space by extrapolating the population-averaged RSF within the sympatric study area. We estimated the relative probability of use with the exponential RSF:

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

where $\beta's$ are the coefficients of the effects of the covariates, X_i, on $\widehat{w}(x)$, the relative probability of use. The predicted RSF values were then rescaled between 0 and 1 with a linear stretch (Johnson et al. 2004, DeCesare et al. 2012). We evaluated the predicted values by calculating a correlation coefficient between the number of used GPS locations within 10 equal-area RSF bins which characterized the available distribution of predicted values from 500,000 random locations within the study area (Boyce et al. 2002, DeCesare et al. 2012).

Lastly, we characterized the distributions of the minimum resolution and linear form of each niche component from the used GPS locations using violin plots (Wickham 2009). This provided an assessment of the seasonal niches solely reliant on the used locations without incorporating multiple spatial grains, functional forms, or an `available` sample. All spatial and statistical analyses were conducted in program R (R Core Team 2016).

Evaluating niche similarity

We evaluated seasonal niche similarity of bighorn sheep and mountain goat niches characterized with RSFs in niche and geographic space as well as the characterizations with used locations. Within niche space we evaluated the confidence interval overlap of the averaged model coefficients for each species as well as the relative similarity according to predictive plots over the range of each covariate. Following recent advances in ecological niche modeling (Warren et al. 2008, Broennimann et al. 2012), we evaluated niche similarity in geographic space by comparing model predicted values from each species with Schoener's D metric (Schoener 1968),

$$D = 1 - \frac{1}{2}\left(\sum_{ij}\left|z_{1ij} - z_{2ij}\right|\right)$$

where z_1 and z_2 represented the stretched population-level RSFs rescaled so that the sum of the predicted values was the same for both species (Broennimann et al. 2012), and *i* and *j* indexed rows and columns, respectively. The D metric ranges between 0 (dissimilar niches) and 1 (identical niches) and can be used with any niche model that produces suitability measures in geographic space (Warren et al. 2008). Moreover, Schoener's D provides a relatively simple measure with a long history of use in both dietary and space use studies, and is typically applied to measures of relative use (Schoener 1968, Warren et al. 2008), such as the relative RSF estimated from a used-available design (Manly et al. 2002).

In addition, we evaluated the ability of one species' niche to predict the other species in geographic space by comparing single bin values of one species to the corresponding grid cells of the other species. More specifically, for each binned RSF value of bighorn sheep, we calculated the proportion of mountain goat bin values that corresponded with a single bighorn sheep bin in geographic space. The method is insensitive to the species direction (e.g., bighorn sheep to mountain goats or mountain goats to bighorn sheep), as one is a transformation of the other. In the case of niche equivalency (e.g., D = 1), there would be perfect alignment between the realized niches in geographic space (Fig. 3.2). In contrast, dissimilar niches would appear random with an equivalency similar to that expected by chance (Fig. 3.2).

Lastly, for the niche characterization with used locations, we compared the distribution shape and mean for each niche component to identify relative differences among species.

Results

Data collection and censoring

Capture efforts began in the spring of 2012 and continued to the winter of 2016, resulting in the instrumentation of 34 female bighorn sheep and 23 mountain goats (15 female, eight males). We censored a single individual of each species monitored ≤ 32 days and an additional 790 locations with a HDOP > 10 and 5,318 locations with a horizontal error estimate > 60 m. Our final seasonal samples contained 31,229 (BHS = 18,997, MTG = 12,232) summer locations from 51 individuals (BHS = 29, MTG = 22), and 65,237 (BHS = 43,548, MTG = 21,689) winter locations from 55 individuals (BHS = 33, MTG = 22; Appendix S3.4). The availability extent (4,389 km^2) encompassed all GPS locations and was buffered by 962 meters, representing the 95th percent quantile of sequential step lengths (Fig. 3.1).

Seasonal niche characterization and similarity

Niche space

For most covariates within the univariate models there were appreciable differences between grains and forms that varied within and among species and season. While the majority of covariates had a clearly top-ranked form and/or grain within the species-season groupings, some grains and/or forms were only marginally higher ranked (Appendix S3.5). When moving from univariate to multivariate models, we changed the summer DST definition from 40 to 50 degrees for bighorn sheep, and changed the grain of SlopeVar from 1000 to 30 m for mountain goats to reduce collinearity with slope (Table 3.2; Appendix S3.5). In winter, we removed SWE which was collinear with elevation for both species (Table 3.2; Appendix S3.5).

There was strong similarity between bighorn sheep and mountain goat weighted mean coefficients in both seasons (Fig. 3.3) and similar relationships with each covariate (Appendix S3.6). The summer niches of both species were characterized by relatively cool aspects with little canopy cover on steep and rugged slopes at high elevations (Fig. 3.3). Slope was the most influential covariate for both species and showed the strongest evidence of niche partitioning. In contrast to our hypotheses, the standardized coefficients suggested the summer bighorn sheep niche was characterized by steeper slopes than that of mountain goats (Fig. 3.3, Appendix S3.6). Moreover, both the linear and quadratic coefficients of slope were positive, indicating positive and accelerating selection for steep slopes by both species rather than an optimal mid-level value for slope. The winter niches of both species were characterized by warmer, southwest slopes, at relatively low elevations with minimal canopy cover, and steep and rugged slopes (Fig. 3.3, Appendix S3.6). Slope was the most influential covariate in winter, yet in contrast to summer, indicated the mountain goat niche was characterized by steeper slopes than that of bighorn sheep. Bighorn sheep also tended to use relatively low elevations compared to mountain goats and had a stronger avoidance of canopy cover in both seasons (Fig. 3.3).

Geographic space

Spearman rank correlations between the RSF bins and the frequency of used locations were high (mean $r_s \geq 0.87$, mean $p \leq 0.02$; Appendix S3.7), indicating strong predictive performance. Not surprisingly, our extrapolations from niche to geographic space indicated similar niches between native bighorn sheep and introduced mountain goats (summer $D = 0.88$, winter $D = 0.87$; Fig. 3.4). The summer niches of both species were centered on rugged and steep terrain at high elevations that was contiguously distributed within the study area (Fig. 3.4). The strong similarity between summer niches was also evident in the cell by cell comparisons of the RSF bins, especially at high bin values (Fig. 3.2). In winter, both species trended to lower elevations, although the stronger effect of elevation for bighorn sheep was evident in the geographic niche representations. Relative to mountain goats, the winter bighorn sheep niche encompassed more low-elevation valley bottoms, although the two niches did overlap on steep, mid-elevation slopes characteristically used by mountain goats. While the bighorn sheep niche was relatively contiguous at low-elevations, the mountain goat niche was patchily distributed throughout the study area and largely excluded valley bottoms (Fig. 3.4). The discrepancies at low elevations also contributed to the larger range of RSF bins of one species associated with each bin of the other species in winter (Fig. 3.2).

Used locations

Our characterizations of seasonal niches from used GPS locations indicated similar distributions for the niche components (Fig. 3.5). Differences were most pronounced for snow water equivalent, which was notably higher for mountain goats relative to bighorn sheep, although this covariate was removed from model predictions because of collinearity with elevation. The remaining niche components showed similar seasonal patterns, with slight differences in the distribution means among species (Fig. 3.5).

Discussion

Our work applied the niche partitioning hypothesis to sympatric mountain ungulates – native bighorn sheep and introduced mountain goats – and indicated similar niches in both niche and geographic space. While both species occur on sympatric native ranges throughout portions of western North America, this study was the first empirical analysis of their sympatric realized niches, and importantly involved native and introduced populations where there is an immediate need to better understand the ecological consequences of introduced mountain goats. Using a variety of methods across niche and geographic space, our work indicated limited evidence of seasonal niche partitioning. Slope was the dominant niche component in both seasons and indicated bighorn sheep occurred on steeper slopes than mountain goats in summer while mountain goats occurred on steeper slopes in winter. In addition, canopy cover was more strongly avoided by bighorn sheep in both seasons and bighorn sheep tended to occur at lower elevations than mountain goats in winter. The remaining niche components were similar among species, resulting in niches that were highly correlated in geographic space.

The conceptual framework initially put forth by Adams et al. (1982) hypothesized mountain goats would occupy the extreme end of habitat-related niche components with partial overlap on sympatric ranges, but did not specify potential seasonal differences. We hypothesized that the Adams et al. (1982) conceptual model would have more relevance in winter and reflect differing wintering strategies between the two species. Regionally, mountain goats tend to select steep slopes at mid-elevations that more readily shed snow (Chadwick 2002, Lowrey et al. 2017), while bighorn sheep move to lower elevations with less snow accumulation (Festa-Bianchet 1988). While we did see mountain goats using relatively steeper slopes in winter, the pronounced differences in slope did not result in notable partitioning in geographic space when combined with the remaining niche components, a finding that was contrary to our hypotheses. In contrast, the niche similarities in summer aligned with our hypotheses as both species tended to use rugged, mountain environments at high elevations. Given the strong seasonal overlap described in our results, we are unable to rule out the possibility of direct or indirect competition. Nonetheless, there are a number of factors that may help to explain the lack of niche partitioning among sympatric mountain ungulates in our study area.

Space use is regarded as an important axis along which a broad range of taxa partition resources (Schoener 1974, Stewart et al. 2002, Jenkins et al. 2007). Nonetheless, species that overlap along the spatial niche axis may yet reduce competition by partitioning niches along temporal or dietary axes (Schoener 1974, Pianka 1974). Both bighorn sheep and mountain goats have evolved as habitat specialists. Given the relatively narrow habitat type within which both species occur, the dietary or temporal niche axes may provide more flexibility in niche partitioning. We are not aware of any studies that have investigated the temporal patterns of sympatric mountain ungulates. However, previous studies have added some support to the presence of dietary partitioning, but definitive conclusions remain elusive. In a review paper, Laundré (1994) concluded that both species have similar diets when broad vegetation classes (grasses, forbs, browse) were compared across studies of allopatric populations, but that diet overlap was reduced when the two species were sympatric. Importantly, however, Laundré (1994) also emphasized the need for additional studies and the inability to draw rigorous conclusions with the available data. Working within a northern subset of our study area, Varley (1994) documented dissimilar summer feeding areas between bighorn sheep and mountain goats, but did not examine their niches as defined here and was again limited to broad vegetation classes within a narrow temporal window.

Although working within a different ‘niche’ framework, the Varley (1994) results highlight scale as an important lens through which to interpret our results. We were specifically interested in population niches and maintaining the ability to directly compare seasonal niches among species. As a result, we defined availability equally for all individuals and seasons to negate the influence of the available sample on conclusions regarding seasonal niche characteristics and niche partitioning (Beyer et al. 2010). Moreover, the population-level inferences are often most relevant to regional managers tasked with monitoring mountain goat expansion and mitigating for any potential negative impacts posed to native species, including bighorn sheep. Similar analyses of sympatric and allopatric species conducted across multiple scales have shown differential patterns in resource selection and niche overlap (Jenkins et al. 2007, DeCesare et al. 2012). While our population-level study design indicated similar seasonal niches, a finer-scale analysis (e.g., within home ranges) in conjunction with behavioral data may indicate niche partitioning at a scale not captured with our broad sample of availability, for example the dissimilar summer feeding areas described by Varley (1994). Nonetheless, we feel the descriptive niche characterizations from the used GPS locations further support our findings of niche similarity, irrespective of scale and availability (Fig. 5).

While our results indicated similar niches, equating niche similarity and overlap with competition can be ‘dubious and misleading’ (Pianka 1974). By definition, resources need to be limiting for niche overlap to result in competition (Gause 1934). Given present densities and distributions of both species in the northeast GYA, the observed niche overlap may not result in exploitive competition, especially in summer when there is an abundance of forage within mountain environments. Niche overlap among sympatric species has been documented in other mountain ungulates, including Asiatic ibex (*Capra ibex*) and blue sheep (*Pseudois nayaur*) in northern India (Namgail 2006), as well as chamois (*Rupicapra rupicapra*) and mouflon (*Ovis gmelini musimon*) in the northern French Alps (Darmon et al. 2012). In both studies researchers found positive associations between sympatric species using abiotic niche components (e.g., terrain features) to describe and predict overlap in niche (Namgail 2006) and geographic space (Darmon et al. 2012). While the generalities are not entirely consistent among published studies of mountain ungulates (see Namgail et al. 2004), the relatively low densities at which mountain ungulates exist on the landscape may minimize the negative effects of overlapping niches, therefore negating the need to partition resources in response to competition.

While our data were broadly overlapping within the study area, because of the difficulty in capturing both species we did not have a large sample of animals that overlapped in both space and time, and were unable to evaluate the direct displacement of one species by the other (i.e., interference competition). Nonetheless, mountain goats have been shown to exhibit a relatively high degree of intraspecific aggressiveness (Côté 2000, Chadwick 2002), and were observed usurping space and resources from bighorn sheep in 39 of 107 (36.5 percent) interactions in a Colorado study (Reed 2001). While mountain goats appear to dominate in interspecific interactions, it is unclear how often these events occur within our study area. Direct encounters were prohibitively difficult to observe within our expansive study area, especially in winter when bighorn sheep and mountain goats were more likely to encounter one another because of the general reduction of suitable habitat. While data on the interspecific interactions of mountain ungulates remains limited, remote trigger camera traps placed at known mineral licks may help to further our understanding of the behavioral interactions between bighorn sheep and mountain goats when seeking a shared, but limited, resource.

Interspecific interactions between bighorn sheep and mountain goats may also be mediated by seasonal movement strategies. Although all niche extrapolations showed strong predictive performance when averaged across individuals, our validation plots highlighted four bighorn sheep for which the winter model had relatively poor predictive performance (Appendix S3.7). All four sheep remained at relatively high elevations during winter months and may be indicative of varying wintering strategies within regional bighorn sheep. While continued research is beginning to describe bighorn sheep seasonal movements, management surveys have previously located bighorn sheep wintering at high elevations (McWhirter unpublished data). Moreover, in the southwest GYA, Courtemanch et al. (2017) recently described an ‘abbreviated migration’ in which bighorn sheep within Grand Teton National Park remain on high-elevation, windswept ridgelines for most of the year, but descend 500 m in spring to gain access to newly emergent forage approximately 30 d prior to spring green up on the high-elevation winter and summer ranges. Seasonal movements and wintering strategies may be an important component of mountain ungulate niche partitioning. While bighorn sheep that undergo elevational migrations between low-elevation winter ranges and high-elevation summer ranges may naturally separate from mountain goats, bighorn sheep that remain at high elevations year-round may increase spatial overlap with non-native mountain goats during the winter months.

At present, the observed spatial and niche overlap does not appear to be negatively impacting demographics as both species have maintained positive growth rates over the period of mountain goat expansion (Flesch et al. 2016, Butler et al. 2017). However, given the similarity in seasonal niches, it is likely that mountain goats will continue to increase their spatial overlap with native bighorn sheep and increase densities where the two species are sympatric presently. While the relative abundance of forage and contagious habitat in summer is unlikely to result in the limited resources required for competition, expanding mountain goats may still negatively impact bighorn sheep in winter when resources are less available and patchily distributed. Moreover, similar niche requirements in winter may increase the likelihood of interspecific interactions, which in addition to displacing bighorn sheep, may also transmit novel respiratory pathogens between species (Gross 2001) and further hinder bighorn sheep restoration efforts. In contrast to our winter hypotheses and previous conceptual models, our results did not indicate meaningful niche partitioning. Our results suggest that reducing densities of mountain goats in hunted populations that are sympatric with bighorn sheep and impeding their expansion may reduce the possibility of competition and disease transfer. Given the current uncertainties regarding the possibility of partitioning at finer spatial scales and along dietary or temporal niche axes, the similarities of the population niches presented here suggests a conservative management approach that liberalizes harvest of introduced mountain goats outside of Yellowstone National Park where hunting was banned in 1894, may be warranted. In concert, additional studies that specifically investigate partitioning at finer scales and along other niche axes will help to further evaluate the possibility of competition and can be used to inform an adaptive management approach. Where applicable and/or feasible, experimental removal of mountain goats would further our understanding of niche flexibility across a broad range with both sympatric and allopatric conditions, and inform interspecific competition between sympatric populations.

As the availability and accessibility of spatial data continues to revolutionize ecological research, we see an opportunity to build from single species habitat maps to applied interspecific research with broad ecological relevance. Our work presented herein exemplifies one such possibility and integrates applicable tools from the habitat suitability and niche modeling fields to evaluate seasonal niche partitioning of native bighorn sheep and introduced mountain goats in the GYA.

Acknowledgments

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Tables and figures

Table 3.1. Covariates used to approximate the realized niches of sympatric bighorn sheep (BHS) and mountain goats (MTG), GYA, 2012 – 2017. Bold type for the hypothesized relationship indicates the relative strength for each species-season combination. For example, both bighorn sheep and mountain goats were hypothesized to have a negative relationship with elevation in winter, but the association was expected to be greater for bighorn sheep than for mountain goats, as indicated by bold type for bighorn sheep.

Abbreviation	**Description**	**Form***	**Spatial grain‡**	**Hypothesized relationship** (summer, winter)	
				MTG	**BHS**
ELEV	Elevation (m)	Li	30	**pos,** neg	pos, **neg**
SLP	Slope (degrees)	Li, Sq	30, 500, 1000	**pos, pos**	pos, neg
SlopeVar†	Slope variance: standard deviation2 of SLP	Li, Ps	30, 500, 1000	**pos, pos**	pos, neg
DST	Distance to steep terrain: Euclidian distance from slops ≥ 30, 40, 50 degrees	Li	30, 500, 1000	**neg, neg**	neg, neg
CanCov	Canopy cover	Li	30, 500, 1000	**neg,** neg	neg, **neg**
NDVI	Time integrated NDVI: mean daily (interpolated) integration of NDVI above the baseline for the duration of the growing season from 2011 - 2014.	Li	250, 500, 1000	pos, pos	**pos, pos**
AspectCos	The inverse cosine of aspect minus 35 degrees	Li	30	pos, neg	pos, neg
SWE	Snow water equivalent: Mean Dec-Jan from 2011 -2014.	Li	1000	na, neg	na, **neg**

* Li = Linear, Sq = Quadratic, Ps = Natural log/pseudothreshold.

‡ Circular buffer in meters.

† The 30 m SlopeVar was generated using a 30 m neighborhood analysis of a 10 m resolution slope raster and served as the base layer to generate SlopeVar at the larger spatial grains.

Table 3.2. The top-ranked covariate grains and forms used to define the realized Grinnellian niches of sympatric bighorn sheep and mountain goats, northeast GYA, 2012–2017.

Season	**BHS**			**MTG**		
	Covariate	**Grain**	**Form**	**Covariate**	**Grain**	**Form**
Summer	Aspect	30	Li	Aspect	30	Li
	CanCov	500	Li	CanCov	1000	Li
	DST50	30	Li	DST50	30	Li
	Ele	30	Li	Ele	30	Li
	NDVI	250	Li	NDVI	1000	Li
	Slope	1000	Sq	Slope	1000	Sq
	SlopeVar	30	Li	SlopeVar	30	Ps
Winter	Aspect	30	Li	Aspect	30	Li
	CanCov	30	Li	CanCov	500	Li
	DST50	30	Li	DST50	30	Li
	Ele	30	Li	Ele	30	Li
	NDVI	1000	Li	NDVI	1000	Li
	Slope	1000	Sq	Slope	30	Sq
	SlopeVar	30	Ps	SlopeVar	30	Ps

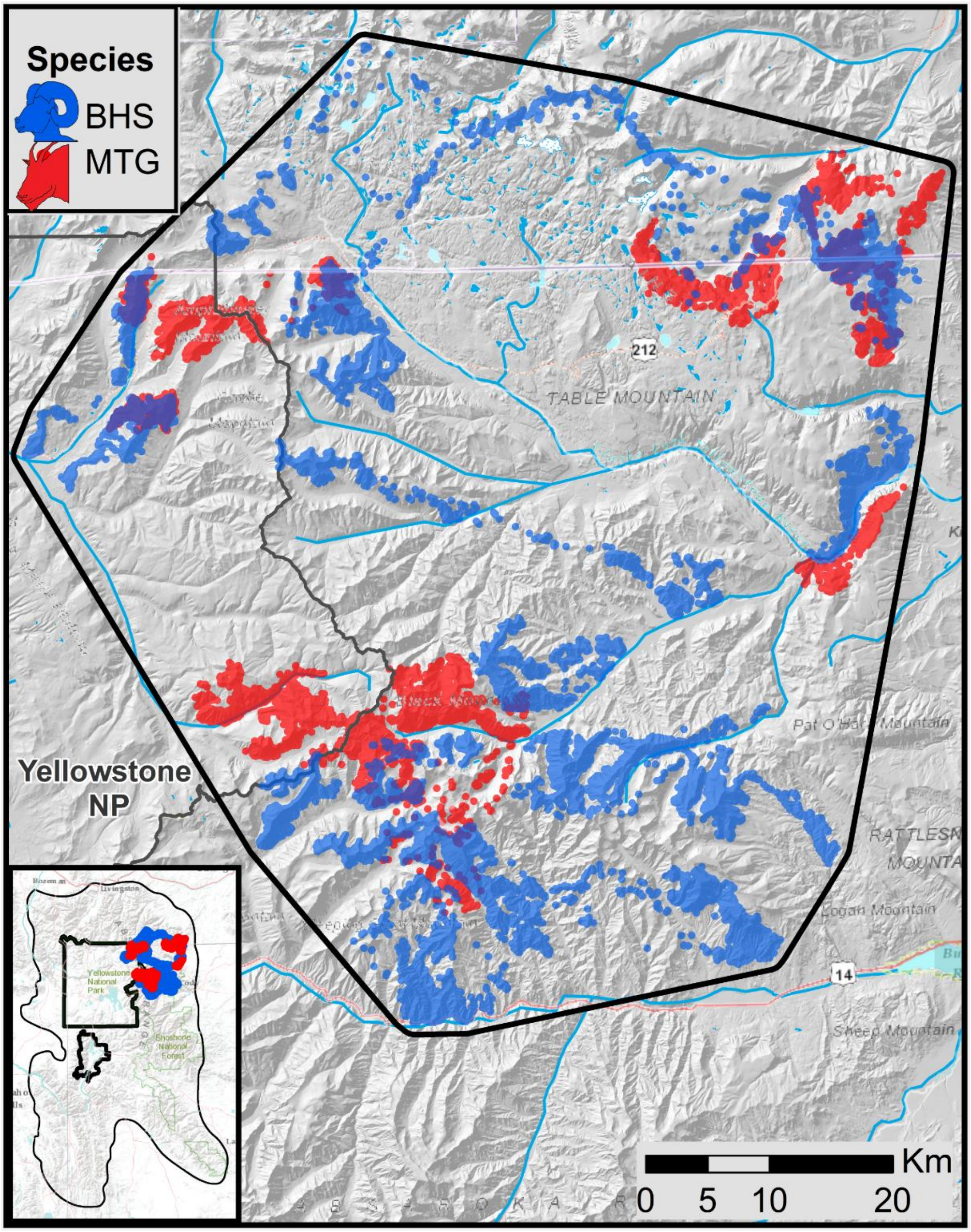


Fig. 3.1. GPS locations of 34 bighorn sheep and 23 mountain goats instrumented in the northeastern GYA, USA, 2012-2017. The study area (black polygon) was defined with a buffered minimum convex polygon around all locations.

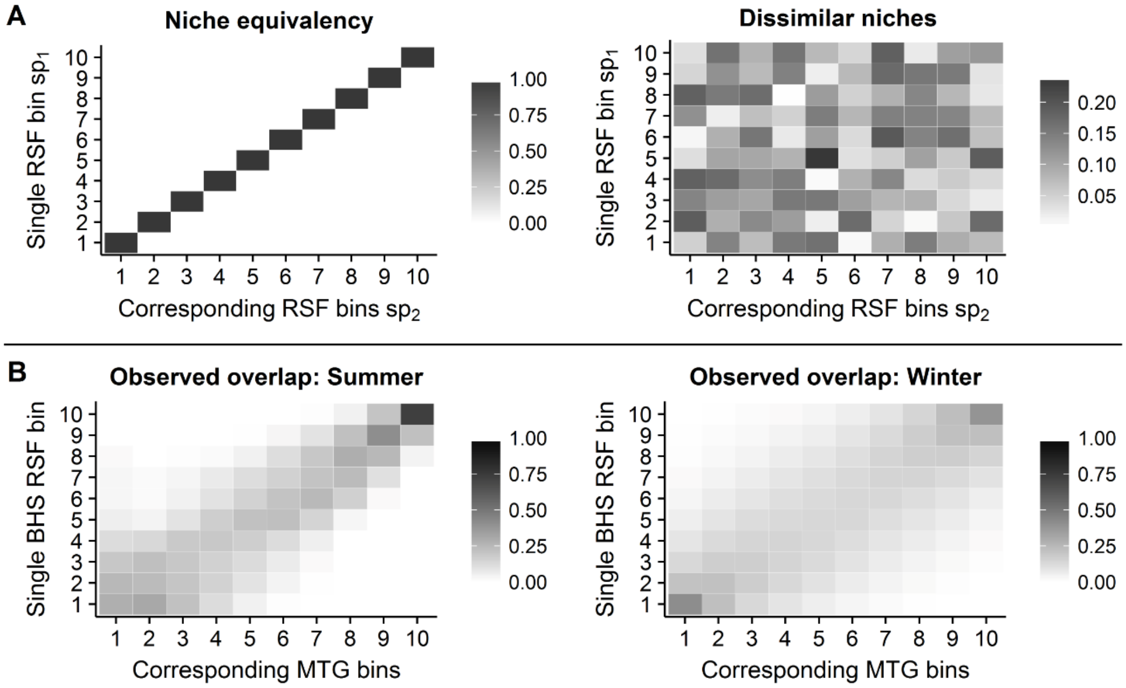


Fig. 3.2. (A) Schematic depiction of the two extremes when comparing niche overlap. Each cell represents the proportion of $species_2$ (sp_2) RSF bins within a single bin of $species_1$ (sp_1). When two niches are equivalent (e.g. D = 1), there will be perfect alignment between the RSF bins. In contrast, dissimilar niches (e.g. D = 0) will appear random with an overlap similar to that expected by chance. Note the different coloring scales between the two panels. (B) Cell by cell comparison of the observed seasonal niche overlap of sympatric bighorn sheep and mountain goats in the northeast, GYA. Each cell represents the proportion of RSF values from one species that corresponds to a single RSF bin of the other species.

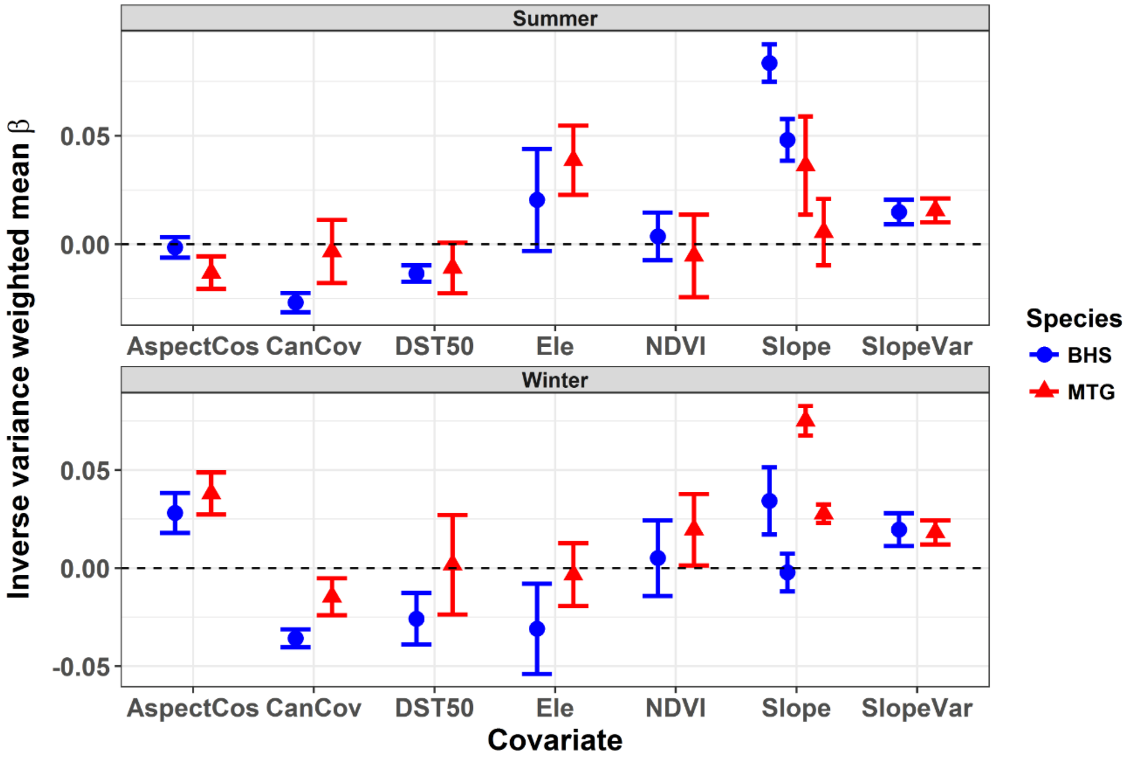


Fig. 3.3. Inverse variance weighted mean coefficients (± 95% CIs) estimated from individual resource selection models using a two-stage framework (with scaled covariates) for sympatric bighorn sheep and mountain goats in the northeast, GYA. Both the linear and quadratic terms are shown for the Slope covariate, respectively.

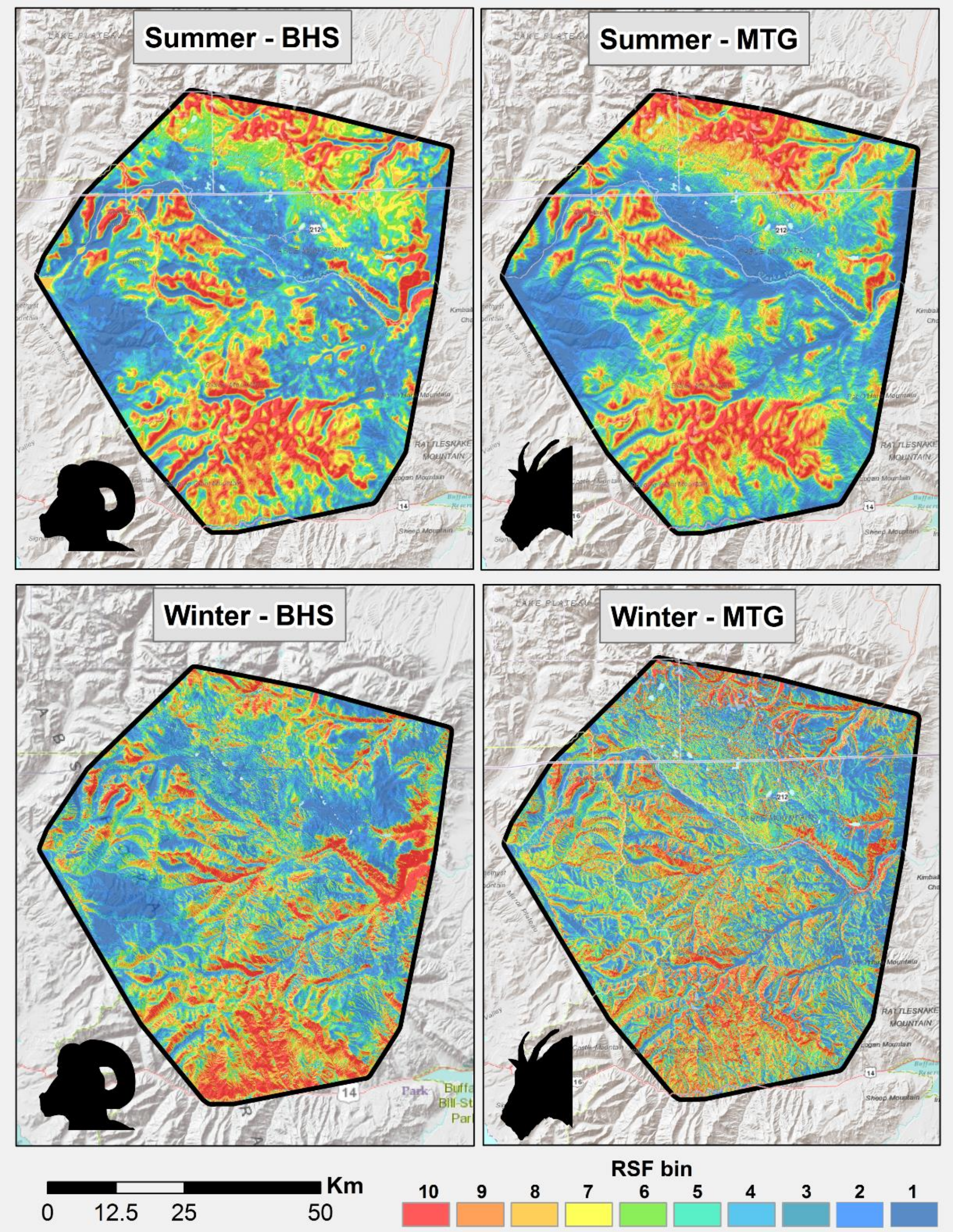


Fig. 3.4. Seasonal geographic realized niche predictions for sympatric bighorn sheep and mountain goats in the northeast, GYA.

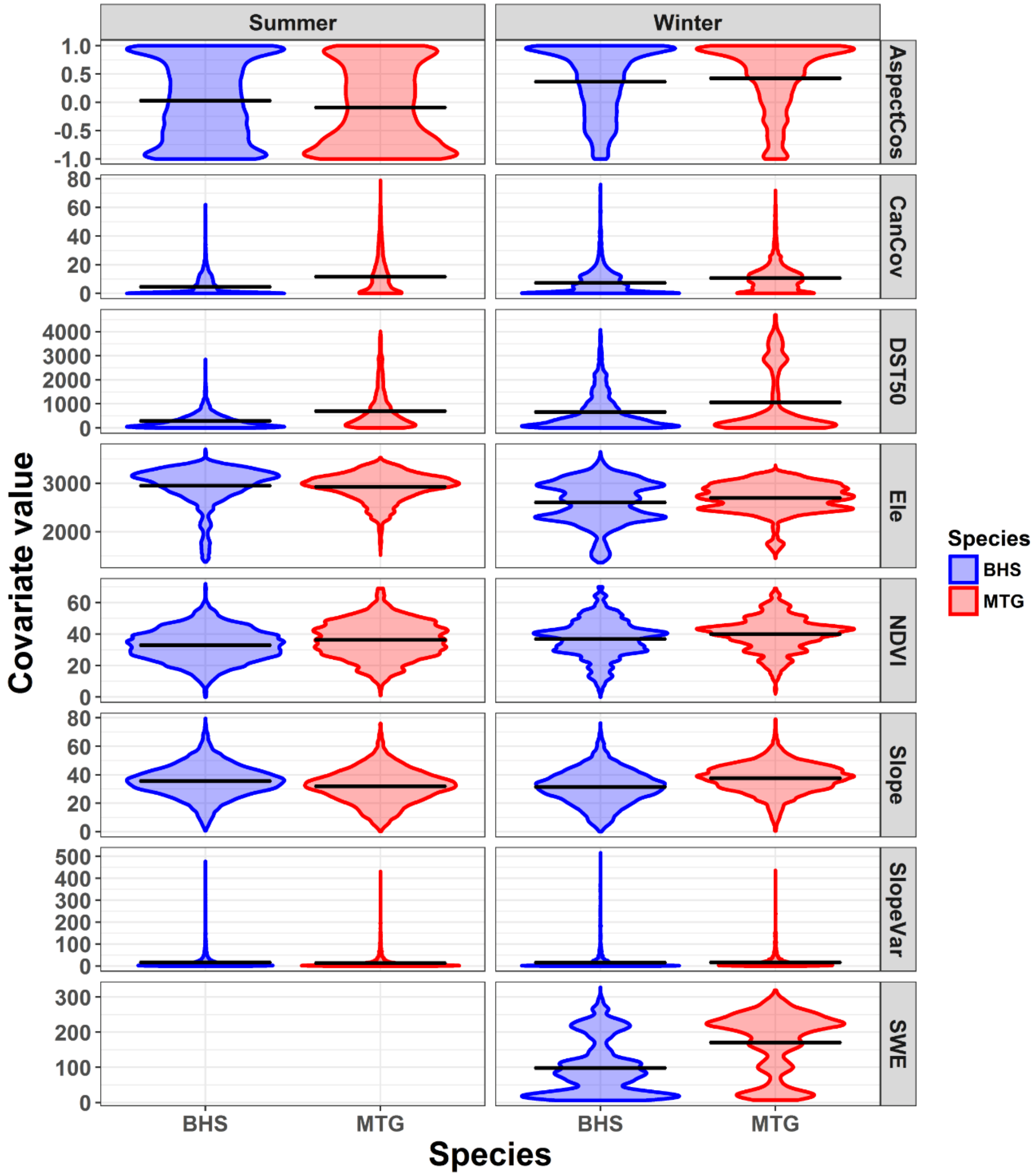


Fig. 3.5. Violin plots showing the distribution of niche components associated with used GPS locations from sympatric bighorn sheep and mountain goats in the northeast, GYA. Distribution means are shown with solid black lines.

CHAPTER THREE APPENDICES

Appendix S3.1: Delineating summer and winter seasons for sympatric bighorn sheep and mountain goats in the northeast Greater Yellowstone Area

We defined summer and winter periods using migration parameters estimated from nonlinear regression modeling of net-squared displacement (NSD; Bunnefeld et al. 2011, Lowrey et al. 2017). Following the described methods for nonlinear regression modeling of NSD we rarified the data to include only a single location for each day and selected the year with the longest continuous monitoring period for each individual bighorn sheep (BHS) and mountain goat (MTG). Animals with < 250 days of monitoring were excluded, leaving 47 animals (BHS = 29 and MTG = 18) for NSD analysis. We measured NSD from each individual's core winter range, defined as the centroid of locations obtained from 15-January to 20-February (Lowrey et al. 2017). The time period was specified to accommodate the varied capture schedule and ensure that animals captured late in the capture season had at least one week of locations from which to estimate a core winter range centroid.

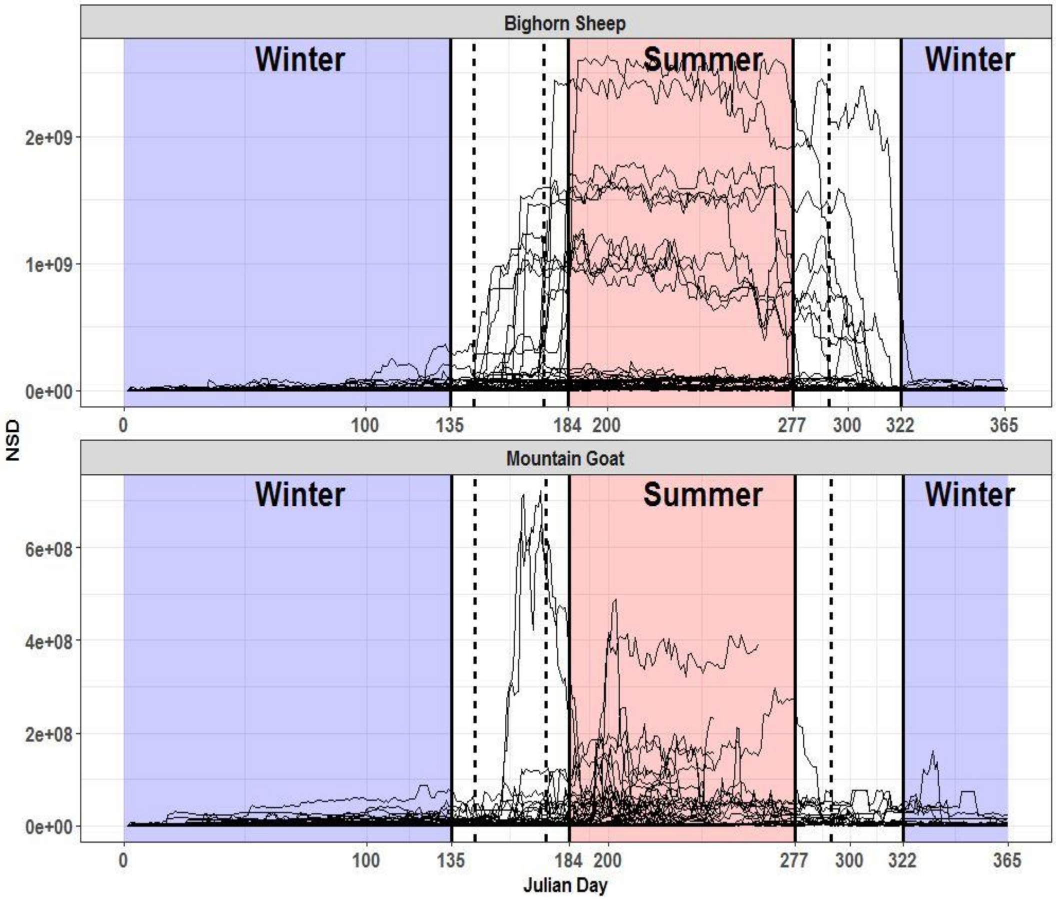
Working with the `migrateR` package for program R (R Core Team 2015, Spitz et al. 2017), we fit 5 movement models (i.e. Bunnefeld et al. 2011) to each individual-year. Exploratory analysis of unconstrained models indicated notable inter- and intra-specific heterogeneity in movement classification as well as parameter estimates for animals classified as migrant or mixed-migrant. Because our interest was in population-level resource selection we set a number of biologically reasonable constraints to the individual NSD models to dampen the observed heterogeneity when defining a single ‘population’ summer and winter period. The constraints were as follows. Theta, the midpoint of the spring migration was specified to occur between 15-April and 15-June. Phi quantifies the duration of movement, specifically the time required to complete 1/2 to 3/4 of the migration, and was specified with a lower and upper bound of 1 to 10 in spring and 1 to 20 in the fall. The length of time spent on the migratory range (rho) had a lower and upper bound of 30 and 200 days, respectively. The distance separating seasonal ranges (delta) was set with a minimum of 5 km. Of the remaining parameters: gamma, the mean NSD of locations in an individual's range was estimated dynamically with no starting value; zeta, an adjustment to delta for the return migration had default lower and upper limits of 0.05 and 0.95, respectively; and kappa, the logarithm of the rate constant had default lower and upper limits of -1.00 and -0.01, respectively (Spitz et al. 2017).

Thirty-two of the 47 animal-years were classified as either migrant or mixed-migrant (Appendix S3.1: Table S3.1). We pooled the migrants and mixed-migrants and estimated population starting and ending dates as the mean of individual theta ± 2 * phi and theta2 ± 2 * phi2 for spring and fall, respectively. Because of the observed heterogeneity in migration timing we added additional temporal buffers to ensure that the majority of all individual migratory movements were included in the population migratory period, and therefore, excluded from the summer and winter modeling periods. The spring and fall start dates were advanced 5 days and the ending dates were lengthened 10 days in spring and 30 days in fall (Appendix S3.1: Fig. S3.1). Inclusive of the additional buffers, spring migration occurred in a 49 day period from 15-May to 3-July and fall migration occurred in a 45 day period from 4-October to 18-November. We removed the days within the migratory periods and defined summer as 3-July to 4-October and winter as 18-November to 15-May (Appendix S3.1: Fig. S3.1).

The summer season was characterized by relatively high NSD and greater variation. In contrast, the winter season was characterized by relatively low NSD that were relatively constant throughout the season (Appendix S3.1: Fig. S3.1). Our quantitative analysis of NSD to delineate summer and winter modeling periods accurately captured the behavioral differences associated with each season and minimized the additional 'noise' associated with transitional movements between summer and winter ranges.

Appendix S3.1: Table S3.1. Movement classifications from nonlinear regression modeling of NSD.

Movement model	BHS	MTG	Total
Disperser	0	1	1
Migrant	9	2	11
Mixed-migrant	13	8	21
Nomad	0	3	3
Resident	7	3	9



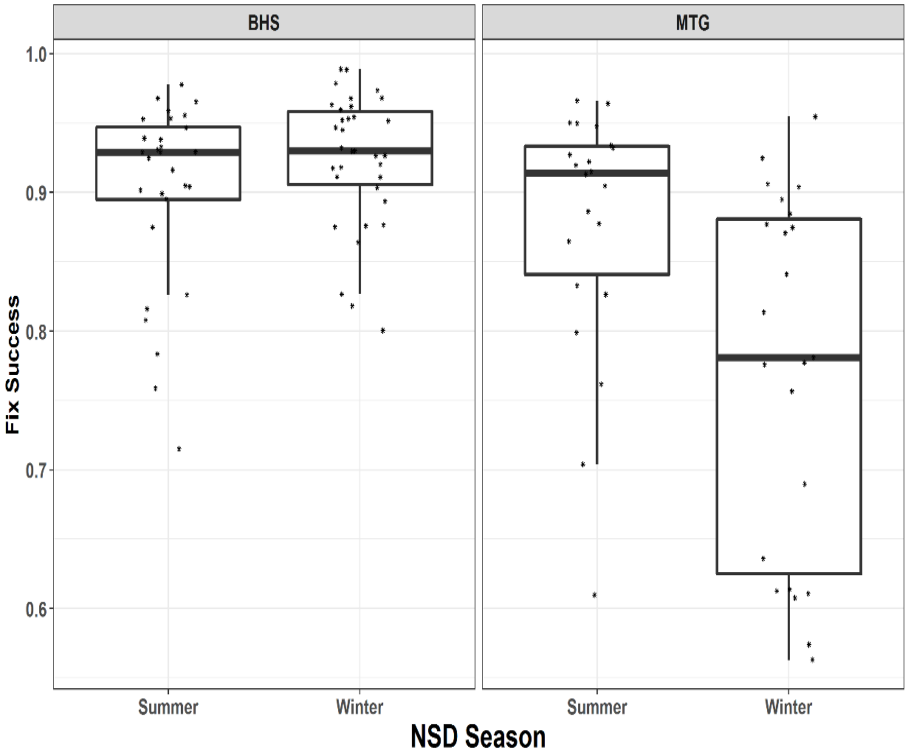
Appendix S3.1: Fig. S3.1. Net-squared displacement distributions for all study individuals, shown separately for bighorn sheep and mountain goats. The population summer and winter seasons were estimated by averaging individual theta values ± 2phi (dashed) and then buffered (solid) to further remove the migratory periods from the summer and winter analysis periods.

Appendix S3.2: Seasonal fix success for sympatric bighorn sheep and mountain goats in the northeast Greater Yellowstone Area

We estimated fix success as the percent of locations that were successfully acquired after accounting for locations that were censored because of spatial imprecision. We did not censor the data based on individual fix success as most individuals had rates greater than the 25% losses found to negatively affect model inferences (Appendix S3.2: Table S3.1; Fig. S3.1; Appendix S3.4: Table S3.1; Johnson and Gillingham 2008). Moreover, although steep slopes can reduce fix success in mountainous terrain (D'Eon et al. 2002), because of the strong seasonal association with steep, alpine environments for both species, it is unlikely these habitats are underrepresented in the dataset in the magnitude necessary to alter the fundamental conclusions regarding mountain ungulate niches (Lowrey et al. 2017).

Appendix S3.2: Table S3.1**.** Seasonal fix success for sympatric bighorn sheep and mountain goats, northeast Greater Yellowstone Area, USA, 2012-2017.

Species	Season	Population fix success
BHS	Summer	91%
BHS	Winter	93%
MTG	Summer	88%
MTG	Winter	78%



Appendix S3.2: Fig. S3.1. Individual (dots) seasonal fix success for bighorn sheep and mountain goats summarized with box plots, northeast Greater Yellowstone Area, USA, 2012-2017. Seasons were defined using net-squared displacement (NSD; Appendix S3.1).

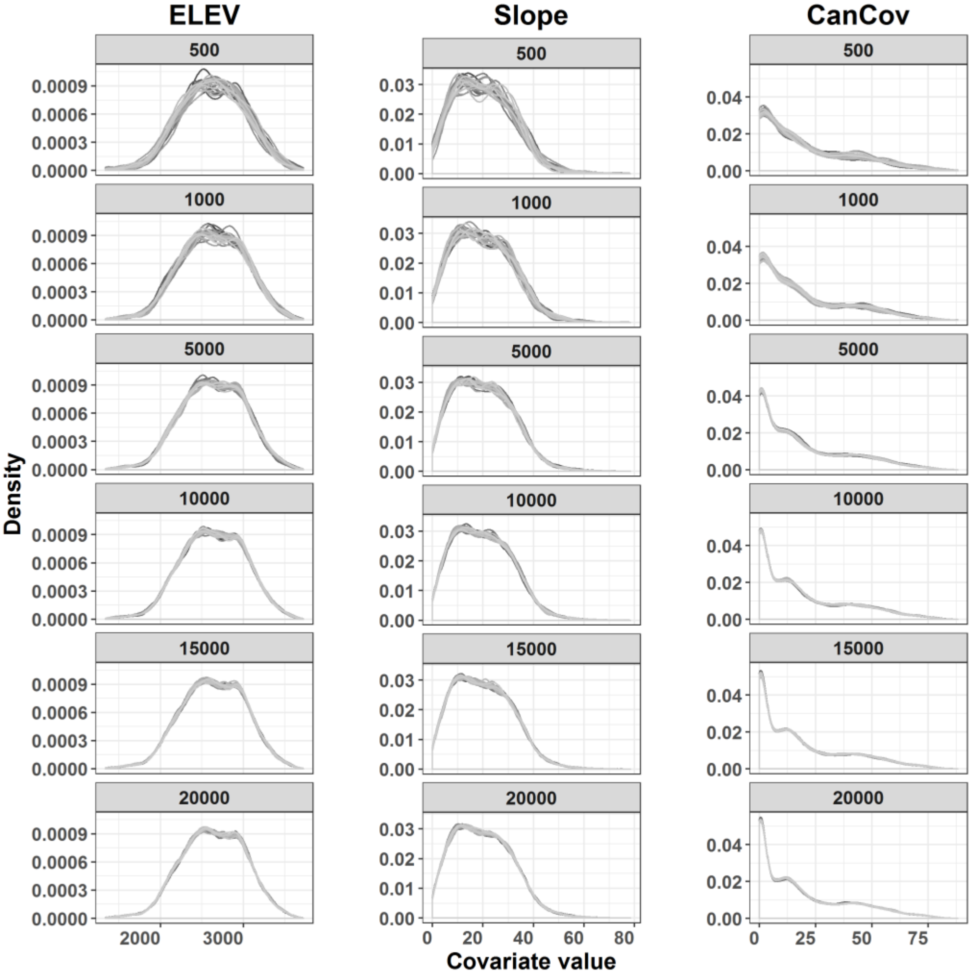
Appendix S3.3. Simulation methods to evaluate multiple sampling intensities when defining a used to available ratio for sympatric bighorn sheep and mountain goats in the northeast Greater Yellowstone Area

Resource selection functions (RSFs) are often used to study patterns in animal resource selection and are commonly fitted using a used-available study design (Manly et al. 2002, Boyce et al. 2002) where ‘used’ locations are collected from GPS collars and ‘available’ locations are randomly generated within an extent deemed ‘available’ given the scale of inquiry (Johnson 1980). The number of available points is often defined in relation to the number of used points (e.g. used:available ratio) and needs to be large enough to allow for model convergence, and to accurately describe the distribution of the covariates of interest within the study area (Northrup et al. 2013).

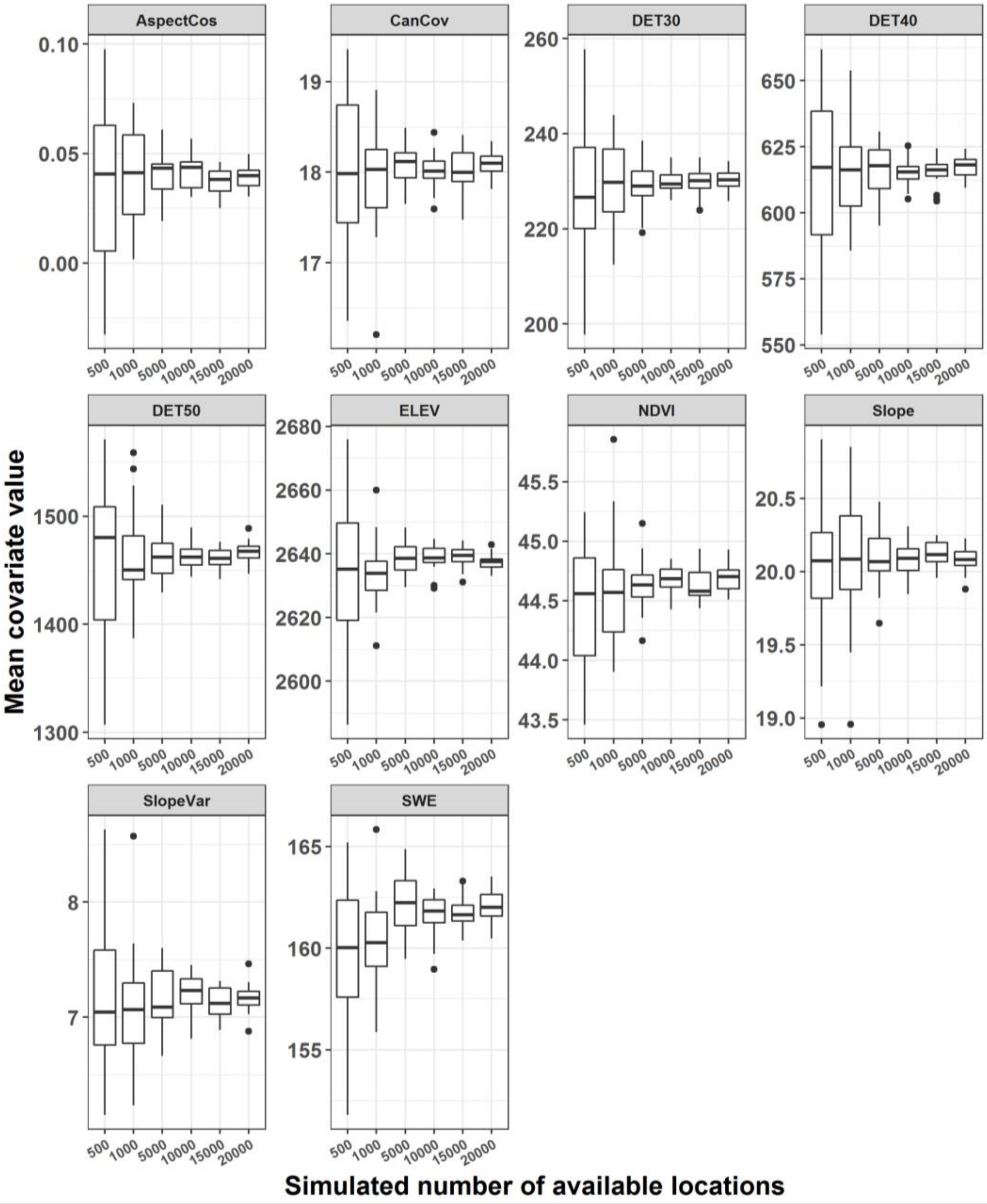
To select the proper sampling intensity for our work with sympatric mountain ungulates in the northeast Greater Yellowstone Area (GYA) we conducted a simulation to identify the number of locations that best described the ‘true’ distribution of the covariates within the study area. We evaluated 6 sampling intensities (500, 1,000, 5,000, 10,000, 15,000, 20,000) of randomly distributed locations within the buffered minimum convex polygon (described in the main article). For each intensity level we ran 25 simulations in which a sample was generated and covariate values were extracted for the sample locations. We extracted values from 10 covariates – AspectCos, CanCov, Elev, DET30, DET40, DET50, Slope, SlopeVar, SWE, and NDVI - all of which were further detailed in the main article (Table 3.1). We evaluated the influence of sampling intensity on the distribution of each covariate by generating density plots (Appendix S3.3: Fig. S3.1) and box-plots (Appendix S3.3: Fig. S3.2). All raster processing and sampling was conducted using the raster package in program R (R Core Team 2015, Hijmans et al. 2016).

Visual examination of the 25 simulations suggested the variance stabilized at 5,000 random locations (Appendix S3.3: Figs. S3.1, S3.2). In some instances, for example CanCov or DET45, 10,000 locations may provide slightly more consistent estimates, but when examined in context of the scale on the y-axis, the differences would likely have a negligible influence on the β coefficients of the fitted models (Lowrey et al. 2017). These results suggest that repeat samples of at least 5,000 random locations provide similar distributions and accurately describe availability within the study area.

After censoring imprecise locations and individuals monitored ≤ 32 days, the number of used locations for each individual ranged from 180–1256 in summer and from 177–2516, in winter. Given the number of used locations, a used to available ratio of 1:10 nearly ensured that all individuals approximated 5,000 available locations. While there were a few individuals with fewer locations, we did not want to over inflate the available sample larger than necessary, nor did we want to unnecessarily remove individuals from the analysis. A 1:10 ratio represents an effective balance between accurately describing availability within the study area and not over inflating the available sample.



Appendix S3.3: Fig. S3.1. Three example density plots of elevation (Ele), slope, and canopy cover (CanCov) obtained from 25 simulations using 6 sampling intensities (indicated at top of each panel). Each line represents the distribution of a single sample from the respective sampling intensity and covariate.



Appendix S3.3: Fig.S3.2. Boxplots of the mean value for 10 covariates obtained from 25 simulations using six different sampling intensities.

Appendix S3.4: Individual summary statistics

Table showing demographics and monitoring periods for all included bighorn sheep (BHS) and mountain goats (MTG). The number of GPS locations and fix success rates are also presented. Means and totals are shown and the bottom of the table.
Appendix S3.4: Table S3.1**.**

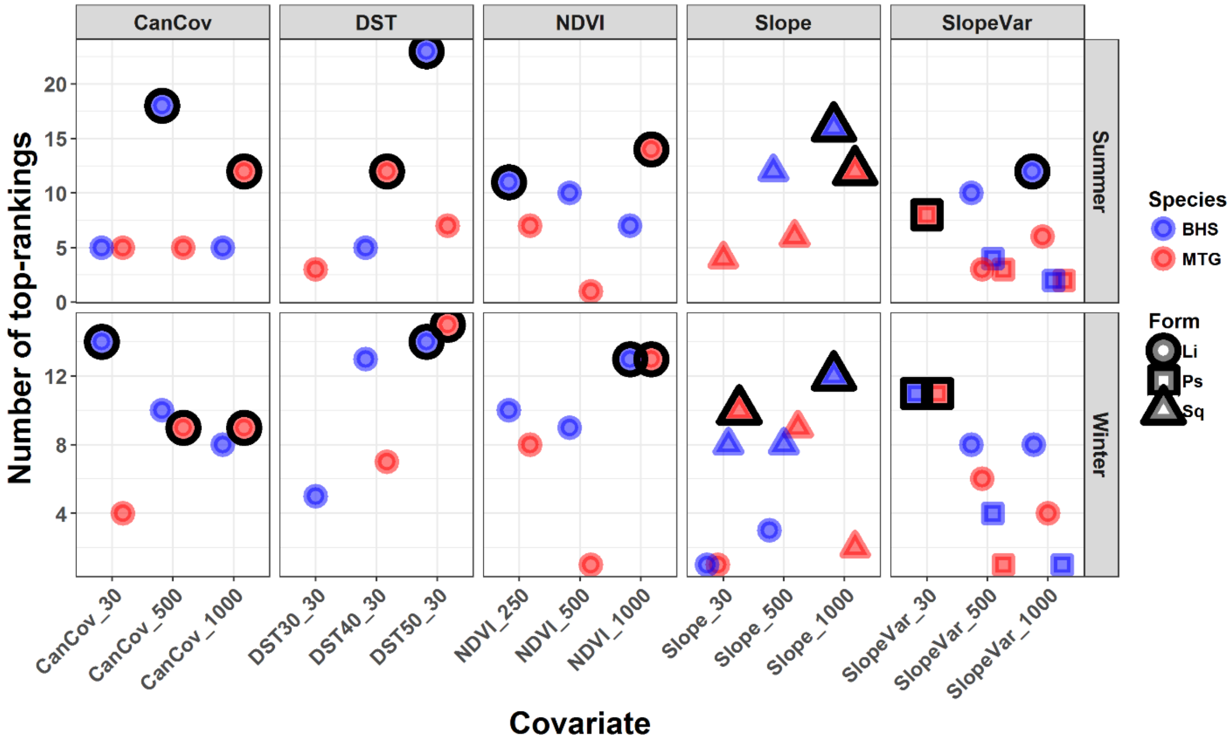
IndID	**Species**	**Number of locations**		**Fix Success rate**	
		Summer	**Winter**	**Summer**	**Winter**
BHS_034	BHS	338	1001	0.904	0.864
BHS_035	BHS	-	177	-	0.801
BHS_037	BHS	499	1081	0.826	0.911
BHS_068	BHS	577	1157	0.956	0.979
BHS_070	BHS	565	1135	0.933	0.960
BHS_071	BHS	460	978	0.759	0.827
BHS_072	BHS	472	1040	0.784	0.877
BHS_073	BHS	432	967	0.715	0.818
BHS_075	BHS	569	1142	0.938	0.963
BHS_076	BHS	359	722	0.965	0.930
BHS_077	BHS	561	1015	0.925	0.918
BHS_078	BHS	579	967	0.953	0.875
BHS_080	BHS	828	2032	0.929	0.945
BHS_081	BHS	846	2052	0.947	0.954
BHS_082	BHS	802	1972	0.899	0.918
BHS_083	BHS	-	459	-	0.952
BHS_084	BHS	872	1996	0.978	0.930
BHS_085	BHS	487	1269	0.931	0.932
BHS_086	BHS	856	2082	0.959	0.968
BHS_087	BHS	808	1993	0.905	0.927
BHS_088	BHS	364	565	0.816	0.894
BHS_106	BHS	1256	2516	0.939	0.947
BHS_109	BHS	727	1736	0.895	0.876
BHS_110	BHS	714	1789	0.875	0.904
BHS_111	BHS	659	1818	0.808	0.920
BHS_112	BHS	-	829	-	0.962
BHS_142	BHS	828	1807	0.929	0.911
BHS_143	BHS	402	1137	0.902	0.953
BHS_145	BHS	-	317	-	0.952

BHS_149	BHS	829	1436	0.929	0.926
BHS_150	BHS	787	1443	0.968	0.968
BHS_153	BHS	776	1449	0.953	0.974
BHS_154	BHS	745	1469	0.916	0.989
MTG_013	MTG	481	734	0.799	0.608
MTG_014	MTG	428	749	0.704	0.614
MTG_015	MTG	564	911	0.932	0.757
MTG_017	MTG	461	608	0.762	0.563
MTG_029	MTG	180	364	0.827	0.781
MTG_030	MTG	327	345	0.878	0.885
MTG_031	MTG	576	882	0.950	0.776
MTG_033	MTG	576	912	0.950	0.814
MTG_036	MTG	585	873	0.966	0.777
MTG_037	MTG	823	2052	0.922	0.955
MTG_039	MTG	223	444	0.934	0.904
MTG_040	MTG	808	1658	0.905	0.925
MTG_041	MTG	584	1002	0.964	0.841
MTG_042	MTG	770	1721	0.948	0.871
MTG_044	MTG	744	1793	0.913	0.906
MTG_045	MTG	678	1210	0.833	0.613
MTG_046	MTG	703	1364	0.865	0.690
MTG_047	MTG	406	550	0.886	0.611
MTG_048	MTG	300	518	0.610	0.574
MTG_049	MTG	510	365	0.915	0.875
MTG_050	MTG	757	1300	0.927	0.877
MTG_051	MTG	748	1334	0.920	0.895
BHS mean		**655**	**1320**	**0.90**	**0.92**
MTG mean		**556**	**986**	**0.88**	**0.78**
Totals		**31229**	**65237**		

Appendix S3.5: Detailed univariate model and collinearity results

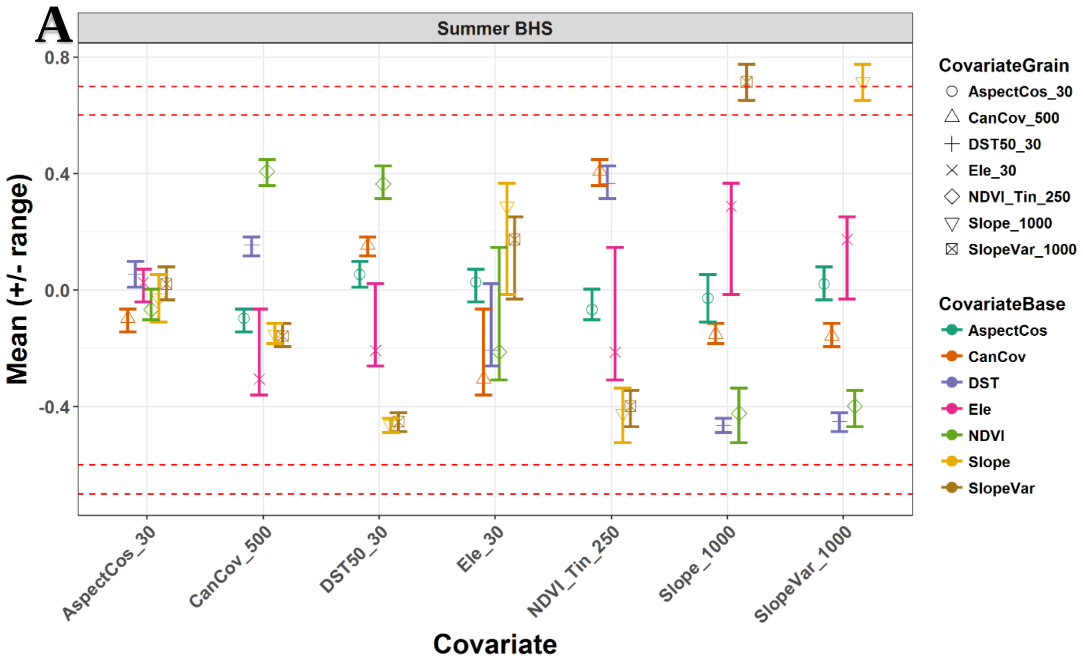
We initiated model building with individual univariate models to select the most explanatory functional form and/or spatial grain for covariates considered with non-linear forms or alternative grains (Table 3.1). For each individual we selected the top-ranked forms and grains using AIC_c (Burnham and Anderson 2002). We then selected the form and grain combination for each covariate that was most top-ranked within the species-season groupings (Appendix S3.5: Fig. S3.1). In instances of a tie, we subjectively defaulted to the smaller spatial grain.

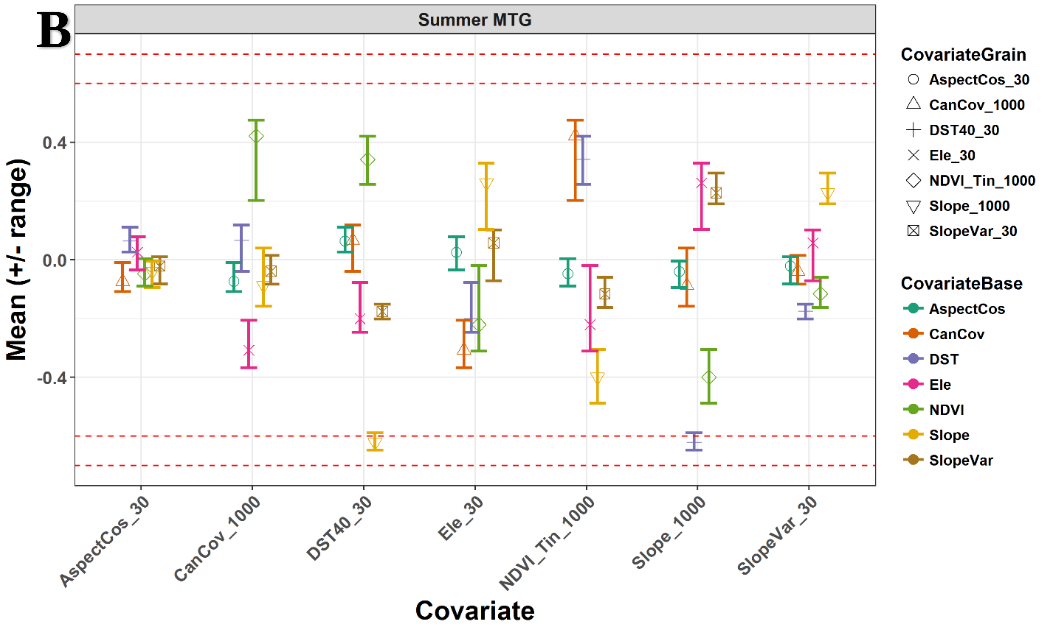
We then combined covariates from tier 1 with covariates not evaluated with multiple forms and/or grains to evaluate collinearly. With the used and available points for each individual we estimated the Pearson correlation coefficient and plotted the mean (± range) across individuals within a species-season group (Appendix S3.5: Fig. S3.2). We made the following changes to reduce collinearity below the |0.6| threshold among the final multivariate models. To reduce the correlation with Slope in summer we changed the DST definition from 40 to 50 degrees for bighorn sheep and changed the grain of SlopeVar from 1000 to 30 for mountain goats. In the winter models we removed SWE which was collinear with Ele for both species (Appendix S3.5: Fig. S3.2).



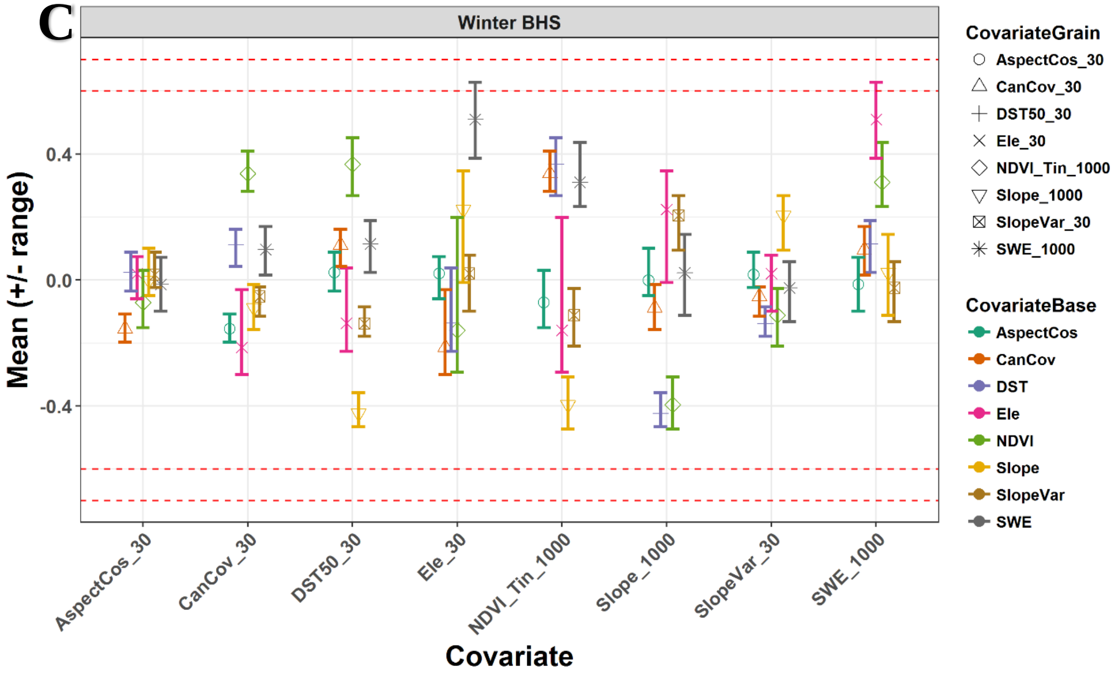
Appendix S3.5: Fig. S3.1. Tier one results showing the number of top-rankings for each functional form and/or spatial grain combination. Black outlines indicate the top-ranked form and/or grain for each covariate when summed across individuals within each species-season grouping.

Appendix S3.1: Fig. S3.2: Mean (± range) seasonal Persons correlation coefficients estimated across individuals within species-season groups for sympatric bighorn sheep (BHS) and mountain goats (MTG) within the northeast, GYA. Summer is shown in panels A and B, while winter is shown in panels C and D. Red dashed lines indicate ±0.6 and ±0.7 correlation thresholds.

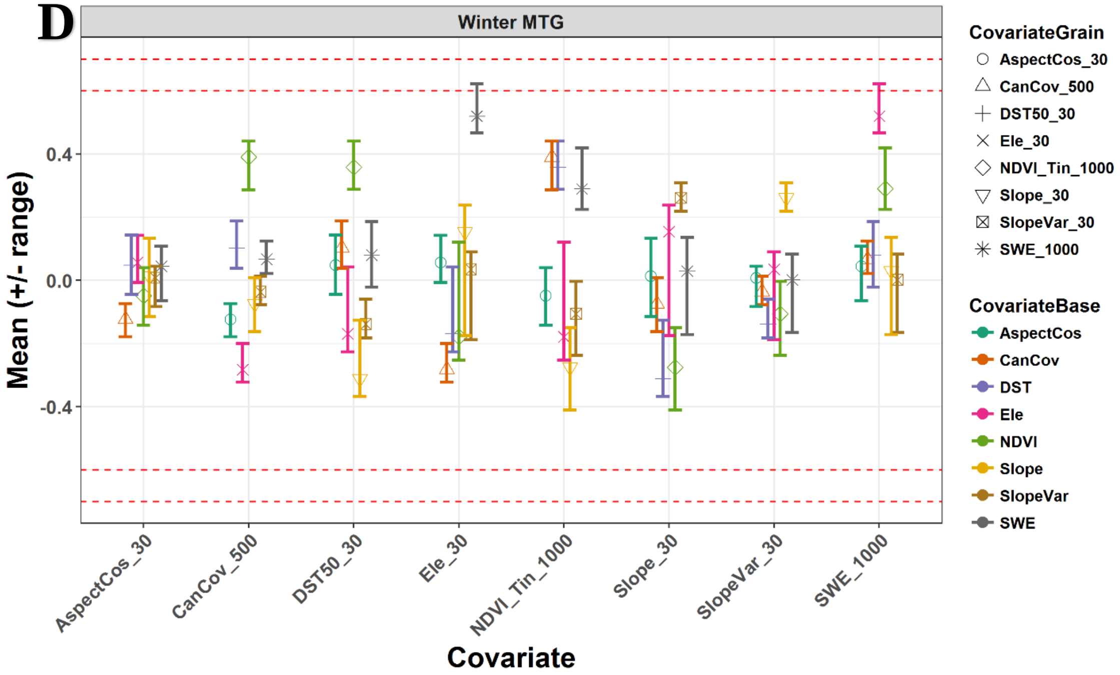




C

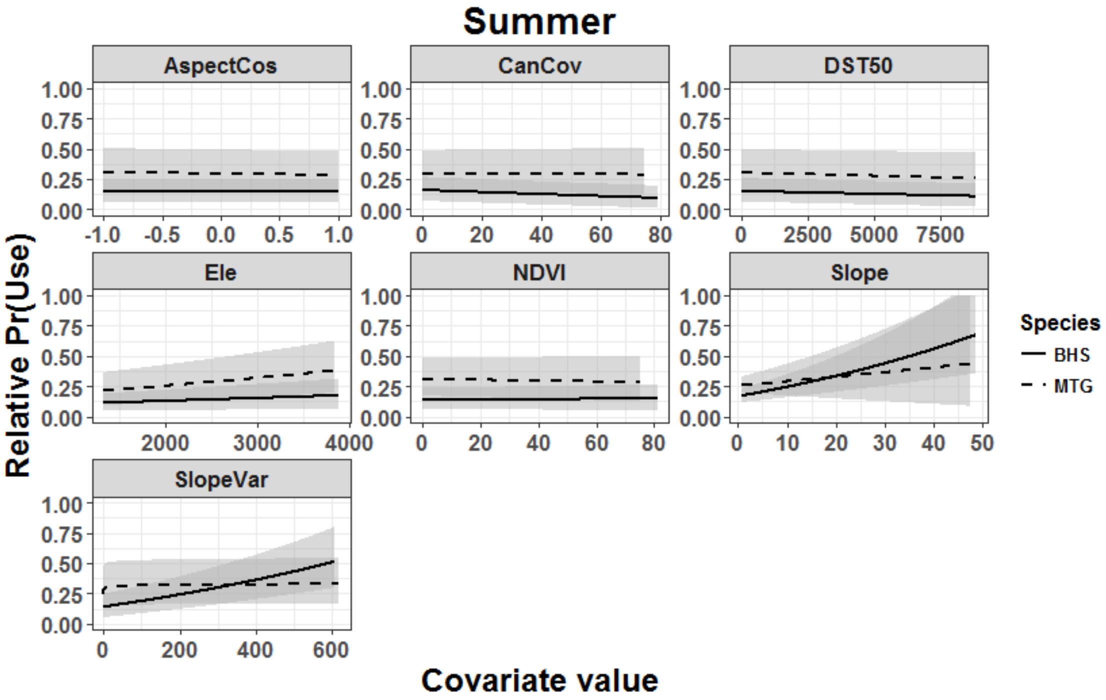

Winter BHS
Mean (+/- range)
0.4
0.0
-0.4
AspectCos_30
CanCov_30
DST50_30
Ele_30
NDVI_Tin_1000
Slope_1000
SlopeVar_30
SWE_1000
Covariate
CovariateGrain
○ AspectCos_30
△ CanCov_30
+ DST50_30
× Ele_30
◇ NDVI_Tin_1000
▽ Slope_1000
⊠ SlopeVar_30
✳ SWE_1000
CovariateBase
AspectCos
CanCov
DST
Ele
NDVI
Slope
SlopeVar
SWE

D

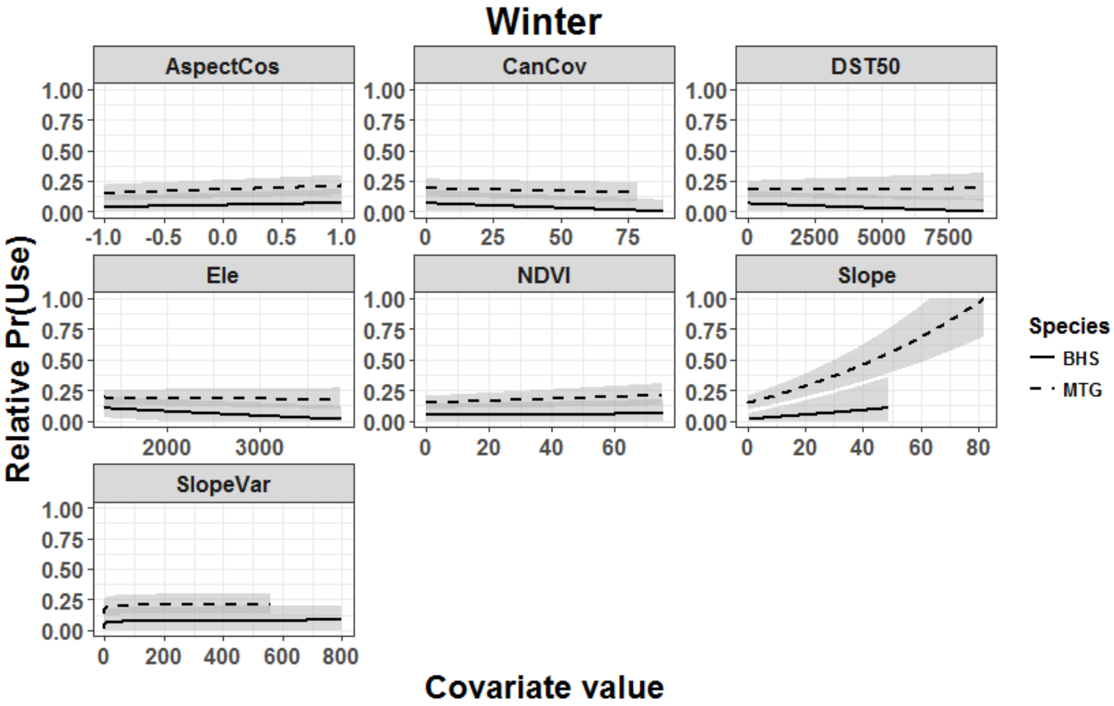

Winter MTG
Mean (+/- range)
0.4
0.0
-0.4
AspectCos_30
CanCov_500
DST50_30
Ele_30
NDVI_Tin_1000
Slope_30
SlopeVar_30
SWE_1000
Covariate
CovariateGrain
○ AspectCos_30
△ CanCov_500
+ DST50_30
× Ele_30
◇ NDVI_Tin_1000
▽ Slope_30
⊠ SlopeVar_30
✳ SWE_1000
CovariateBase
AspectCos
CanCov
DST
Ele
NDVI
Slope
SlopeVar
SWE

Appendix S3.6: Model coefficients and predictive plots

Coefficients for models fit with scaled (i.e. subtract the mean and divide by the standard deviation; Appendix S3.6: Table S3.1) and unscaled (Appendix S3.6: Table S3.2) covariate values. Seasonal predictive plots (Appendix S3.6: Figs. S3.1 and S3.2) for each species were created by predicting over the observed range of each covariate while holding the remaining covariates at their mean value.



Appendix S3.6: Fig. S3.1.



Appendix S3.6: Fig. S3.2.

Appendix S3.6: Table S3.1.

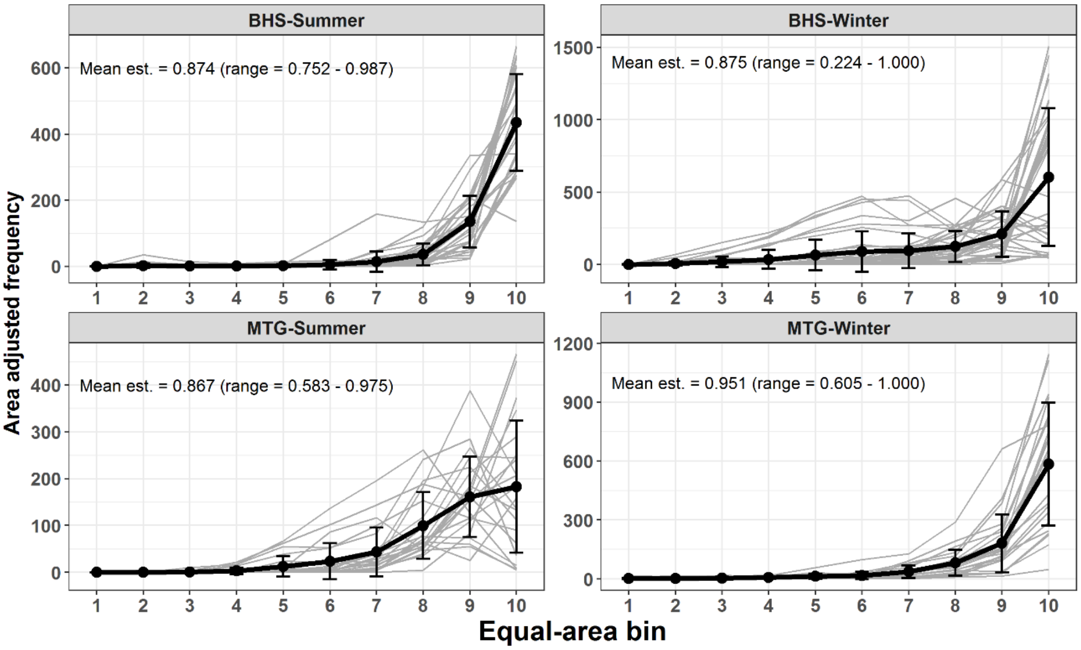
Scaled coefficient estimates						
Season	Species	CovGen	Grainsize	Form	PopBetas	PopSE
Summer	BHS	Intercept		Li	0.043	0.005
	BHS	AspectCos	30	Li	-0.001	0.002
	BHS	CanCov	500	Li	-0.027	0.002
	BHS	DST50	30	Li	-0.013	0.002
	BHS	Ele	30	Li	0.020	0.012
	BHS	NDVI	250	Li	0.004	0.006
	BHS	Slope	1000	Li	0.083	0.004
	BHS	SlopeSq	1000	Sq	0.048	0.005
	BHS	SlopeVar	30	Li	0.015	0.003
	MTG	Intercept		Li	0.079	0.007
	MTG	AspectCos	30	Li	-0.013	0.004
	MTG	CanCov	1000	Li	-0.003	0.007
	MTG	DST50	30	Li	-0.011	0.006
	MTG	Ele	30	Li	0.039	0.008
	MTG	NDVI	1000	Li	-0.005	0.010
	MTG	Slope	1000	Li	0.036	0.012
	MTG	SlopeSq	1000	Sq	0.006	0.008
	MTG	SlopeVar	30	Ps	0.016	0.003
Winter	BHS	Intercept		Li	0.092	0.005
	BHS	AspectCos	30	Li	0.028	0.005
	BHS	CanCov	30	Li	-0.036	0.002
	BHS	DST50	30	Li	-0.026	0.007
	BHS	Ele	30	Li	-0.031	0.012
	BHS	NDVI	1000	Li	0.005	0.010
	BHS	Slope	1000	Li	0.034	0.009
	BHS	SlopeSq	1000	Sq	-0.002	0.005
	BHS	SlopeVar	30	Ps	0.020	0.004
	MTG	Intercept		Li	0.062	0.003
	MTG	AspectCos	30	Li	0.038	0.005
	MTG	CanCov	500	Li	-0.015	0.005
	MTG	DST50	30	Li	0.002	0.013
	MTG	Ele	30	Li	-0.003	0.008
	MTG	NDVI	1000	Li	0.020	0.009
	MTG	Slope	30	Li	0.075	0.004
	MTG	SlopeSq	30	Sq	0.028	0.002
	MTG	SlopeVar	30	Ps	0.018	0.003

Appendix S3.6: Table S3.2.

Unscaled coefficient estimates						
Season	Species	Covariate	Grain size	Form	Estimate	SE
Summer	BHS	Intercept	-	Li	0.071022	0.097301
	BHS	AspectCos	30	Li	-0.001930	0.003421
	BHS	CanCov	500	Li	-0.001673	0.000141
	BHS	DST50	30	Li	-0.000010	0.000001
	BHS	Ele	30	Li	0.000047	0.000030
	BHS	Slope	1000	Li	-0.020747	0.002399
	BHS	Slope	1000	Sq	0.000701	0.000061
	BHS	NDVI	250	Li	0.000194	0.000391
	BHS	SlopeVar	30	Li	0.000908	0.000152
	MTG	Intercept	-	Li	-0.202454	0.080746
	MTG	AspectCos	30	Li	-0.018554	0.005423
	MTG	CanCov	1000	Li	-0.000204	0.000506
	MTG	DST50	30	Li	-0.000008	0.000004
	MTG	Ele	30	Li	0.000100	0.000021
	MTG	Slope	1000	Li	-0.000374	0.004178
	MTG	Slope	1000	Sq	0.000120	0.000120
	MTG	NDVI	1000	Li	-0.000485	0.000747
	MTG	SlopeVar	30	Ps	0.008293	0.001454
Winter	BHS	Intercept	-	Li	0.254141	0.106614
	BHS	AspectCos	30	Li	0.040785	0.007397
	BHS	CanCov	30	Li	-0.001875	0.000123
	BHS	DST50	30	Li	-0.000019	0.000005
	BHS	Ele	30	Li	-0.000086	0.000029
	BHS	Slope	1000	Li	0.004949	0.002619
	BHS	Slope	1000	Sq	-0.000010	0.000077
	BHS	NDVI	1000	Li	0.000240	0.000759
	BHS	SlopeVar	30	Ps	0.010400	0.002211
	MTG	Intercept	-	Li	-0.006261	0.082797
	MTG	AspectCos	30	Li	0.054286	0.007812
	MTG	CanCov	500	Li	-0.000903	0.000302
	MTG	DST50	30	Li	0.000002	0.000009
	MTG	Ele	30	Li	-0.000011	0.000021
	MTG	Slope	30	Li	-0.001987	0.000736
	MTG	Slope	30	Sq	0.000171	0.000013
	MTG	NDVI	1000	Li	0.001492	0.000738
	MTG	SlopeVar	30	Ps	0.009550	0.001608

Appendix S3.7. Detailed methods and validation of geographic niche interpolations within the northeast Greater Yellowstone Area

We sampled the available distribution of the stretched RSF values using 500,000 random locations and generated equal-area bins for each species-season grouping. We then extracted predicted values to the used locations and assigned each point to the respective equal-area bin. For each individual, we then summed the number of locations in each bin and calculated the Spearman rank correlation coefficient (r_S; Appendix S3.7: Fig. S3.1; Boyce et al. 2002).



Appendix S3.7: Fig. S3.1. Seasonal model validation results for sympatric bighorn sheep (BHS) and mountain goats (MTG), northeast, GYA. The mean population estimates (± 95% CIs) are shown with thick black lines and individuals are shown in light grey. The mean (± range) correlation coefficient among individuals is also reported for each species-season grouping.

CHAPTER FOUR

CONTRASTING SEASONAL MOVEMENTS IN NATIVE AND RESTORED POPULATIONS: A CASE FOR CONSERVING MIGRATORY PORTFOLIOS

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

Author: Blake Lowrey

Contributions: Conceived the study, coordinated execution of the field studies, performed the analyses, interpreted results, and wrote the manuscript.

Co-Author: Kelly M. Proffitt

Contributions: Coordinated execution of the field studies, provided comments on the manuscript and provided data.

Co-Author: Douglas E. McWhirter

Contributions: Coordinated execution of the field studies, provided comments on the manuscript and provided data.

Co-Author: P. J. White

Contributions: Provided comments on the manuscript and provided data.

Co-Author: Alyson B. Courtemanch

Contributions: Provided comments on the manuscript and provided data.

Co-Author: Sarah R. Dewey

Contributions: Provided comments on the manuscript and provided data.

Co-Author: Hollie M. Miyasaki

Contributions: Provided comments on the manuscript and provided data.

Co-Author: Kevin L. Monteith

Contributions: Provided comments on the manuscript and provided data.

Co-Author: Julie S. Mao

Contributions: Provided comments on the manuscript and provided data.

Co-Author: Jamin L. Grigg

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Abstract

1. Migration evolved as a behavioral strategy to enhance fitness through exploiting spatially and temporally variable resources and avoiding predation or other threats. Globally, landscape alterations have resulted in declines to migratory populations across taxa. Given the long time periods over which migrations evolved in native systems, it is unlikely restored populations embody the same migratory complexity that existed before population reductions or regional extirpation.
2. We characterized seasonal movement strategies between core seasonal ranges using GPS data collected from 209 female bighorn sheep (*Ovis canadensis*) across 18 restored, augmented, and native herds within contiguous mountain landscapes.
3. Restored and augmented herds were predominantly characterized by elevational migrations over relatively short geographic distances (e.g., 10 km). Native herds had similar elevational movements, but over longer geographic distances, upwards of 25 km in some herds. Resident individuals were observed in all three herd types. Individual variation is seasonal movement strategies was relatively limited in restored and augmented herds but more prevalent in native herds, which maintained a portfolio of seasonal movement strategies with respect to both elevation and geographic distances.
4. *Synthesis and applications.* Migrations within native herds are the culmination of a complex evolutionary history, and maintain a portfolio of seasonal movements that translocation efforts have not been able to recreate within restored and augmented herds. The complementary dynamics among individual movement strategies can

promote resilience, stability, and productivity. The loss of migratory portfolios may serve as an additional factor limiting demographic performance in restored and augmented herds or in native herds where disturbance has disproportionally impacted a single strategy. Our work highlights the difficulty in restoring historic seasonal movement patterns and the importance of preserving native systems with intact migratory portfolios. We encourage management experiments that attempt to increase individual heterogeneity and mirror the movement portfolios of native herds.

Key words

Bighorn sheep, individual heterogeneity, migration, *Ovis canadensis*, portfolio effects, restoration, translocation

Introduction

Seasonal migration has evolved as a complex behavioral strategy to enhance fitness and results from the interaction between individuals (e.g., learned behavior), their genes, and the environment, notably spatiotemporal variation in resources and interspecific threats (e.g., predation; Fryxell & Sinclair 1988; Dingle & Drake 2007; Hebblewhite & Merrill 2009). Migration is widespread across taxonomic groups and increasingly recognized as fundamental to maintaining populations and communities through effects on population productivity and the lateral transport of nutrients within and across ecosystems (Helfield & Naiman 2001; Bolger *et al.* 2008; Holdo *et al.* 2011; Milner-Gulland, Fryxell & Sinclair 2011). Moreover, identifying and maintaining migration corridors is an urgent management priority for state (WYGF 2016) and federal

(USDOI 2018) agencies, and has been noted as one of the most difficult conservation challenges of the 21st century (Berger 2004).

Globally, habitat loss, barriers along migratory routes, overexploitation, and climate change have resulted in steep declines of migratory behavior, and for many species, subsequent population declines (Bolger *et al.* 2008; Wilcove & Wikelski 2008; Milner-Gulland, Fryxell & Sinclair 2011). The loss of migration spans nearly all taxonomic groups and has important implications across multiple biological levels of organization as well as direct relevance to economic and social concerns (Harris *et al.* 2009; Wilcove 2010). Once lost, restoring migrations has been met with limited success, as the source of the initial extirpation (e.g., habitat loss or fragmentation) persists on the landscape (Wilcove 2010). Although a few hopeful examples have shown some capacity to restore migrations after mitigating impediments to animal movement, the gains generally come at high economic costs and represent a diminished resemblance of historic migratory patterns (Ellis *et al.* 2003; Bartlam-Brooks, Bonyongo & Harris 2011). Given the evolutionary period over which migrations have developed, it is unlikely that restored populations express the same migratory complexity that existed before population reductions or regional extirpation, although there are few empirical evaluations.

Bighorn sheep (*Ovis canadensis*) are an iconic mountain ungulate that occur throughout western North America but have struggled to rebound to historic numbers and distributions after over-harvest and the introduction of non-native respiratory pathogens from domestic livestock (Buechner 1960; Cassirer *et al.* 2017). Throughout their range, previous studies have documented varied seasonal movements from resident to long-distant migrants involving all or a subset of individuals within a herd (i.e., partial migration; Woolf, O'Shea & Gilbert 1970; Martin 1985; DeCesare & Pletscher 2006; Sawyer *et al.* 2016; Courtemanch *et al.* 2017). Migratory movements clearly influence other large ungulates (e.g., White *et al.* 2007; Bolger *et al.* 2008; Sawyer *et al.* 2009; Tucker *et al.* 2018), yet our current understanding of bighorn sheep migration stems from management surveys or limited tracking of animals instrumented with VHF collars sampled from single populations. Moreover, bighorn sheep are particularly interesting for studies of migration because of the widespread use of translocations as a management strategy to expanded distributions into historic ranges and augment existing herds (Singer, Papouchis & Symonds 2000; Wild Sheep Working Group 2015). For example, as of 2015, nearly 1,500 restoration efforts resulted in the translocation of more than 21,500 bighorn sheep in North America (Brewer *et al.* 2014).

While restoration efforts have resulted in modest increases in distribution and abundance, bighorn sheep still occupy only a small fraction of their former range and occur predominantly in restored herds that number fewer than 100 individuals (Buechner 1960; Singer, Papouchis & Symonds 2000). Although factors related to disease, competition, and habitat quality routinely inform translocation efforts, seasonal migration strategies have received less attention, despite evidence that the tendency to migrate has been associated positively with bighorn sheep translocation success (Singer, Papouchis & Symonds 2000; Singer, Zeigenfuss & Spicer 2001). To better understand the influence of translocation history on bighorn sheep migratory movements, a broad-scale characterization of migratory patterns across herds representing varied management histories (e.g., native, augmented, and restored) would allow us to evaluate our ability to maintain and restore migratory behaviors that existed prior to local reductions or extirpation. Such knowledge could help inform ungulate conservation and management, particularly translocation and augmentation programs.

Migration is thought to be maintained though the enhanced demographic performance associated with the benefits of a migratory strategy (e.g., prolonged access to high-quality forage and/or reduced predation risk; Fryxell & Sinclair 1988; Dingle & Drake 2007). Over evolutionary time, one could expect selection for a single strategy that best maximizes individual fitness. In juxtaposition, partial migration has been well documented across migratory taxa (Chapman *et al.* 2011), suggesting that fitness trade-offs between strategies can result in demographic balancing and the coevolution of multiple strategies rather than a single, most fit migratory strategy (Hebblewhite & Merrill 2011). To explore the dichotomy of the natural maintenance of a single verses multiple migratory strategies, we used GPS location data to evaluate the presence and diversity of migratory movements along elevational and geographic gradients among native, augmented, and restored bighorn sheep herds. We viewed migratory patterns along a continuum of seasonal movement strategies, including resident and migrant individuals (e.g. Cagnacci *et al.* 2011). We hypothesized that migrations in native herds would span relatively large elevational and geographic distances, and possess a greater degree of variation in seasonal movement strategies among individuals within a herd. In contrast, we hypothesized migrations within augmented and restored herds would be limited with respect to elevation and geographic distance and exhibit less individual variation in seasonal movements. Our hypotheses build from the increasingly well documented presence of multiple strategies within a herd (i.e., partial migration; Chapman *et al.* 2011) and suggest that the long and continuous evolutional history of native herds would provide relatively more time to discover and exploit new areas as well as develop divergent individual strategies. Restored and augmented herds, in contrast, have had less time to develop significant migrations or individual variation in seasonal movements. Our approach represents a broad empirical assessment of seasonal movements in bighorn sheep and provides an evaluation of translocation efforts in restoring seasonal movements in areas where bighorn sheep were locally extirpated or greatly reduced.

Materials and methods

Study areas

Our study herds were broadly distributed across Montana, Wyoming, Idaho, and Colorado in the western USA (Fig 4.1). Within each state, we used capture locations to group individuals into herd units, which generally adhered to regional management units (i.e., state hunting districts or national park boundaries; Appendix S4.1). We used herd histories to classify study herds as native, augmented, or restored (Table 4.1). Native herds were never extirpated or augmented and maintained a constant evolutionary history on the landscape. Augmented herds retained a native component that was bolstered through translocations because of concerns over long-term persistence and low abundance. Restored herds were within historic bighorn sheep range, but created through translocations after extirpation of the native component. The average numbers of years since the first translocation in restored and augmented herds was 34 (SD = 12.7) and 46 (SD = 12.3) years, respectively.

The heterogeneity and phenological patterns of the landscapes occupied by each study herd were consistent with systems where migratory behavior was expected. All herds were located in contiguous mountainous landscapes within temperate latitudes and experienced strong seasonal variation in annual climate and spatiotemporal variation in resource availability and quality. Winter months were characterized by cold temperatures with moisture predominantly occurring as snow, whereas summer was characterized by relatively warm temperatures with plant phenology advancing from low to high elevations. All herds had similar heterogeneity in landscape topography and a minimum elevational gradient of 1,120 meters (mean = 1,852, SD = 421). High elevations contained alpine and sub-alpine flora, mid-elevations were predominantly characterized by mixed coniferous forests, and low elevations consisted of a mosaic of shrub communities and agriculture production.

All herds contained a suite of native carnivore species, including black bears *(Ursus americanus*), coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and golden eagles (*Aquila chrysaetos*). With the exception of herds studied in Colorado and Idaho, grizzly bears (*Ursus arctos horribilis*) were also present. Wolves (*Canis lupus*) were present in all study areas outside of Colorado. Most bighorn sheep herds were sympatric with one or more additional ungulates, including mule deer

(*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), and mountain goats (*Oreamnos americanus*).

Data collection and seasonal movement characterizations

Animal capture occurred between 2008 and 2017. We used ground darting, drop nets, and helicopter net-gunning to capture adult (>1 yr old) female bighorn sheep, primarily during winter months. Animals were instrumented with store-on-board or remote download GPS collars programmed to record locations at varied intervals ranging from 1 to 13 hours. Where metrics were provided by the GPS collar manufacturer, we censored GPS locations with an HDOP > 10 (D'eon & Delparte 2005) and a horizontal error > 100 m. We then randomly selected a single location per animal for each day to ensure an equal fix rate across individuals and herds.

We characterized seasonal movements between summer and winter core ranges. We defined core ranges using the location data collected from 15-Jan to 28-Feb and 15-Jul to 15-Aug for winter and summer, respectively. The core periods were defined to ensure that individuals would be within the respective seasonal range and also accommodate the varied capture schedule across herds. We censored individuals with fewer than 10 days of GPS locations within either core seasonal period. In the few instances where we had multiple years of data for an individual, we selected core seasonal ranges from the first year's data that included both the winter and summer periods and excluded data from subsequent years. We characterized geographic distance by measuring the Euclidian distance between centroids (mean coordinates) of the two core seasonal ranges. We characterized elevational distance as the seasonal difference between the mean elevation of GPS locations within the respective seasonal periods. Lastly, we described herd-level movements using the median elevation and geographic distance and individual variation within a herd according to the 10th and 90th percent distribution quantiles across individuals.

Results

We characterized seasonal movements for 209 female bighorn sheep across 18 herds in four states (Table 4.1). We obtained data for an average of 12 (range: 6–19) individuals per herd with native, augmented and restored herds well distributed across the range of sample sizes (Table 4.1). Resident individuals, with little to no elevational and geographic distance between core seasonal ranges, occurred in all three herd types. Seasonal movements that largely spanned elevational gradients (i.e., elevational migrations) were the most common migratory strategy. Herd-level (i.e., median points) migrations in restored and augmented herds were characterized by movements that spanned roughly 1,000 m in elevation across geographic distances of 10 km. Native herds had a greater range of herd-level elevational movements, which occurred over longer geographic distances in many herds (Fig 4.2). While 15 and 11 km marked the near maximum geographic distance for restored and augmented herds, respectively, native herds tended to move over longer geographic distances, including a maximum median distance of 27 km (Fig 4.2).

There were notable differences in individual variation within a herd across the three herd types. As predicted, relative to native herds, restored and augmented herds had less variation among individuals with respect to elevational and geographic distance (Figs 4.2 and 4.3). The differences were most pronounced for geographic distances, where the majority of native herds had a range of variation between the 90th and 10th percent distribution quantiles that was 2 to 4 times greater than in restored or augmented herds (Fig 4.3). Moreover, individual movements in native herds spanned a continuum of elevation and geographic distances, while the limited variation in restored and augmented herds was largely driven by the resident and migrant behaviors characteristic of partially migratory herds (Appendix S4.2).

Discussion

This study presents a broad-scale characterization of seasonal movement strategies for bighorn sheep from restored, augmented, and native herds using metrics of elevation and geographic distance between core seasonal ranges, and is a novel attempt to generalize migration patterns across multiple herds with different management histories. While elevational migrations were common among all herd types, there was variation in the distances over which elevational migrations occurred. In addition to migrating longer geographic distances, seasonal movements in native herds possessed individual heterogeneity that was up to four times greater than restored or augmented herds, representing a portfolio of seasonal movements (sensu Schindler *et al.* 2010) along elevation and geographic continuums and the maintenance of multiple rather than a single migratory strategy. While restoration efforts, largely through translocations, have restored elevational migrations in some areas, our results indicate restoration efforts have not successfully restored long-distance migrations or the more diverse portfolio of individual strategies observed in native herds.

Seasonal movements within unaltered systems are the culmination of a long evolutionary history resulting in genetic, physiological, behavioral, and life-history traits that facilitate the successful interaction between individuals and the biotic and abiotic factors in their environment (Alerstam *et al.* 2003; Bowlin *et al.* 2010; Chapman *et al.* 2011). Elevational migrations that track regional phenological patterns and prolong access to intermediate vegetation growth stages are well documented in large herbivores (Merkle *et al.* 2016). Compared to long-distance migrations, elevational movements, which can occur over relatively short distances (e.g., 10 km), appear to be more easily restored in bighorn sheep as the ‘green wave’ of newly emergent vegetation may provide an enticing guide from low elevation winter ranges to high elevation summer ranges (Aikens *et al.* 2017). In contrast, our results suggest that long-distance migrations that span broad areas and traverse complex landscapes may be more difficult to restore. Recent work with bighorn sheep and moose (*Alces alces*) suggests that migratory behavior likely is socially learned and culturally transmitted (Jesmer *et al.* 2018). The herd memory influencing migration patterns in native herds represents a complex set of interactions that are responsible for developing and maintaining long-distance migrations (Alerstam *et al.* 2003; Chapman *et al.* 2011). Within restored and augmented herds, the herd memory required for long-distance migrations does not appear to have been recreated through translocation efforts.

Where known, seasonal movements of source herds used for translocations provide additional insights when interpreting our results. For example, the two restored herds with resident movements patterns (e.g., Paradise and Petty Creek; Fig 4.1; Appendix S4.2) were sourced from landscapes where seasonal migrations were inhibited by barriers to animal movement and a lack of topographic relief (Table 4.1). When sourced from non-migratory herds, translocated animals placed in novel mountain environments without a remnant native component appear to retain their resident strategy rather than develop seasonal migrations (Leech *et al.* 1996; Warren *et al.* 1996), which may lead to reduced demographic performance (Wiedmann & Sargeant 2014). Resident strategies can be an important component of partially migratory herds, but herds with a single resident strategy may persist with poor demographic performance within mountain environments where the demographic benefits of migratory movements (i.e., Hebblewhite & Merrill 2009; Merkle *et al.* 2016) are not realized. In addition to missing possible energetic benefits, resident herds are more likely to experience detrimental epizootics resulting from higher pathogen transmission rates on a single year-round range (Singer, Zeigenfuss & Spicer 2001). While non-migratory source herds can help in restoring resident herds and increase local abundance, they may be ill suited in restoring seasonal migrations in mountain landscapes.

The three herd types also had striking differences in individual variation in seasonal movements, with a range of variation in native herds that was greater than that observed in restored or augmented herds. Within the context of socially learned and culturally transmitted migratory behavior, individuals in native herds have learned and maintained a portfolio of seasonal movement strategies that have likely been lost in many restored and augmented herds (Jesmer *et al.* 2018), and not fully recreated through translocation efforts. Given that seasonal movements can functionally expand range capacity through behavior (Sawyer *et al.* 2016), the loss of movement portfolios likely has demographic consequences with implications for management and restoration. Originally formalized in fisheries research, the 'portfolio' concept recognizes the value of individual heterogeneity in reducing risk in a variable environment through the complementary dynamics of asynchronous vital rates (Markowitz 1952; Schindler *et al.* 2010). Akin to species richness in community ecology (Tilman, Reich & Knops 2006), a portfolio of individual movements can promote increased resilience, stability, and productivity resulting from the asynchronous dynamics among a myriad of strategies or life-history traits (Schindler *et al.* 2010; Griffiths *et al.* 2014). While restored and augmented herds were able to develop elevational migrations and have some tendency to maintain a partial migration, the lack of a portfolio of seasonal movements may be an additional factor limiting demographic performance in restored populations.

Within native herds, the portfolio of seasonal movements is often associated with a more diffuse distribution of individuals across the landscape, potentially minimizing the effects of disease through reducing transmission rates (Singer, Zeigenfuss & Spicer 2001). A diffuse distribution can also buffer individuals from other density mediated limits to growth such as interspecific competition and predation (Singer, Papouchis & Symonds 2000; Sawyer *et al.* 2016) as well as stochastic threats such as avalanches (Courtemanch *et al.* 2017). In addition, spatial and temporal variation in weather severity may differentially impact any one strategy, resulting in strategy-specific vital rates that are inherently volatile (Kaitala, Kaitala & Lundberg 1993). Yet, when viewed as an aggregate portfolio of seasonal movements, volatility in herd-level demographic processes may be greatly reduced (Schindler *et al.* 2015). At present, the portfolio concept has largely been applied to the varied life-history traits of anadromous fishes, yet provides an intuitive lens with which to view the benefits of maintaining and promoting migratory portfolios across taxa, including terrestrial ungulates.

In addition to observing a reduced migratory portfolio in restored and augmented herds, the loss of migratory portfolios may also occur through anthropogenic disturbance in native herds. For example, bighorn sheep in Grand Teton National Park (GTNP) are a native herd with a limited migratory portfolio containing resident individuals (Fig 4.2; Appendix S4.1). Bighorn sheep in GTNP remain on high-elevation, windswept ridgelines for most of the year, but descend 500 m in spring to gain access to newly emergent forage approximately 30 days prior to spring green up on the high-elevation winter and summer ranges (Courtemanch *et al*. 2017). Although only a single strategy persists today, historic migration patterns also involved elevational movements between the current year-round ranges and low elevation winter ranges in the surrounding valleys (Whitfield 1983). While Courtemanch *et al*. (2017) suggested that the remnant bighorn sheep persist through adopting an alternative high elevation resident strategy, within the context of the portfolio concept and our observations of other native herds within the Greater Yellowstone Area, an alternative explanation is that both strategies existed historically, and that the elevational component was unable to persist with the continued loss of low elevation winter ranges do to anthropogenic development. While likely reduced from historic abundances prior to the loss of elevational migrations, the portfolio of seasonal movement strategies has allowed the herd to persist, although within a reduced range. As components of native migratory portfolios are lost through anthropogenic activities (i.e., development, harvest, etc.) that disproportionally effect a single strategy, native herds may become more susceptible to other threats.

Within migratory ungulates there has been a focus on ecological (e.g., spatial, temporal, demographic) differences between resident and migratory components of partially migratory herds (i.e., Hebblewhite & Merrill 2009; Middleton *et al.* 2013; Rolandsen *et al.* 2016). Nonetheless, a growing body of literature is beginning to describe differences within the migratory component with relevance to conservation and management. For example, mule deer migrating from winter ranges in the Red Desert of southwest Wyoming have three distinct strategies delineated by geographic distance, each with varying trade-offs related to anthropogenic risk and intraspecific competition (Sawyer *et al.* 2016). Individual differences in migratory distance have been noted in other ungulates including elk (White *et al.* 2010; Middleton *et al.* 2013), additional populations of mule deer (Monteith *et al.* 2011), and white-tailed deer (Fieberg, Kuehn & DelGiudice 2008). As GPS technology continues to enhance our ability to track and map animal movements, there are an increasingly large number of seasonal movements that do not fit within traditional definitions of migration (Dingle & Drake 2007). Indeed, rather than adopt a dichotomous classification, seasonal movements are being increasingly interpreted along a behavioral continuum spanning resident and migrant strategies (Cagnacci *et al.* 2011; Sawyer *et al.* 2016). This is exemplified by our observations of a gradient of strategies along both elevational and geographic continuums, and provides additional insights when describing migratory metrics (e.g., timing) and differences in demographic performance among migrant individuals in a herd.

While nearly a century of bighorn sheep restoration has resulted in modest increases in distribution and abundance, seasonal movements in restored herds do not mirror the complexity observed in native herds. Complex and varied seasonal movements in bighorn sheep and other terrestrial ungulates may have demographic benefits through realized portfolio effects and we encourage further work that links demography with individual migration strategies and with population-level variation of such. Our work highlights the difficulty in restoring historic seasonal movement patterns and the importance of preserving native systems with intact migratory portfolios. Nonetheless, targeted management experiments that more directly link the seasonal movement patterns in source herds with landscape heterogeneity in restored landscapes may be an additional tool to build heterogeneity into restored or augmented herds. In addition to increasing the abundance and distribution of bighorn sheep on the landscape, we suggest there may be value in simultaneously increasing the diversity of seasonal movement strategies, and in so doing, building resilience to future perturbations and mirroring the movement portfolios observed in native herds.

Authors' contributions

B.L. and R.A.G. conceived the idea and methodological approach; B.L. performed the analysis; All authors were involved in field efforts to collect and provide data, contributed critically to the draft manuscripts, and gave final approval for publication.

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Figures and Tables

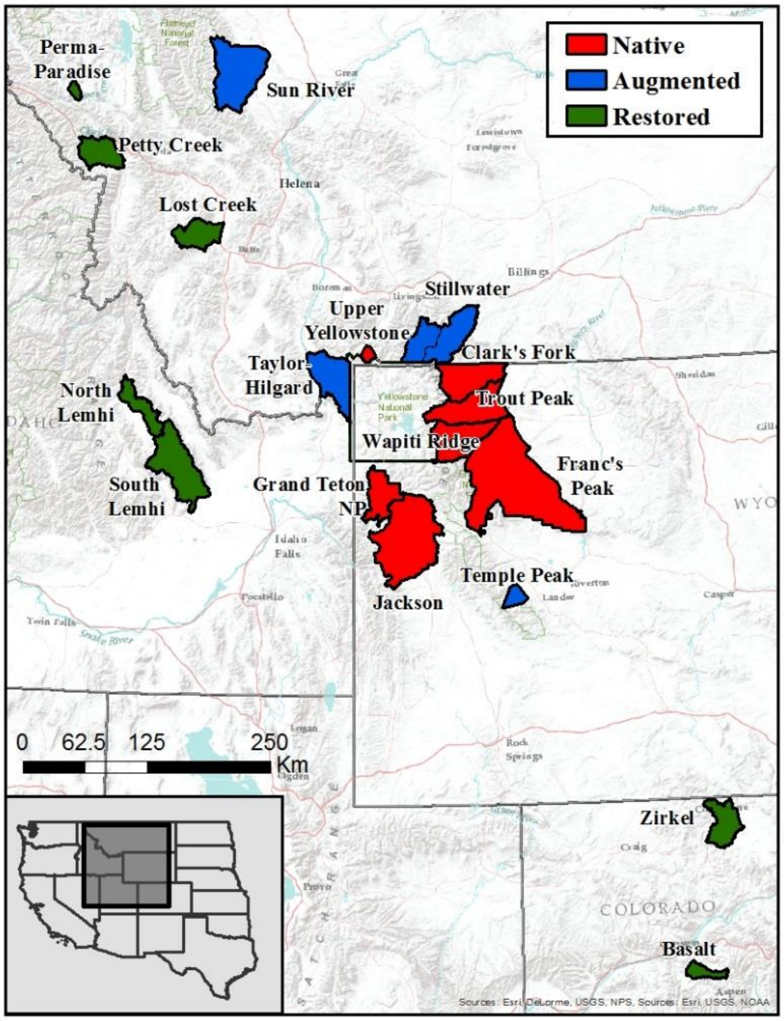

Fig 4.1. Native (red; N = 7), augmented (blue; N = 4), and restored (green; N = 7) herd units used to characterize female bighorn sheep migration patterns, Montana, Wyoming, Idaho, and Colorado, USA, 2008−2017.

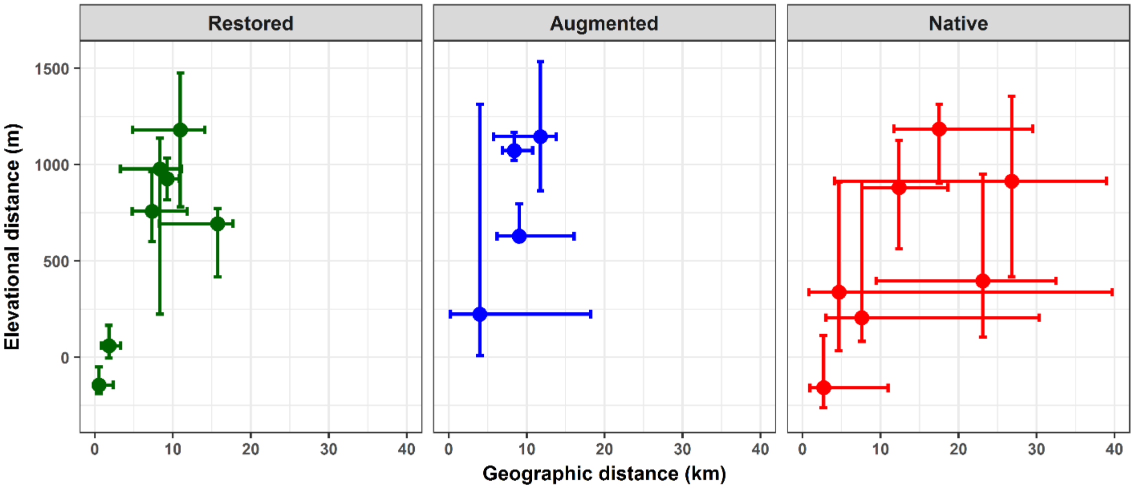

Fig 4.2. Migration characterizations with respect to elevational and geographic distance between core seasonal ranges for restored (green), augmented (blue), and native (red) herds of female bighorn sheep, in Wyoming, Montana, Idaho, and Colorado, 2008−2017. Closed circles represent herd-level median values. Individual variability is described with the 10th and 90th percent distribution quantiles. Herds with elevational distance below zero had a winter range that was higher than the summer range. Paradise and Petty Creek are the lower left restored herds, while Grand Teton National Park is the lower left native herd.

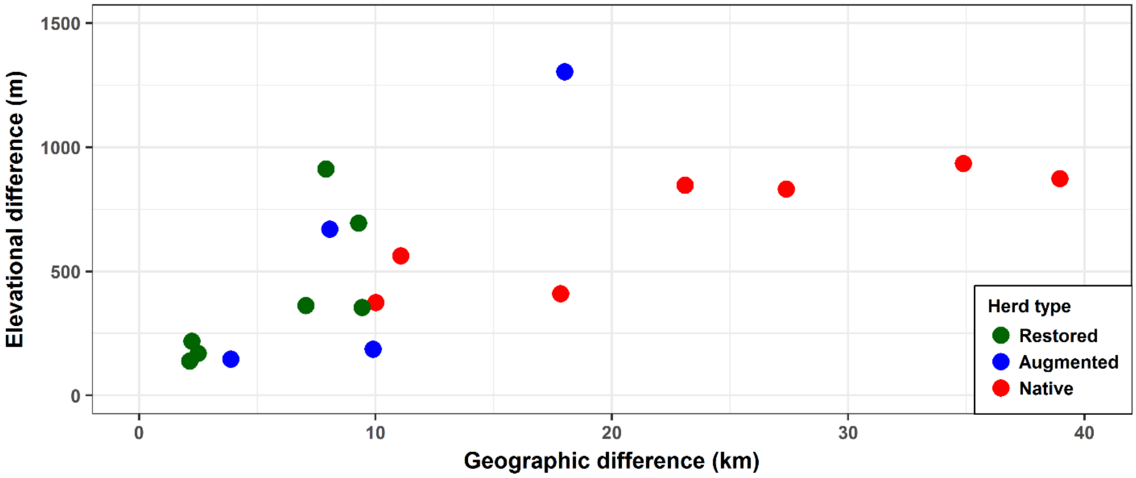

Fig 4.3. Range of variation in elevational and geographic distances among individuals within a herd, Wyoming, Montana, Idaho, and Colorado, 2008−2017. Each point represents the difference between the 90th and 10th percent quantile for restored (green), augmented (blue), and native (red) herds of female bighorn sheep.

Table 4.1. Summary information for the study herds, Montana, Wyoming, Idaho, and Colorado, USA, 2008−2017.

State	Herd units					Translocation history		
	Name	**N**	**Mgmt. unit[1]**	**Pop estimate[2]**	**Herd type**	**Year**	**Number**	**Source[3]**
MT	Perma-Paradise	14	HD-124	352	Restored	1979	14	WHI
						2011	22	WHI
MT	Petty Creek	14	HD-203	160	Restored	1968	16	MT-422
						1985	4	NBR
MT	Lost Creek	10	HD-213	100	Restored	1967	25	MT-422
						1985	2	MT-121
MT	Hilgard	15	HD-302	280	Augmented	1988	19	MT-121
						1989	5	MT-121
						1989	19	MT-213
						1993	26	WHI
MT	Sun River	12	HD-422, 424	150	Augmented	1960	8	MT-422
MT	Stillwater	13	HD-501, 502	75	Augmented	1968	2	MT-422
						1970	2	MT-422
						1984	3	NBR
MT	Upper Yellowstone	10	HD-305, northwest YNP	320	Native	−	−	−
WY	Clark's Fork	19	HD-1, northeast YNP	600	Native	−	−	−
WY	Trout Peak	11	HD-2	700	Native	−	−	−
WY	Wapiti Ridge	7	HD-3	850	Native	−	−	−
WY	Franc's Peak	17	HD-5, 22	840	Native	−	−	−
WY	Grand Teton NP[4]	14	GTNP	100	Native	−	−	−
WY	Jackson	16	HD-7	450	Native	−	−	−
WY	Temple Peak[4]	8	-	50-75	Augmented	1960	1	WY-Whiskey
						1964	20	WY-Whiskey
						1965	20	WY-Whiskey
						1966	18	WY-Whiskey
						1971	13	WY-Whiskey
						1972	39	WY-Whiskey

						1987	54	WY-Whiskey
ID	North Lemhi	9	37A, 29	129	Restored	1986	18	OR-Lostine
						1988	13	ID-36A
						1989	23	ID-36B
ID	South Lemhi	6	51, 58	40	Restored	1983	19	WY-Whiskey
						1984	22	WY-Whiskey
CO	Zirkel	7	S73	120-130	Restored	2004	26	CO-S65
						2005	14	CO-S65
CO	Basalt	7	S44	70	Restored	1972	18	CO-S10

[1] The aggregation of management units within each herd unit is further described in Appendix S4.1

[2] Estimates were provided by area biologists and determined from local knowledge, minimum counts, and recent trends.

[3] WHI: Wild Horse Island; NBR: National Bison Range

[4] Temple Peak is a non-hunted herd without a management unit.

CHAPTER FOUR APPENDICES

Appendix S4.1: Detailed description of the herd unit delineations

The delineation of herd units to describe seasonal migration patterns and variability is a critical step in our analysis that highlights the importance of scale in ecology (Wiens 1989). While we recognize the scale-dependence of our results (e.g. Levin 1992), we feel the herd units detailed herein are an appropriate aggregate based on a number of factors. We delineated herd units using regional management units (i.e. hunting districts or national park boundaries) which provided a similar grouping system that could be applied across the broad study region. Moreover, management units are the most relevant administrative unit for regional managers and are often used to summarize other herd attributes (i.e. vital rates, abundance, disease prevalence, etc.). By linking our work with management units, our results are directly applicable to regional management efforts and represent the same spatial scale.

We grouped individual bighorn sheep into herd units based on the capture location. In most instances the ‘herd unit’ was synonymous with local management units, although there were a few exceptions where we lumped adjacent management units and/or individuals to better reflect groupings based on the GPS locations and local geography. We recognize the subjective nature of these decisions and have provided detailed descriptions of the areas where lumping occurred. There was no lumping within the Colorado or Idaho herd units.

Montana herd units

Perma-Paradise (HD-124), Petty Creek (HD-203), Lost Creek (HD-213), and Taylor-Hillgard (HD-302) herd units were all characterized by a single management unit (Fig S4.1.1). The Sun River herd unit was an aggregate of individuals captured in HD-424 and HD-422, both of which had 6 animals. The adjacent management units (HD-421 and HD-423) were also used by instrumented bighorn sheep (Fig S4.1.1). There were four individuals captured in the northwest corner of Yellowstone National Park (YNP), roughly 9 km from the animals within the Upper Yellowstone (HD-305). We aggregated animals captured in northwest YNP with those in Upper Yellowstone (HD-305) to make a single herd unit with 10 individuals. All animals in Stillwater were captured within a single management unit (HD-502) but separated into two adjacent units (HD-501) in summer (Fig S4.1.1). These animals were considered a single herd unit with 13 individuals.

Wyoming herd units

Animals in Wyoming were broadly distributed across the Absaroka mountains with additional discontinuous herd units in the Teton, Gros Ventre, and Wind River ranges (Fig S4.1.2). The Clark's Fork herd unit contained a total of 19 collared individuals, which included two animals captured within the northeast corner of YNP and another single individual capture roughly 2 km north of the MT-WY border as this is a "shared" or trans-boundary herd. While the individual was captured in MT, we included it within Wyoming's Clark's Fork herd (Fig S4.1.2). The Trout Peak (HD-2) and Wapiti Ridge (HD-3) herd units are separated by the North Fork of the Shoshone River. These herds share some common winter ranges, and in one instance an individual captured in HD-2 was more strongly associated with HD-3 according GPS locations. Although the capture location was within HD-2, we grouped the individual with HD-3, the Wapiti Ridge herd unit (Fig S4.1.2). The Franc's Peak herd unit included 17 collared individuals, of which three were captured in HD-22, the management unit adjacent to HD-5 to the southwest. Lastly, Temple Peak is not a hunted herd and does not have a designated management unit but was aggregated as a single herd with 8 collard individuals. The remaining herd units, Jackson (HD-7) and Grand Teton NP were characterized by a single management unit.

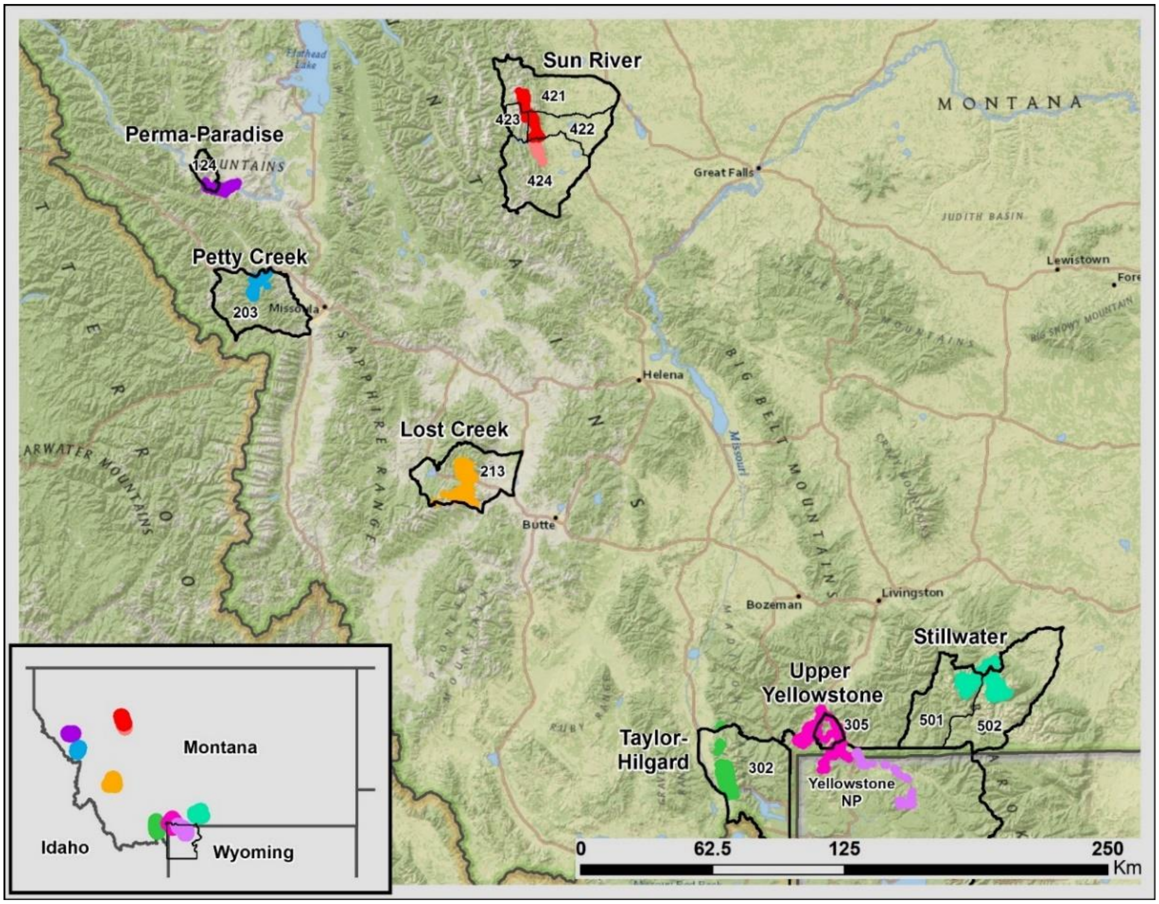

Fig S4.1.1 Montana herd units. Within the Sun River herd unit we aggregated individuals captured within HD-424 (pink) and HD-422 (red). Within the Upper Yellowstone herd unit we aggregated individuals captured in HD-305 (dark pink) and northwest YNP (light pink).

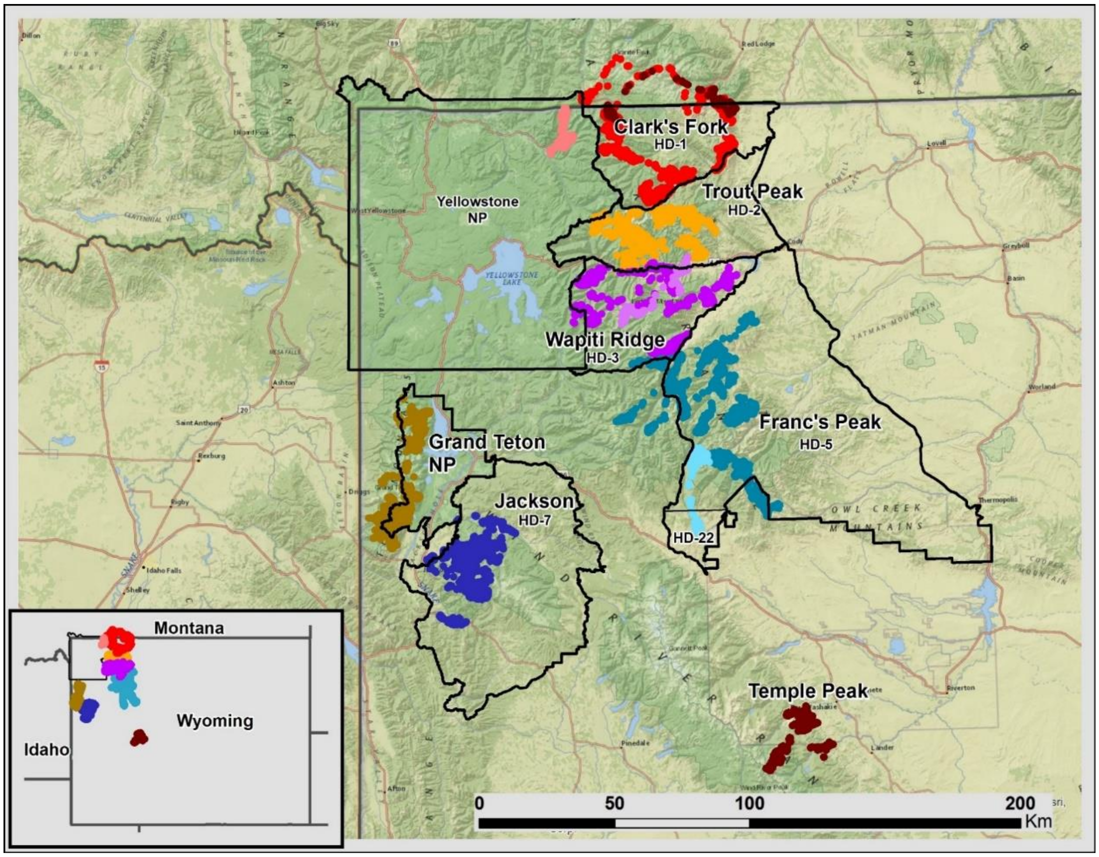

Fig S4.1.2 Wyoming herd units. The Clark's Fork herd unit contained 16 individuals in HD-1 (red), two individuals captured in northeast YNP (pink), and one individual captured just north of the MT-WY boarder (dark red). The Wapiti herd contained six individuals from HD-3 (dark pink) and one individual that was captured in HD-2, but more strongly associated with HD-3 (light pink). The Franc's Peak herd was an aggregate of HD-5 (blue) and HD-22 (light blue).

Appendix S4.2: Individual migration characterizations

The individual migration characterizations for restored (Fig S4.2.1), augmented (Fig S4.2.2), and native (Fig S4.2.3) herds help to show the patterns driving herd-level variability. Within restored and augmented herds, herd-level variability was driven by the resident and migratory behaviors of partially migratory herds as seen in Basalt (Fig S4.2.1) and Temple Peak (S4.2.2). In contrast, native herds have a continuum of individual movements with respect to elevational and geographic distances, representing a portfolio of seasonal movement strategies (Fig S4.2.3).

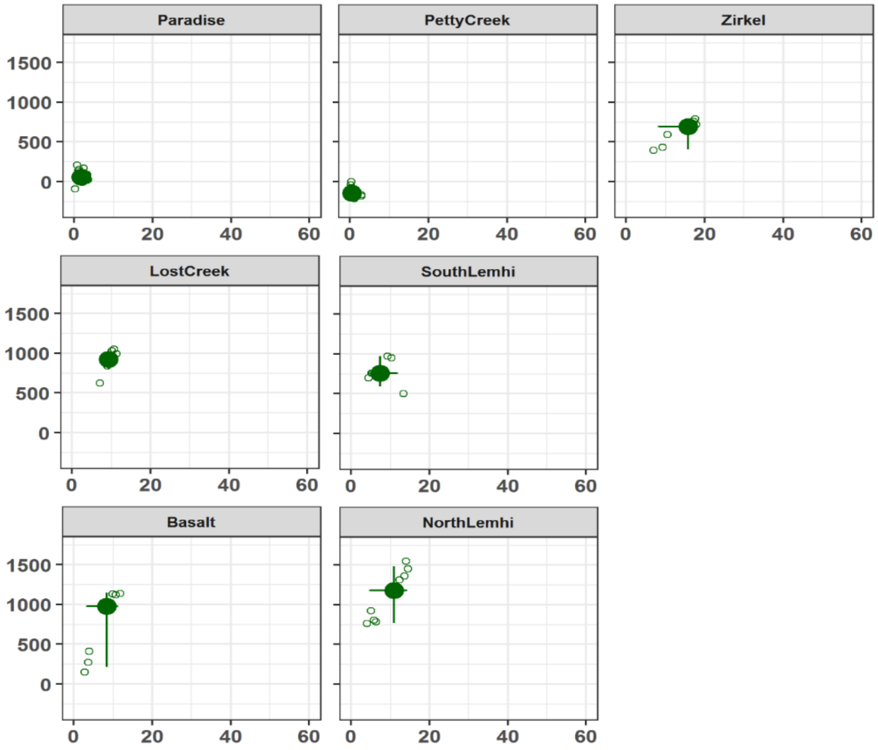

Fig S4.2.1 Restored herd-level (solid circles) and individual (open circles) migration characterizations. Lines represent the herd-level 10th and 90th percent distribution quantiles for each axis.

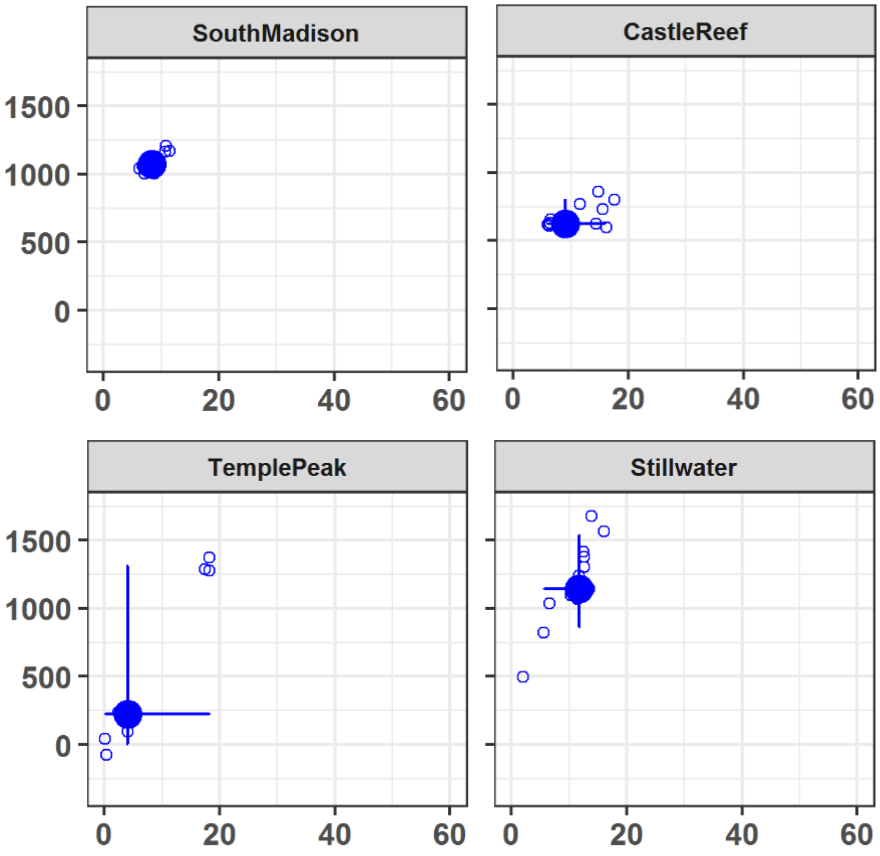

Fig S4.2.2 Augmented herd-level (solid circles) and individual (open circles) migration characterizations. Lines represent the herd-level 10th and 90th percent distribution quantiles for each axis.

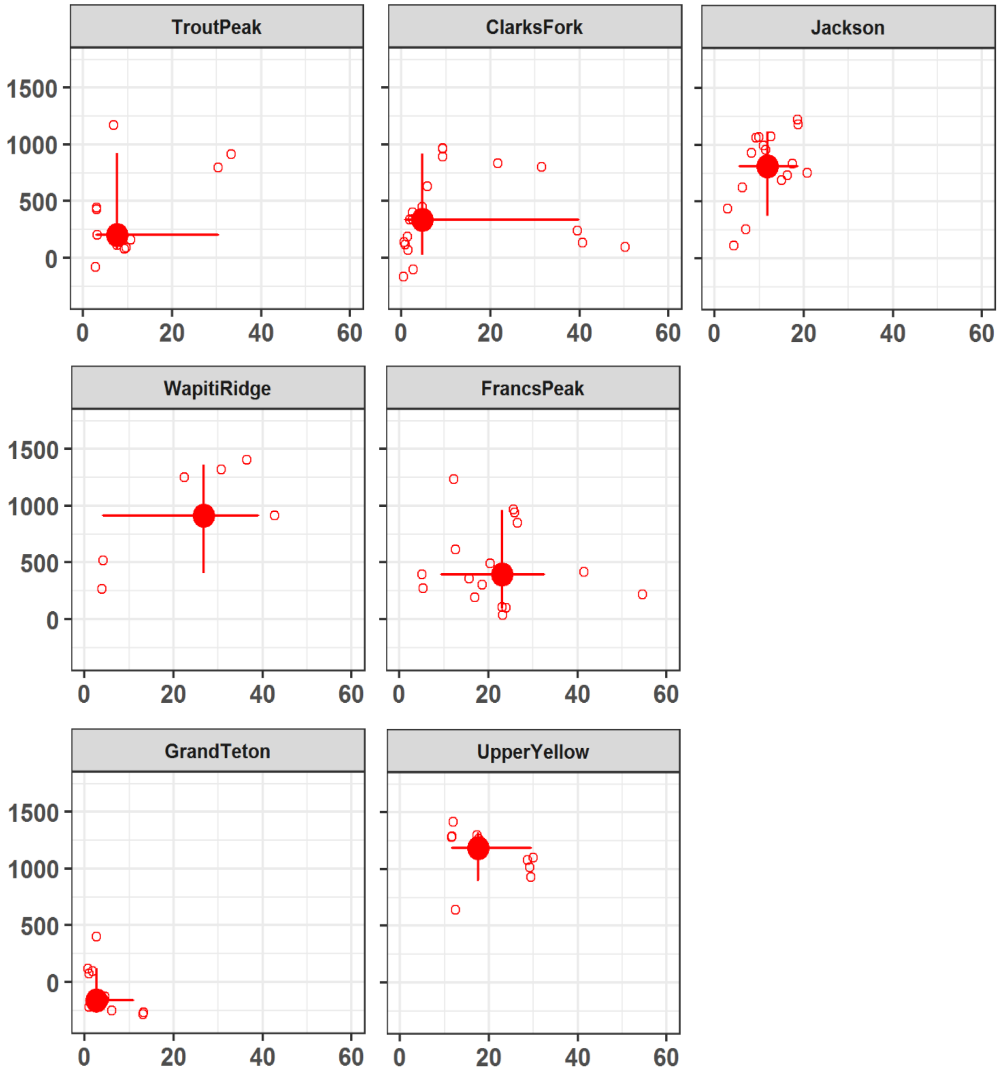

Fig S4.2.3 Native herd-level (solid circles) and individual (open circles) migration characterizations. Lines represent the herd-level 10th and 90th percent distribution quantiles for each axis.

CHAPTER FIVE

INDIVIDUAL VARIATION CREATES DIVERSE PORTFOLIOS OF SEASONAL MOVEMENT PATTERNS AND RANGES IN A MIGRATORY UNGULATE

Contribution of Authors and Co-Authors

Manuscript in Chapter 5

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Contributions: Provided analytical assistance, comments on the manuscript and provided data.

Co-Author: Sarah R. Dewey

Contributions: Provided comments on the manuscript and provided data.

Co-Author: Robert A. Garrott

Contributions: Conceived the study, coordinated execution of the field studies, interpreted results, and edited and commented on the manuscript.

Manuscript Information

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Abstract

Individual variation in migration patterns is being increasingly well documented, largely due to advances in GPS technology aiding our ability to track animals over small temporal and expansive spatial scales. Both ecological theory and empirical results across many migratory taxa have demonstrated population-level demographic benefits resulting from a diversity of individual behaviors and the congruent diversity in seasonal ranges. Nonetheless, individual variation has received relatively less attention in migratory ungulates, where research has largely focused on the dichotomous behaviors (e.g., resident and migrant) in partially migratory populations. We characterized individual variation in migratory behaviors and movements using GPS data from 362 female bighorn sheep (*Ovis canadensis*) across 17 (restored = 4, augmented = 6, native = 7) populations in Montana and Wyoming, USA. We characterized migratory portfolios according to behavior (interpreted along elevational and geographic continuums), behavioral switching rates, spatial fidelity to seasonal ranges, and population spread. Native populations, which have been extant on the landscape for many generations, had more diverse portfolios of migratory behaviors, increased behavioral switching rates, and were diffusely spread across both summer and winter ranges. In contrast, restored populations which had a limited evolutionary history on the landscape, were largely non-migratory with a narrow behavioral portfolio, less behavioral switching, and were generally concentrated in both summer and winter ranges. Our results build from recent research describing social learning and cultural transmission as the primary mechanism through which migration evolves in ungulates. In addition to increased migratory

propensity and foraging efficiency, native populations had diverse portfolios of migratory behaviors and ranges with potential synergistic benefits associated with individual heterogeneity and resulting portfolio effects. In addition to increasing the abundance and distribution of bighorn sheep on the landscape, we suggest there is value in simultaneously increasing the diversity of seasonal movement strategies and ranges, and in so doing, building resilience to future perturbations and respiratory disease die-offs, and mirroring the movement portfolios observed in native populations of bighorn sheep.

The last word of ignorance is the man who says of an animal or plant: what good is it?... If the biota, in the course of eons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering.

Aldo Leopold
A Sand County Almanac (1949)

Introduction

Animal migration is one of the most inspiring and important aspects of ecology, yet habitat destruction, barriers along migratory routes, overexploitation, and climate change have resulted in steep declines of migratory behavior across many taxonomic groups (Bolger et al. 2008, Wilcove and Wikelski 2008, Milner-Gulland et al. 2011). While migration continues to decline broadly, GPS technology has enhanced our ability to track animals over small temporal and expansive spatial scales, and in so doing, highlighted the prevalence and diversity of migratory behaviors in native systems that are less impacted by anthropogenic disturbances. Both among and within species, large aggregates of spatial data have detailed more nuanced individual migratory behaviors that are not described by the classic examples of migration (Dingle and Drake 2007, Cagnacci et al. 2011). For example, individuals can migrate over a continuum of elevational and geographic distances that vary within and among populations (Singh et al. 2012, Sawyer et al. 2016, Lowrey et al. In review). In addition, partial migration, where a subset of individuals migrate seasonally while others remain resident on shared ranges, is the most common migratory behavior (Chapman et al. 2011). Moreover, within partially migratory populations individual behavior can be conditional on both endogenous and exogenous factors, resulting in individuals switching strategies across years (Lundberg 1987, Chapman et al. 2012, Eggeman et al. 2016, Spitz et al. 2018).

The importance of individual heterogeneity is being increasingly well documented in the field of ecology (e.g., Marra et al. 1998, Bolnick et al. 2011, Dingemanse and Dochtermann 2013). Within the context of migration, understanding and describing individual heterogeneity has important implications for the ecology, conservation, and evolution of migratory organisms. Recently, the portfolio concept, as well as measures of migratory diversity, connectivity and population spread, have provided theoretical and empirical evidence of the presence and importance of individual heterogeneity in migratory patterns across aquatic and avian taxa. For example, the portfolio concept illustrates the demographic benefits of a diverse portfolio of individual life history traits of anadromous fishes. While the dynamics of a single life history trait are inherently volatile, when viewed in aggregate, asynchrony among life history traits results in more stable abundances through time and reduced risk (Schindler et al. 2010, Griffiths et al. 2014).

Similar demographic benefits have been described in birds. For example, avian species with low migratory diversity (i.e. full migrants or full residents) and restricted winter ranges, are more likely to experience population declines (Gilroy et al. 2016). In contrast, partially migratory species that occupied multiple non-breeding (i.e., winter) ranges over a large area were more resilient to anthropogenic habitat loss, likely driven by the relatively diverse migratory network and non-restricted (i.e., broad population spread) winter ranges (Gilroy et al. 2016). Avian intraspecific variation is also characterized through migratory connectivity, which describes the extent to which individuals from a common breeding range migrate to the same nonbreeding range (Webster et al. 2002, Webster and Marra 2005). In the extreme case, when all individuals from a single breeding area migrate to the same nonbreeding area, migratory connectivity is considered strong. In contrast, when all individuals migrate to different nonbreeding areas, migratory connectivity is considered weak (Webster et al. 2002). The diversity in individual ranges associated with weak migratory connectivity is thought to increase resiliency, genetic diversity, and population stability (Webster et al. 2002), and is common in long-distance avian migrants (Finch et al. 2016).

Within migratory ungulates, the study of individual heterogeneity has largely focused on the ecological (e.g., spatial, temporal, demographic) differences between resident and migratory components of partially migratory species (i.e., Hebblewhite and Merrill 2009, Middleton *et al.* 2013, Rolandsen et al. 2016), and behavioral switching rates between the two dichotomous strategies (Eggeman et al. 2016, Spitz et al. 2018). Aided by increasing aggregates of GPS data, however, recent work has begun to describe different strategies among the migrant component of partially migratory populations. For example, three distinct migratory strategies (short, moderate, and long distance routes) were delineated for mule deer (*Odocoileus hemionus*) migrating from winter ranges in the Red Desert of southwest Wyoming, each with varying trade-offs related to anthropogenic risk and intraspecific competition (Sawyer et al. 2016). In addition, Lowrey et al. (In review) described a continuum of migratory movements of female bighorn sheep (*Ovis canadensis*) over a wide range of both elevational and geographic distances between seasonal ranges. While individual variation is often noted in ungulate migrations (e.g. White et al. 2010, Monteith et al. 2011, Middleton et al. 2013), the application of metrics to describe and characterize individual heterogeneity in migration patterns and population spread lags behind other migratory taxa, yet has potentially important implications for demography, disease transmission, and inter- and intra-specific competition.

Within partially migratory populations, individual plasticity in migratory behavior (i.e., resident or migrant) can further diversify population-level migratory portfolios. Behavioral switching is common in birds and fish (Alerstam and Lindström 1990, Chapman et al. 2012), with switching rates of 45 percent noted for some passerines (Hegemann et al. 2015). Within ungulates, migratory behaviors are often assumed to be fixed, yet recent work has begun to describe the prevalence of switching in many species (Fieberg et al. 2008, Gaidet and Lecomte 2013, White et al. 2014, Eggeman et al. 2016), highlighting the conditional nature of migratory behavior in ungulates (Spitz et al. 2018; although see Sawyer et al. In review). Switching can also be expressed spatially through low fidelity to consecutive seasonal ranges (i.e., summer-summer or winter-winter).

While behavioral switching is congruent with a lack of fidelity to consecutive seasonal ranges, the use of non-overlapping ranges can also occur when individuals maintain a single migratory behavior, yet migrate to different ranges seasonally. Low fidelity to seasonal ranges between years without behavioral switching may be an additional individual characteristic that further diversifies population-level migratory portfolios.

Bighorn sheep occur throughout western North America but have struggled to rebound to historic numbers after overexploitation, competition with livestock, and the introduction of respiratory pathogens from domestic animals (Buechner 1960). While native populations have persisted on the landscape, many existing populations are the result of management translocations into formerly occupied ranges where the native component was extirpated, or augmentations into remnant populations suffering from low abundance estimates or poor demographic performance. Recently, comparisons across restored and native populations of bighorn sheep found that migration is socially learned and culturally transmitted in ungulates, and that the loss of ‘population memory’ through extirpation can result in restored populations that are largely non-migratory and have a lesser ability to track plant phenology (Jesmer et al. 2018). In addition, using similar comparisons across populations with different management histories (i.e., restored, augmented, native), Lowery et al. (In review) found that native populations had more individual variation with respect to elevational and geographic distances, but did not formally classify migratory behavior or characterize other components of migratory diversity.

Within the context of socially-learned migration in ungulates, we developed multiple predictions regarding individual heterogeneity with respect to migratory behavior, behavioral plasticity, spatial fidelity, and population spread. We predicted that, 1) native populations, because of their long and uninhibited history on the landscape would have a relatively diverse portfolio of classified migratory behaviors, including resident, and multiple migrant strategies, which evolved over many generations. In contrast, restored populations, with a constrained evolutionary history on the landscape, would be characterized by a limited migratory portfolio with only a few migratory behaviors expressed. Given the increased migratory propensity observed in native ungulates (Jesmer et al. 2018, Lowrey et al. In review), we predicted that, 2) migratory behaviors in native populations would be more plastic, resulting from the increased opportunity to switch between resident and migratory behaviors. In contrast, in restored populations we predicted there would be limited behavioral switching as the reduced migratory propensity results in less opportunity to switch behaviors within largely resident populations. With respect to spatial fidelity we predicted that, 3) the enhanced memory in native populations would result in the use of multiple seasonal ranges (i.e. low fidelity) without a behavioral switch, and that restored populations would be characterized by relatively high fidelity resulting from a limited population memory of diverse seasonal landscapes capable of meeting physiological requirements. Lastly, with regard to population spread, we predicted that, 4) individual home ranges in native populations would be diffusely distributed across seasonal ranges, resulting in broader population spread within a season. In contrast, we predicted that restored populations would be characterized by short distances between individual home ranges and minimal population spread. Recognizing the large losses of the native component that prompted the restoration of augmented populations, we predicted that metrics of individual variation in augmented populations would mirror restored populations. We evaluated these predictions using 633 seasonal migrations from 362 individuals across 17 native, augmented and restored populations in Montana and Wyoming, USA (http://www.mtbighorninitiative.com).

Methods

Study areas

Our study populations were broadly distributed across the northern Rocky Mountains in western Montana and Wyoming, USA (Figure 5.1) and represent a continuum of management histories and population characteristics (Table 5.1). We used capture locations and recovered GPS data to group female bighorn sheep into populations following regional management units (i.e., state hunting districts or national park boundaries; Appendix S5.1). We defined native populations as those that were never extirpated or augmented and thus have maintained a constant evolutionary history on the landscape. Augmented populations retained a native component that was bolstered through translocations because of concerns over long-term persistence and low abundance. Restored populations were within historic bighorn sheep range, but created through translocations after extirpation of the native component. The number of translocation events ranged from 1 to 7 per population (mean = 3.6, SD = 2.19) with a total number of translocated animals ranging from 7 to 165 (mean = 51.8, SD = 68.52;

Table 5.1; Appendix S5.2). The number of years since the initial translocation event ranged from 37 to 51 (mean = 44.25, SD = 7.27) for restored populations and from 30 to 74 (mean = 54, SD = 16) for augmented populations (Table 5.1). Disease events were documented in some of the study populations within each of the management histories with an average mortality of 53.6 percent (Table 5.1; Appendix S5.2).

The heterogeneity and phenological patterns of the landscapes occupied by each study population were consistent with systems where migratory behavior was expected. All populations were located in contiguous mountainous landscapes within temperate latitudes and experienced strong seasonal variation in annual climate and spatiotemporal variation in resource availability and quality. There were no notable differences in phenological patterns or metrics of landscape heterogeneity across the study populations (Appendix S5.3). Winter months were characterized by cold temperatures with moisture predominantly occurring as snow, whereas summer was characterized by relatively warm temperatures with plant phenology advancing from low to high elevations. High elevations contained alpine and sub-alpine flora, mid-elevations were predominantly characterized by mixed coniferous forests, and low elevations consisted of a mosaic of shrub communities and agriculture production. All populations contained a suite of native carnivore species, including grizzly bears (*Ursus arctos horribilis*), black bears *(Ursus americanus*), wolves (*Canis lupus*), coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and golden eagles (*Aquila chrysaetos*). Most bighorn sheep populations were sympatric with one or more additional ungulates, including mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), and mountain goats (*Oreamnos americanus*).

Animal capture and data collection

Animal capture occurred between 2008 and 2018. We used ground darting, drop nets, and helicopter net-gunning to capture adult (> 1 yr old) female bighorn sheep, primarily during winter months. Animals were instrumented with store-on-board or remote download GPS collars programmed to record locations at varied intervals ranging from one to 13 hours. Where metrics were provided by the GPS collar manufacturer, we censored GPS locations with an HDOP > 10 (D'eon & Delparte 2005) and a horizontal error > 100 m.

Seasonal periods and migratory behavior classification

Non-linear modeling of net-squared displacement (NSD) has been widely used to categorize the seasonal movements of migratory species (Bunnefeld et al. 2011, Singh et al. 2012, Eggeman et al. 2016), but can be sensitive to the type of migratory movement (Singh et al. 2016) and often requires post-hoc inspection or subjective decisions to get the most biologically reasonable classification (Mysterud et al. 2011). Moreover, the method requires a complete animal-year, inclusive of two seasonal movements between winter and summer ranges (e.g., winter → summer → winter), and cannot incorporate partial animal-years in which only a single seasonal movement occurred (e.g., winter → summer). In addition, while NSD has been expanded to incorporate metrics of elevation in delineating migratory behavior (Spitz et al. 2015), it is not possible to characterize migratory behaviors with respect to elevation and geographic metrics simultaneously.

However, within diverse mountain landscapes, elevation and geography can function independently along a migration route, and be equally important in classifying migratory behaviors (Lowrey et al. In review, Spitz et al. 2015). Lastly, NSD methods are confined to relatively few migratory behaviors, yet migrations are being increasingly defined across a continuum of behaviors beyond the classifications afforded by the NSD approach (Sawyer et al. 2016, Barker et al. 2018, Lowrey et al. In review).

As an alternative to the analysis of NSD, we implemented *k*-means clustering, one of the most widely used clustering techniques (Jain 2010), to classify the seasonal movements of bighorn sheep. While novel in the context of migratory ungulates, clustering techniques are broadly applied across many diverse ecological disciplines (Jain 2010) and have been used to distinguish behavioral states of other species, for example diving behaviors of white sharks (*Carcharodon carcharias*; Jorgensen et al. 2012). Rather than require a full animal-year, we characterized migratory patterns between winter and summer core seasonal ranges. We defined core seasonal ranges using a maximum of the first 60 days of GPS locations between 1-January and 10-May for winter, and the GPS locations between 1-July and 31-August for summer. The core periods were defined to ensure that individuals would be within the respective seasonal range and accommodate the varied capture schedules across populations (Appendix S5.4). While the 10-May cutoff for winter was relatively late, the large majority of individuals were captured in January – March. Moreover, the few individuals that were captured in early May were on known winter ranges prior to spring migration (Appendix

S5.4). We censored individual-years with fewer than 10 days of monitoring within either core seasonal period.

For each animal-year, we characterized migratory distance by measuring the Euclidian distance between seasonal range centroids, and characterized elevational distance as the absolute value of the difference between the mean elevation associated with the GPS locations within the respective seasonal periods (Lowrey et al. In review). In this way, the seasonal movements of each animal-year were characterized by a single point with respect to elevational (i.e. the y-axis) and geographic (i.e. the x-axis) distances. We then scaled and centered the distances and created a distance matrix by measuring the Euclidian distance in 2-D space to assess similarity across all animal-years, and selected an optimal number of *k* groups such that the total within group sum squares was minimized and distances between groups were maximized. The *k*-means approach was beneficial in that it incorporated partial animal-years with a single movement between seasonal ranges, combined metrics of both elevation and geography into behavioral classification, and was not confined to a pre-defined set of migratory behaviors.

Measures of individual heterogeneity and migratory diversity

To describe the portfolio of migratory movements, we calculated the proportion of individuals within each migratory behavior for all populations. To account for the presence of multiple seasonal movements for a single individual, we used 500 bootstrap iterations to sample a single seasonal movement from each individual and calculated the proportion of individuals within each strategy for each iteration. In addition, we used Shannon’s H diversity index to provide a quantitative measure of migratory diversity

(Appendix S5.4). We calculated behavioral switching rates as the proportion of individuals with ≥ 2 years of monitoring that switched behaviors in consecutive years, and also summarized the behaviors between which switching occurred. Because behavioral switching is associated with a congruent change in consecutive seasonal ranges, we characterized spatial fidelity for the years where no behavioral change occurred. In this way, we characterized spatial fidelity (Euclidian distance between consecutive seasonal ranges) between years with a consistent migratory behavior. Lastly, to characterize seasonal population spread, we calculated pairwise Euclidean distance matrices between individual home ranges centroids for each season (Gilroy et al. 2016). All analyses were conducted in the R environment for statistical computing (R Core Team 2018) in combination with the `sf` package for spatial analysis (Pebesma 2018), `factoextra` (Kassambara and Mundt 2017) and the `stats` (R Core Team 2018) package for *k*-means clustering, and the `tidyverse` (Wickham 2017) suite for data wrangling and visualization.

Results

We recovered GPS data from 412 individuals across 17 (restored = 4, augmented = 6, native = 7) populations in Montana and Wyoming. We censored 49 individuals with early mortalities or GPS collar failures that occurred prior to any movement between seasonal ranges. From the remaining 362 individuals we aggregated 633 seasonal movements with a mean of 1.74 seasonal movements (range = 1 to 4) for each individual. An optimal value of *k* = 4 groups provided the best balance between minimizing the within group distances and maximizing among group distances (Appendix S5.5). The four groups were largely delineated according to geographic distance and contained residents, as well as short-, mid-, and long-distance migrants, all of which traversed a range of elevational gradients (Figure 5.2). One average, the diversity of the migratory portfolios increased along the continuum from restored to native populations (Figure 5.3, Appendix S5.3), with the exception of Grand Teton National Park (GTNP), which was a native population predominantly characterized by high elevation residents. Resident behavior was common across all management histories and tended to occur at low elevations in restored populations (Figure 5.4). In contrast, residents in native populations predominantly occurred at high elevations, although some low-elevation residents were documented. Short-distance seasonal movements were characterized by geographic distances of 5 – 20 km between seasonal ranges and were present across all management histories. Mid-distance migrants were characterized by a range of geographic distances but did not exceed 35 km, and were absent from restored populations. Lastly, long-distance migrants were only present in native populations and were characterized by geographic distances between 30 – 50 km. Interestingly, many of the long distance migrations were between high elevation summer and winter ranges with little difference in elevation (Figure 5.4).

There were 224 individuals with at least two years of monitoring that we included in the characterizations of behavioral switching. Across all management types, nine percent of the individuals with multiple years of monitoring switched strategies, although switching rates were notably less common in restored populations (mean = 6.25%, SD = 12.5%) than in augmented (mean = 15.2%, SD = 11.4%) or native (mean = 18%, SD =

11.4%) populations (Figure 5.5). The majority of the observed switches (58 percent) where characteristic of partially migratory populations and occurred between resident and migrant behaviors. The remaining switches (42 percent) were between the three migratory behaviors. Across years without a migratory change in behavior, there was generally high fidelity to consecutive seasonal ranges across all management histories with seasonal range centroids that were separated by < 2 km (Figure 5.6). Lastly, with respect to population spread, individuals within restored populations were largely concentrated on a single range with an average of < 3 km between individual home ranges centroids (Figure 5.7). Augmented populations were slightly more spread with an average of 7.8 and 5.4 km between summer and winter home ranges, respectively. In contrast, native populations were diffusely spread across the landscape with an average of 20 km between individual home ranges in both seasons (Figure 5.7).

Discussion

We provided a detailed characterization of individual migratory heterogeneity using multiple metrics with restored, augmented, and native bighorn sheep populations across the northern Rocky Mountains of Montana and Wyoming, USA. Our results showed higher migratory diversity in native bighorn sheep populations that have maintained a consistent presence on the landscape for generations. Native populations had more diverse portfolios of migratory behaviors, including newly documented high elevation long-distance migrants, increased switching rates between migratory behaviors, and were diffusely spread across both summer and winter ranges. In contrast, restored populations were largely non-migratory resulting in a limited behavioral portfolio, had less switching between years, and were generally concentrated in both summer and winter ranges. There was more variation among augmented populations with mixed results regarding individual variation. While some populations were almost exclusively short distant migrants, others were partially migratory with short- and mid-distance behaviors, but still had relatively constrained distributions on seasonal ranges. Importantly, these differences were observed across populations within similar landscapes with respect to landscape heterogeneity and phenological patterns (Appendix S5.3). Using a similar comparison across native and restored populations of bighorn sheep and moose (*Alces alces*), recent work has highlighted social learning and cultural transmission as the primary mechanisms through which ungulate migration evolves (Jesmer et al. 2018). Our results build from these findings and suggest that the landscape 'knowledge' that has develop over generations in native populations not only increases migratory propensity and foraging efficiency (Jesmer et al. 2018), but also results in diverse portfolios of migratory behaviors.

Bighorn sheep typically occupy rugged and heterogeneous mountain landscapes where observed phenological patterns represent the complex interaction of both broad- and fine-scale factors. Rather than develop a single, most fit behavior, it appears the migratory patterns of bighorn sheep reflect the complexity of their mountain environment and exploit multiple landscape patterns across varied spatial scales. While we did not directly measure demographic performance across the three management histories beyond estimates of abundance (Table 5.1), ecological theory and empirical results from other migratory taxa indicates individual variation has realized demographic benefits. For example, although annual patterns of weather (i.e., winter severity, rate of spring green-up) or predation may disproportionately impact any one behavior from year to year, a diverse portfolio of migratory behaviors can buffer the aggregate population and result in more stable demographic performance over time (Webster et al. 2002, Griffiths et al. 2014, Gilroy et al. 2016). The presence of multiple behaviors in native populations indicates that each behavior has sufficient demographic benefits to persist over time and not experience complete negative directional selection.

There were three native populations without long-distance migrations (Jackson, and Upper Yellowstone, and Whiskey Mountain) and one population (Grand Teton NP) with only residents and short-distant migrants. Although it is possible these migrations exist but were not documented in our sample, the reduced diversity in these native populations is likely due to disease events or anthropogenic disturbances which resulted in large population losses. The Jackson, Upper Yellowstone and Whiskey Mountain populations have all experienced die-offs associated with contagious respiratory pathogens with mortality estimates of up to 80 percent (Table 5.1; Appendix S5.2). While the migratory behaviors of the lost population component are unknown, it seems possible that large mortality events could result in the loss of specific migratory behaviors among individuals that are in close association (Lowrey et al. In review). The limited migratory portfolio in Grand Teton NP was historically more diverse. In addition to high elevation residents, there were also elevational migrations between the current year-round ranges and low elevation winter ranges (Whitfield 1983), which have undergone significant anthropogenic development, resulting in the loss of the elevational migration behavior

(Whitfield 1983, Courtemanch et al. 2017). The native populations with all four migratory behaviors have no known population declines resulting from disease or anthropogenic disturbances. Although die-offs may have occurred when domestic sheep were first introduced, the varied distributions and movement behaviors of native bighorn sheep as well as the inaccessibility of some areas in the Absarokas likely minimized the impact of introduced pathogens. While the occurrence of multiple partially migratory augmented populations indicates some ability to retain or restore (Lowrey et al. In review) migratory diversity, fully restoring the migratory portfolios observed in native populations remains a formidable conservation challenge that has yet to be widely achieved (Harris et al. 2009, Lowrey et al. In review, Jesmer et al. 2018).

There are a number of hypothesis that relate migratory behavior to disease dynamics (Altizer et al. 2011). Migrants are predicted to have higher disease prevalence and diversity because of the increase potential of ‘sampling’ a diversity of habitats and inter- or intra-specific populations along the migratory route (migratory sampling; Teitelbaum et al. 2018). In contrast, migration can also provide an escape from densely occupied seasonal ranges where pathogens have accumulated (migratory escape), or selectively cull infected individuals that are unable to withstand the physiological stresses of migration (migratory culling), both of which could reduce disease prevalence or diversity in migratory populations (Johns and Shaw 2015). The majority of empirical studies have focused on birds and found mixed results with respect to migratory behavior and pathogen prevalence (Teitelbaum et al. 2018). In addition to migratory movements, dispersal and the increased movement rates associated with the rut are an additional mechanism that can facilitate pathogen transmission between bighorn sheep populations as well as between bighorn sheep and domestic livestock (Borg et al. 2016). Across our study region, recent work indicates a broad distribution of respiratory pathogens within all management histories (Butler et al. In press). Given the importance of respiratory disease to bighorn sheep management, we encourage additional work that examines the relationship between migratory and pathogen diversities. However, bighorn populations with dense seasonal aggregations are known to have a greater risk of pneumonia epizootics (Sells et al. 2015), likely resulting from increased transmission rates among conspecifics (Manlove et al. 2017). The diffuse seasonal ranges (i.e., broad population spread) associated with native populations may help to minimize risk of pneumonia epizootics through reducing transmission rates and lowering densities across multiple seasonal ranges. In contrast, the lack of multiple seasonal ranges in restored populations creates a vulnerability to future die-offs if new pathogens enter a population or added stressors cause resident pathogens to become virulent.

The migratory behaviors of the source populations used for restoration and augmentation is an important consideration that is complicated by the web of historic bighorn sheep translocations throughout North America (Brewer et al. 2014). For example, many restored and augmented populations have multiple sources, which themselves are also an aggregate of historic translocations. While the majority of the source populations in our study populations were migratory (Table 5.1), current migratory patterns often may not reflect historic complexity and may be limited in scope. Moreover, many of the source populations are partially migratory, containing seasonal residents and migrants who share ranges during the winter months when captures for translocations typically occur. In these instances, the migratory behavior of the translocated individuals with respect to resident or migrant classifications are unknown. While migratory propensity is lower for migrant individuals translocated into novel landscapes (Jesmer et al. 2018), the use of resident source populations likely further reduces individual heterogeneity in restored or augmented recipient populations (Lowrey et al. In review). For example, although initially started from migratory populations in the early 1900’s, Wildhorse Island and the National Bison Range populations in western Montana now contain exclusively resident populations that have been used as source populations throughout western North America (MTFWP 2010). While translocations from resident source populations may meet management objectives of reducing local densities, they are unlikely to diversify migratory portfolios when used for augmentations (Lowrey et al. In review). This is exemplified in the restored Perma-Paradise population, which was reestablished with bighorn sheep translocated from Wildhorse Island and has remained resident for the last 30 yrs.

Interestingly, among restored populations, Darby Mountain was unique in that resident bighorn sheep occupied high-elevation year-round ranges akin to the resident behaviors observed in native populations. The Darby Mountain population was initiated from two translocations totaling 60 individuals during the winters of 1981 and 1987 from Whiskey Mountain, a partially migratory population. The translocated animals were transported via helicopter in wooden crates to historic-high elevation winter ranges (WYGF 1980). Although sourced from low- to mid- elevation ranges in Whiskey

Mountain, the resident behavior appears to be transferable to high elevations where the population has remained stable, albeit at low abundances (Table 5.1). The restoration of the Darby Mountain population indicates that alternative approaches to bighorn sheep restoration may help to diversify migratory portfolios through adding high-elevation residents. Moreover, restoring resident populations to historic high-elevation ranges may reduce epizootics as high-elevation ranges are largely separated from domestic livestock during winter and can reduce the probability of comingling events.

Building from theoretical and empirical evidence that describes population-level benefits of individual heterogeneity across multiple disciplines and taxa, we encourage future work that links demography with population-level migratory diversity and environmental conditions in terrestrial ungulates. In addition, matching known migratory behaviors with unoccupied bighorn sheep habitats may help to diversify the migratory portfolios of restored, and in some cases, augmented bighorn sheep. Recognizing the diversity of suitable bighorn sheep habitats, a single-species habitat model that aggregates across migratory behaviors may miss many of the nuances associated with behavior-specific seasonal ranges. For example, when high and low elevation residents are aggregated in habitat models (i.e., resource selection functions), the result would be an 'average' resident model that poorly predicts both resident behaviors. We suggest a two-pronged approach that first creates behavior-specific habitat models and then matches known migratory behaviors to unoccupied areas as an alternative restoration approach that may more efficiently infuse migratory diversity into restored populations, potentially with synergistic benefits associated with individual heterogeneity and resulting portfolio effects. Expanding existing bighorn sheep populations within contagious mountain ranges helps to mirror the diffuse population spread observed in native herds and has shown positive results in Montana (MTFWP 2013) and California (U.S. Fish and Wildlife Service. 2007, Johnson et al. 2011). These efforts could be aided by behavior-specific habitat models to help inform translocations, notably areas of high elevation winter range. In addition to increasing the abundance and distribution of bighorn sheep on the landscape, we suggest there is value in simultaneously increasing the diversity of seasonal movement strategies and ranges, and in so doing, building resilience to future perturbations and respiratory disease die-offs from resident and novel pathogens, and mirroring the movement portfolios observed in native populations of bighorn sheep.

Tables and figures

Table 5.1. Management histories, population estimates, and translocation and disease histories for the 17 populations of female bighorn sheep, Montana and Wyoming, USA, 2008-2018.

State	Herd units				
	Name	**N**	**Management units^1**	**Population estimate^2**	**Herd type**
MT	Hilgard	49	HD-302	280	Augmented
MT	Lost Creek	26	HD-213	100	Restored
MT	Perma-Paradise	23	HD-124	352	Restored
MT	Petty Creek	14	HD-203	160	Restored
MT	Spanish Peaks	13	HD-301	172	Augmented

MT	Stillwater	20	HD-501, 502	75	Augmented
MT	Sun River	17	HD-422, 424	150	Augmented
MT	Upper Yellowstone	10	HD-305, northwest YNP	320	Native
WY	Clark's Fork	22	HD-1, northeast YNP	600	Native
WY	Darby Mountain[4]	5	–	60	Restored
WY	Franc's Peak	32	HD-5, 22	840	Native
WY	Grand Teton NP[4]	29	–	100	Native
WY	Jackson	40	HD-7	450	Native
WY	Temple Peak[4]	23	–	50-75	Augmented
WY	Trout Peak	19	HD-2	700	Native
WY	Wapiti Ridge	44	HD-3	850	Native
WY	Whiskey Mountain	23	HD-9, 10	850	Native

Name	**Translocation history**				**Disease[5]**	
	Year	**Number**	**Source[3]**	**Migratory behavior of source population**	**Year**	**Percent Mortality**
Hilgard	1988	19	MT-121	Migratory	1987	90
	1989	5	MT-121	Migratory		
	1989	19	MT-213	Migratory	1997	70
	1993	26	WHI	Resident		
Lost Creek	1967	25	MT-422	Migratory	1991	>50
	1985	2	MT-121	Migratory	2010	60
Perma-Paradise	1979	14	WHI	Resident	None	–
	2011	22	WHI	Resident		
Petty Creek	1968	16	MT-422	Migratory	None	–
	1985	4	NBR	Resident		
Spanish Peaks	1944	2	HD-101		None	–
	1947	2	HD-422	Migratory		
	1963	6	NBR	Resident		
Stillwater	1968	2	MT-422	Migratory	Pre-1920	Unk
	1970	2	MT-422	Migratory		
	1984	3	NBR	Resident		
Sun River	1960	8	MT-422	Migratory	1925	Unk
					1932	Unk
					1984	30
					2010	>50
Upper Yellowstone	–	–	–	–	1981	60
					2012	Unk
					2014	Unk
Clark's Fork	–	–	–	–	None	–
Darby Mountain[4]	1981	35	WY-Whiskey	Partial	None	–
Franc's Peak	–	–	–	–	None	–
Grand Teton NP[4]	–	–	–	–	None	–
Jackson	–	–	–	–	1934	80
					2001-2004	60
					2012	40
Temple Peak[4]	1960	1	WY-Whiskey	Partial	1992	60
	1964	20	WY-Whiskey	Partial		

	1965	20	WY-Whiskey	Partial		
	1966	18	WY-Whiskey	Partial		
	1971	13	WY-Whiskey	Partial		
	1972	39	WY-Whiskey	Partial		
	1987	54	WY-Whiskey	Partial		
Trout Peak	–	–	–	–	None	–
Wapiti Ridge	–	–	–	–	None	–
Whiskey	–	–	–	–	1990	30-40
					2010	20

[1] The aggregation of management units within each herd unit is further described in Appendix S5.1

[2] Estimates were provided by area biologists and determined from local knowledge, minimum counts, and recent trends.

[3] WHI: Wild Horse Island; NBR: National Bison Range

[4] Non-hunted population without a management unit.

[5] All disease events were associated with respiratory pathogens with the exception of Upper Yellowstone in 1981 when pink eye was documented.

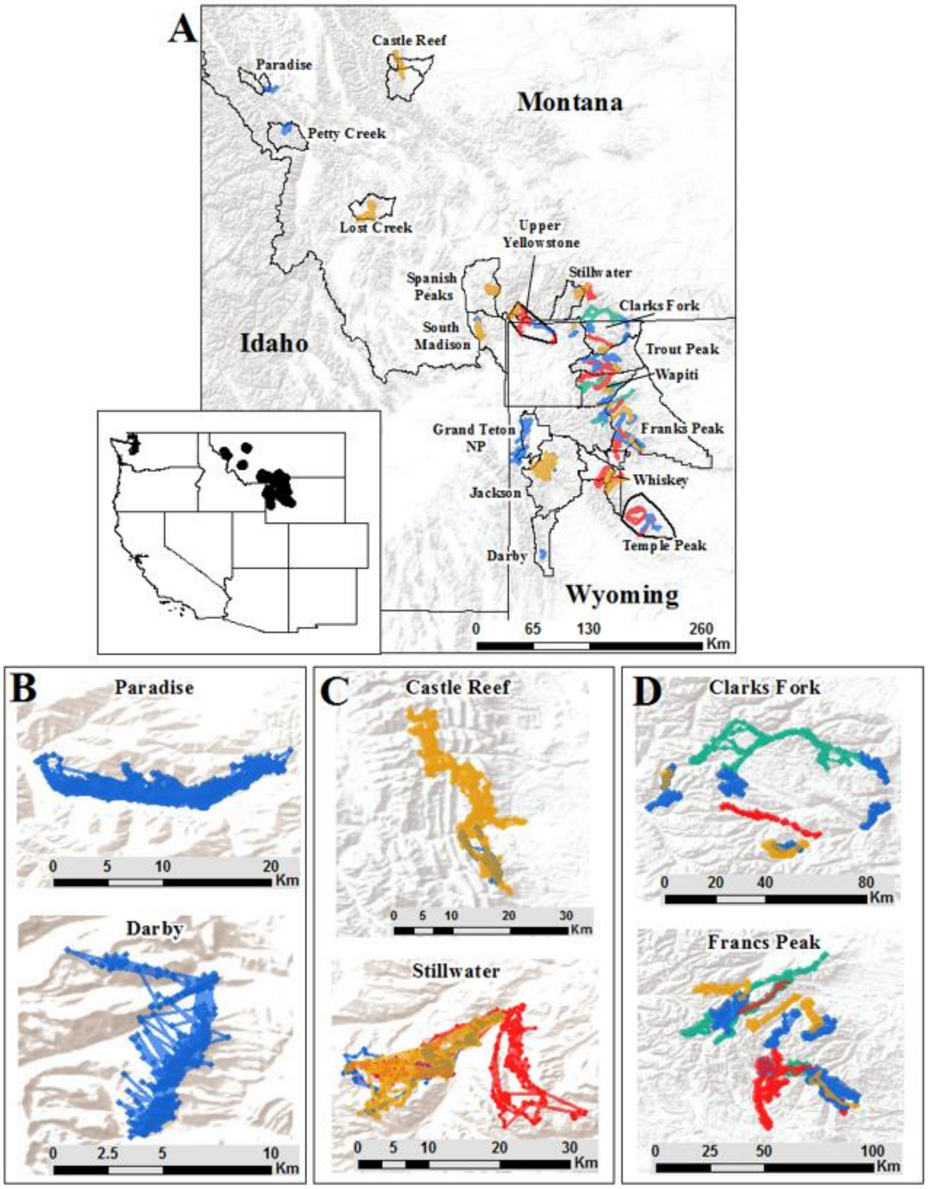

Figure 5.1. (A) Study regions across Montana and Wyoming, USA, 2008 – 2018. Paths are shown for short- (yellow), mid- (red), and long-distance (green) migrants. The movements of residents (blue) are characterized as the paths between locations within the mean spring and fall migratory periods across all migrant individuals (spring = 21-May to 16-June; fall = 26-Sept – 28-Oct). Population classifications are further detailed in Appendix S5.1. Panels B – D show two detailed example populations within restored, augmented and native management histories, respectively.

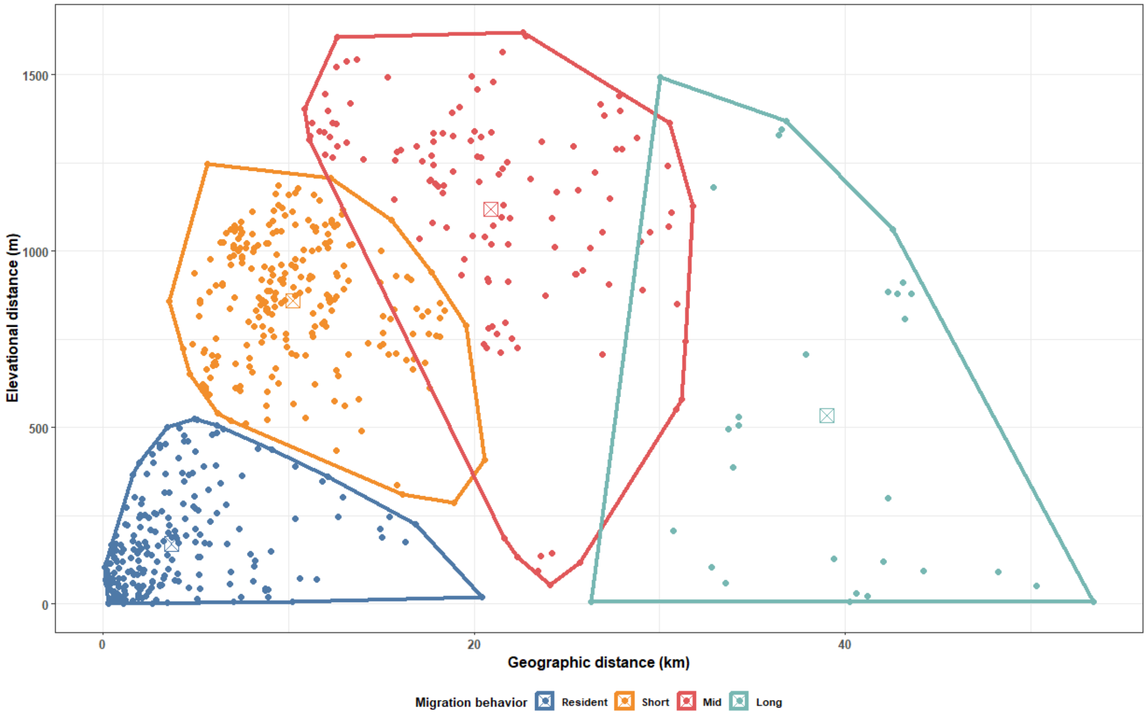

Figure 5.2. Migratory behavior classifications of 633 seasonal movements between core seasonal range centroids for female bighorn sheep, Montana and Wyoming, USA 2008 – 2018. The resident and three migratory behaviors are shown in 2-D space with respect to elevation and geographic distances between seasonal ranges. Group centroids are show with a crossed box. Although distances were measured between centered and scaled covariates, native units are presented above.

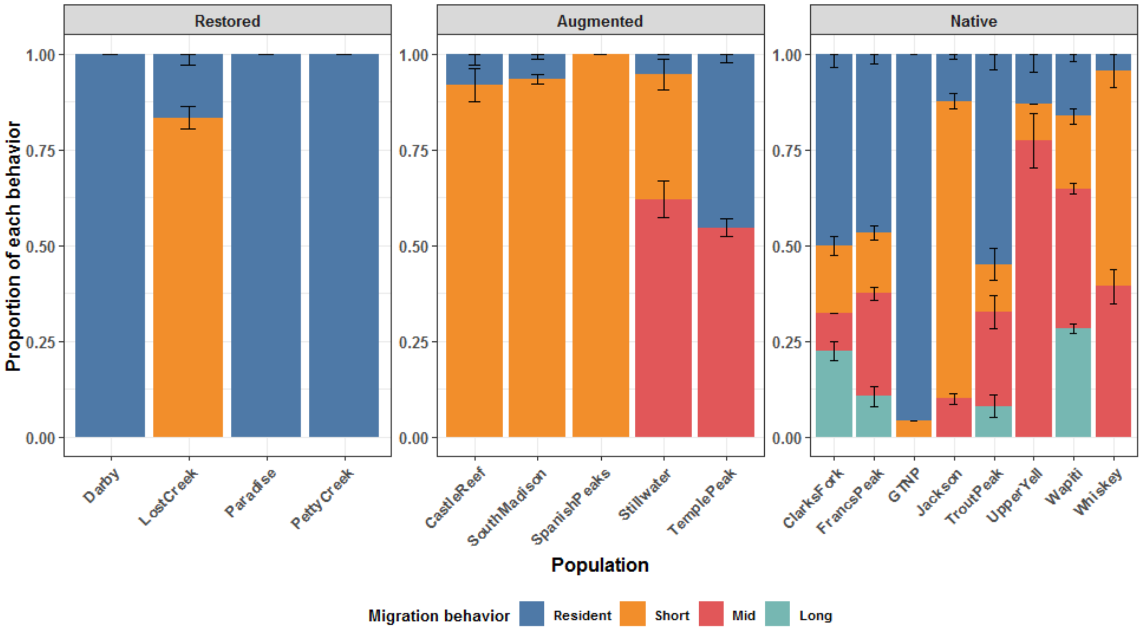

Figure 5.3. The mean proportion of each migratory behavior for restored, augmented, and native bighorn sheep populations, Montana and Wyoming, USA 2008 – 2018. Error bars represent the standard error across 500 bootstrap iterations and pertain to the lower behavior at each boundary.

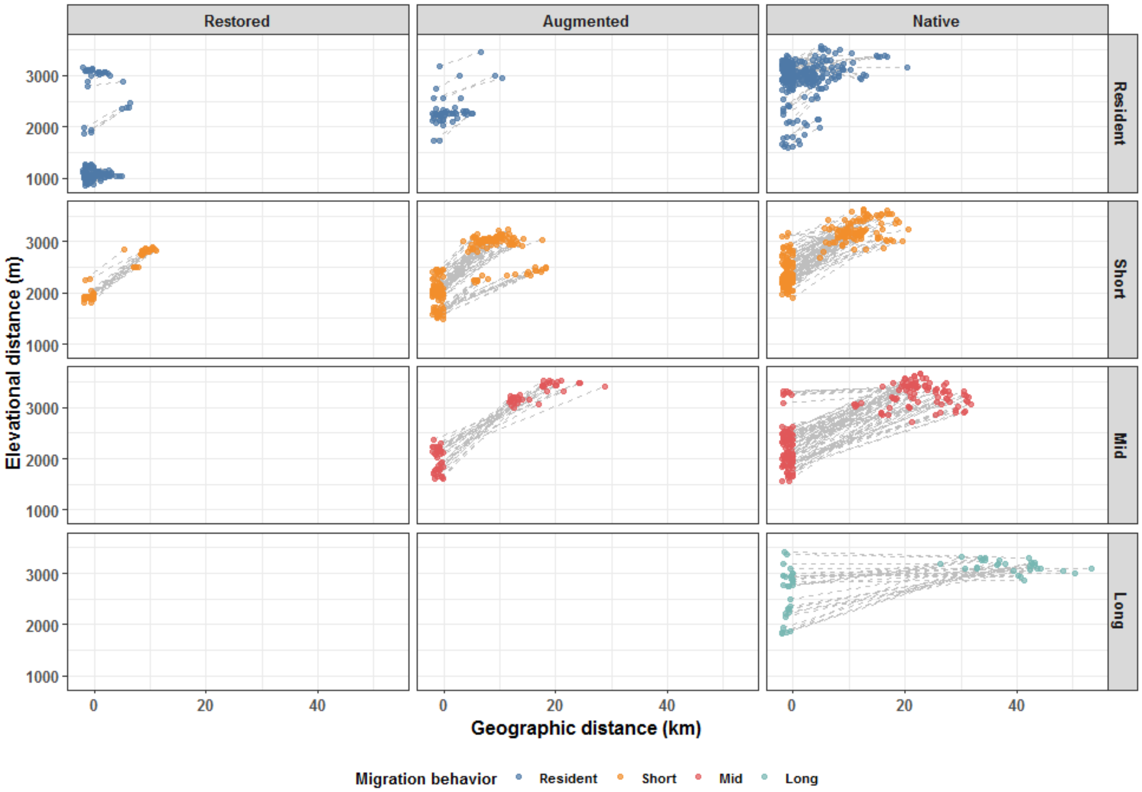

Figure 5.4. Seasonal movement portfolios of female bighorn sheep as characterized by elevational and geographic distances between winter and summer home range centroids, Montana and Wyoming, USA 2008 – 2018. Migratory behaviors are separated by rows, while columns separate population management histories. The elevation of each seasonal range as well as the geographic distance between seasonal ranges (referenced with zero as the starting point in winter) is shown for each individual-year (grey lines).

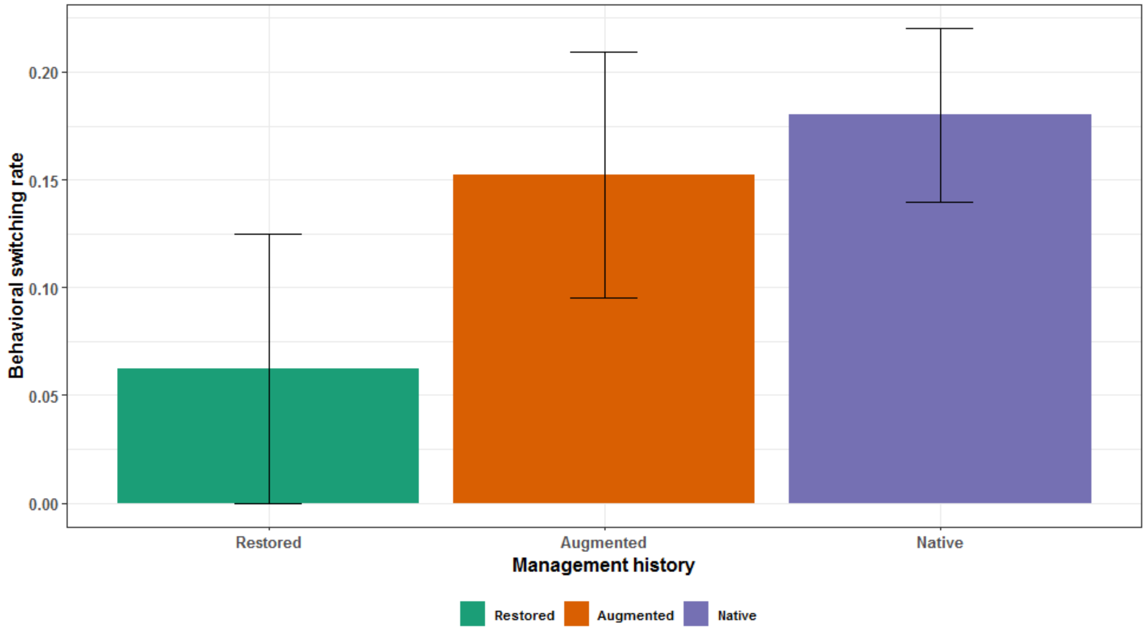

Figure 5.5. Average (± SE) behavioral switching rates for all restored, augmented, and native populations of bighorn sheep, Montana and Wyoming, USA 2008 – 2018.

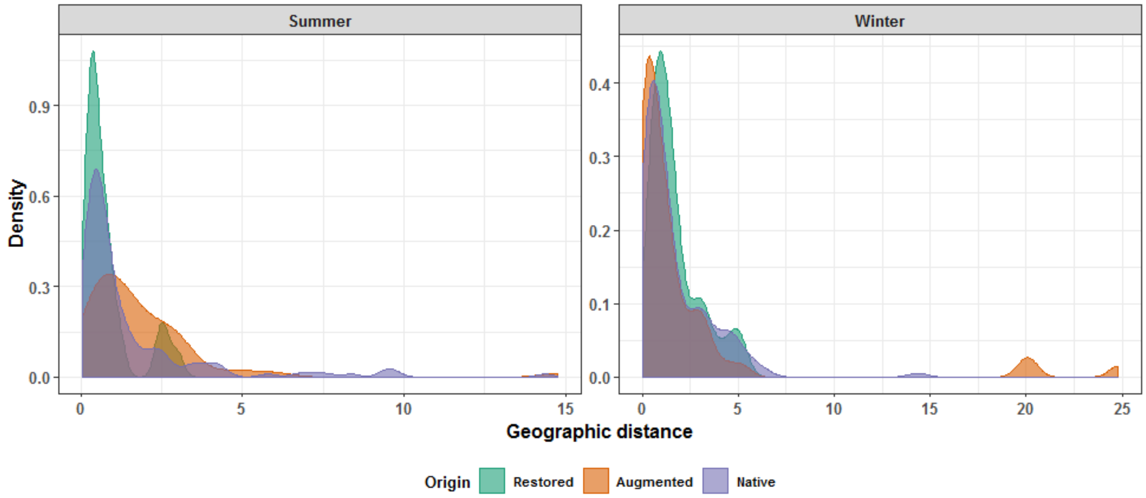

Figure 5.6. Density plots showing the distribution of the geographic distances between consecutive seasonal ranges for restored, augmented, and native populations of bighorn sheep, Montana and Wyoming, USA, 2008-2018.

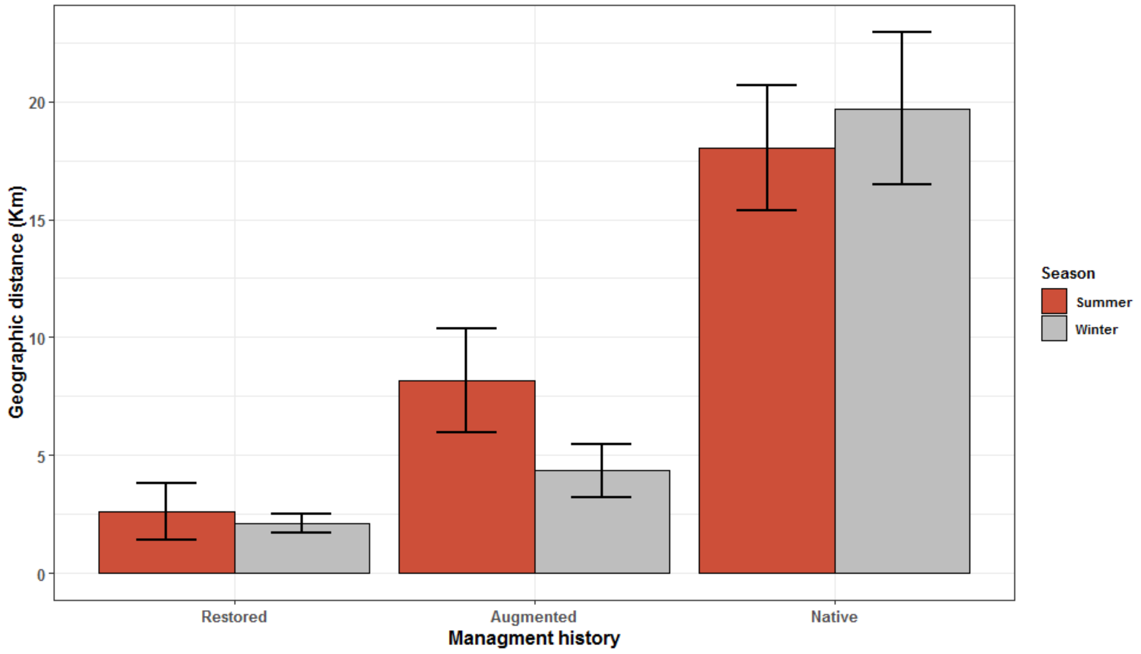

Figure 5.7. Bar plots describing the average (± SE) pairwise distances between female bighorn sheep individual home range centroids in summer (red) and winter (grey) seasons, Montana and Wyoming, USA, 2008-2018.

Acknowledgements

This study would not have been possible without the dedicated effort of the many state and federal agencies who have diligently worked to conserve and restore bighorn sheep for the last half century. Primary funding for this work was provided by the Wyoming Game and Fish Department, Federal Aid in Wildlife Restoration Grant W-159-R to Montana Fish Wildlife and Parks and the annual auction sale of a Montana bighorn sheep hunting license, the National Park Service (Yellowstone and Grand Teton National Parks), Canon USA Inc. (via the Yellowstone Park Foundation), Greater Yellowstone Coordinating Committee, the United States Forest Service (Bridger-Teton, Shoshone, and Caribou-Targhee National Forests), and Wyoming Governor’s Big Game License

Coalition. Additional funds and scholarships were provided by Montana State University, Wyoming Wild Sheep Foundation, Montana Wild Sheep Foundation, Wild Sheep Foundation, Idaho Safari Club International, Idaho Bureau of Land Management, the Kevin Hurley Wild Sheep Biology Award, the Jack Creep Preserve Foundation, and the Shikar Safari Club.

CHAPTER FIVE APPENDICES

Appendix S5.1: Detailed description of population delineations

We delineated population units using regional management units (i.e. hunting districts or national park boundaries) which provided a similar grouping system that could be applied across the broad study region. Management units are the most relevant administrative unit for regional managers and are often used to summarize other population attributes (i.e. vital rates, abundance, disease prevalence, etc.). By linking our work with management units, our results are directly applicable to regional management efforts and represent the same spatial scale.

We grouped individual bighorn sheep into population units based on the capture location. In most instances the ‘population unit’ was synonymous with local management units, although there were a few exceptions where we lumped adjacent management units and/or individuals to better reflect groupings based on the GPS locations and local geography. We recognize the subjective nature of these decisions and have provided detailed descriptions of the areas where lumping occurred.

Montana populations

Paradise (HD-124), Petty Creek (HD-203), Lost Creek (HD-213), Spanish Peaks (HD-301), and Taylor-Hillgard (HD-302) populations were all characterized by a single management unit (Figure S5.1.1). The Castle Reef population was an aggregate of individuals captured in HD-424 and HD-422. The adjacent management units (HD-421 and HD-423) were also used by instrumented bighorn sheep (Figure S5.1.1). There were four individuals captured in the northwest corner of Yellowstone National Park (YNP), roughly 9 km from the animals within the Upper Yellowstone (HD-305). We aggregated animals captured in northwest YNP with those in Upper Yellowstone (HD-305) to make a single population. All animals in Stillwater were captured within a single management unit (HD-502) but separated into two adjacent units (HD-501) in summer (Figure S5.1.1). These animals were considered a single population.

Wyoming populations

Animals in Wyoming were broadly distributed across the Absaroka mountains with additional discontinuous populations in the Teton, Gros Ventre, Wind River, and Wyoming ranges (Figure. S5.1.2). We aggregated two animals captured within the northeast corner of YNP with the Clark's Fork population as well as a single individual captured roughly 2 km north of the MT-WY boarder (Figure S5.1.2). The Trout Peak (HD-2) and Wapiti Ridge (HD-3) populations are separated by the North Fork of the Shoshone River. These populations share some common winter ranges, and in one instance an individual captured in Trout Peak was more strongly associated with Wapiti Ridge according GPS locations. Although the capture location was within Trout Peak, we grouped the individual with Wapiti Ridge (Figure S5.1.2). The Franc's Peak population also included three individuals captured in HD-22, the management unit adjacent to Franc's Peak to the southwest. Whiskey Mountain was an aggregate of HD-10 and HD-9. Lastly, Temple Peak is not a hunted population and does not have a designated management unit. Single management units characterized each the remaining populations, Jackson (HD-7), Darby Mountain (HD-24), and Grand Teton NP.

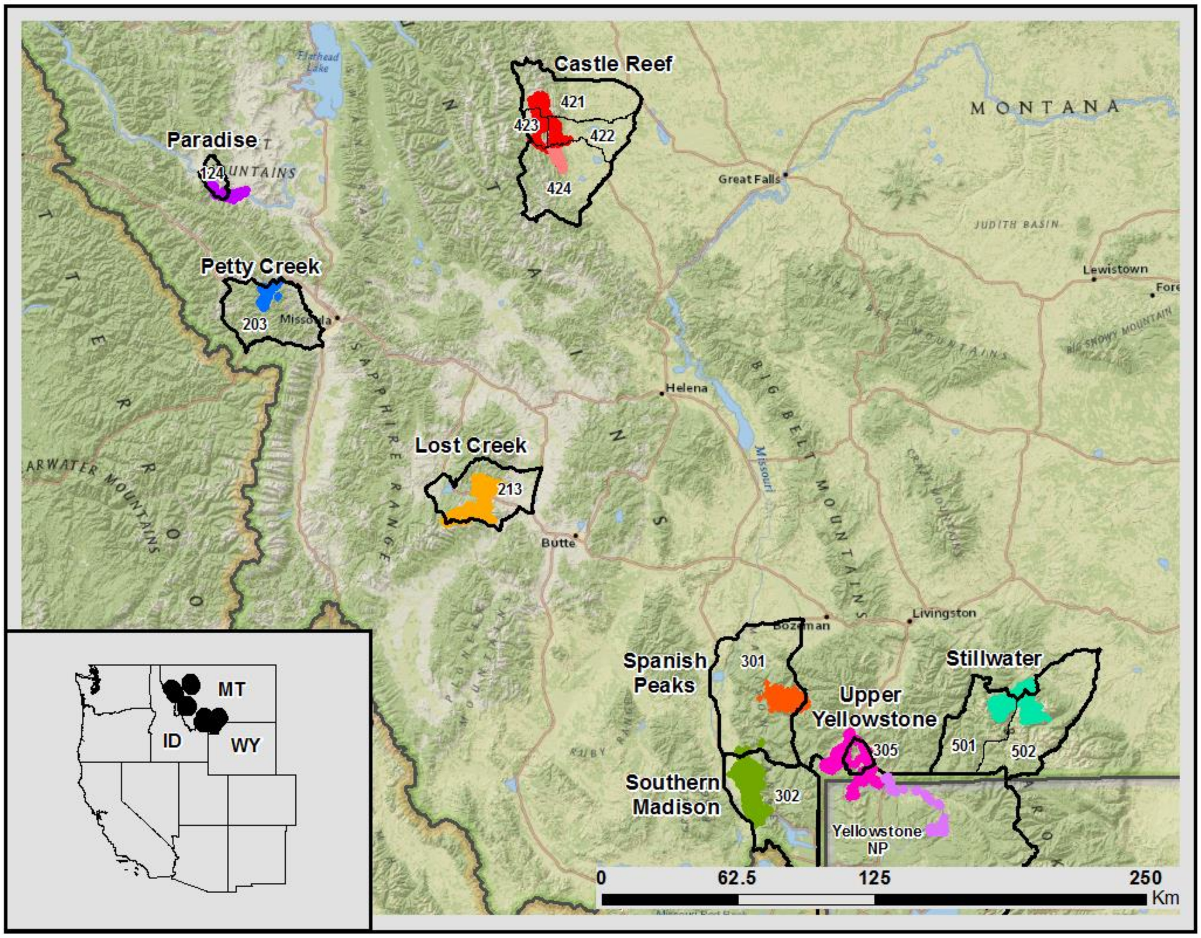

Figure S5.1.1 Montana populations, 2008-2018. Within the Castle Reef population, we aggregated individuals captured within HD-424 (pink) and HD-422 (red). Within the Upper Yellowstone population we aggregated individuals captured in HD-305 (dark pink) and northwest YNP (light pink).

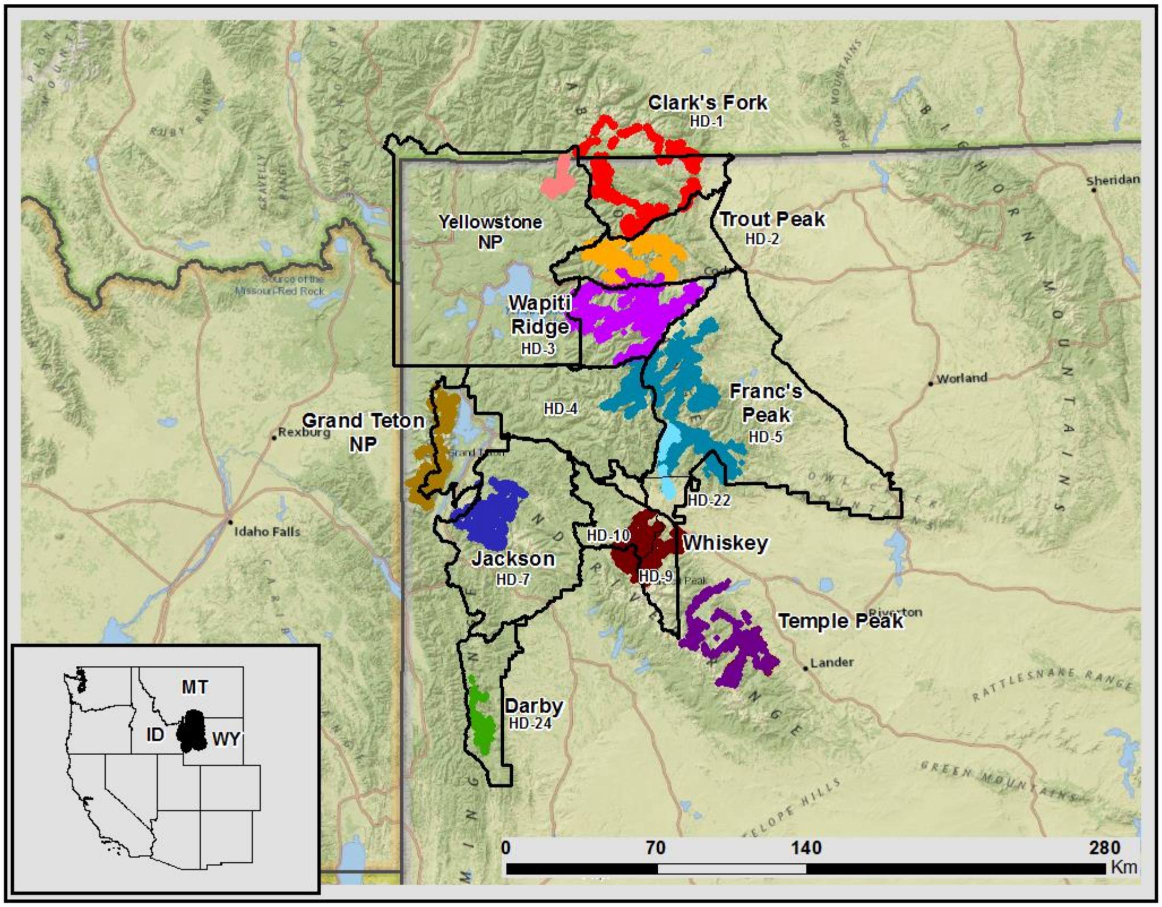

Figure S5.1.2 Wyoming populations, 2008 - 2018. The Clark's Fork population contained individuals captured in HD-1 (red), and two individuals captured in northeast YNP (pink). The Franc's Peak population was an aggregate of HD-5 (blue) and HD-22 (light blue).

Appendix S5.2: Population translocation and disease die-off summaries

Disease events were document across all management histories and had an average severity of 53.6 percent mortality (Figure S5.2.1). There were an average of 1.75 and 3.4 translocations for restored and augmented populations respectively (Figure S5.2.2). Temple Peak received the most individuals (N = 165) while Stillwater received a minimum of seven individuals. The sex ratio of the translocated animals is not well documented across all populations. In general, when only a few individuals were translocated they were all males (MTFWP 2010). When larger groups were translocated there were often varied proportions of males, females and age classes (MTFWP 2010).

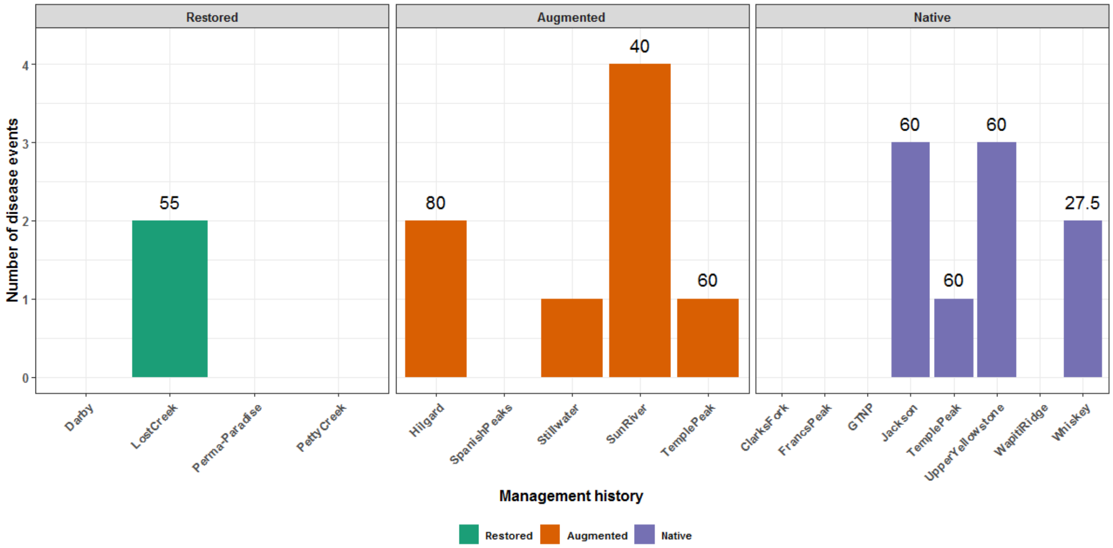

Figure S5.2.1 Number of disease events for all study populations. Where known, the average severity (percent mortality) is shown above each population.

Figure S5.2.2 Number of translocated individuals for restored and augmented populations. The number of translocation events is shown above each population.

Appendix S5.3: Summaries of landscape heterogeneity and phenology

The association between migratory patterns and landscape heterogeneity is well documented in ungulates. While homogeneous landscapes are associated with residency, landscape heterogeneity with respect to phenological patterns and topographic relief promotes migratory behavior as individuals track annual patterns or exploit seasonal refuges (Mueller et al. 2011, Merkle et al. 2016, Hsiung et al. 2018). To evaluate the importance of local landscape characteristics on migratory diversity, we first adapted Shannon's H diversity index to calculate an index of migratory diversity:

$$H = -\sum_{i=1}^{s} p_i \, ln(p_i)$$

where S was the total number of migratory behaviors, and $p_i$was the proportion of each migratory behavior i (Krebs 1999). The results provide a quantitative measure of diversity that reflects migratory portfolio diversity presented in Figure 3 in the body of the manuscript. As expected, Shannon's H-index increased along the continuum from restored to native populations (Figure S5.3.1).

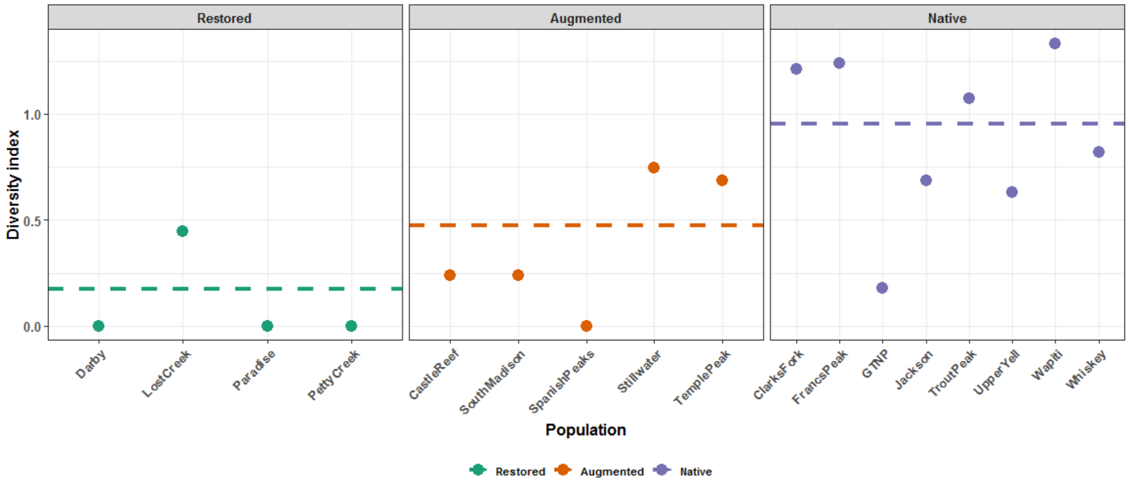

Figure S5.3.1 Shannon's H-index for the 17 populations of restored, augmented, and native bighorn sheep. The mean H-index for each management history is shown with a dashed horizontal line.

We generated multiple metrics of heterogeneity and phenology across our broad study region. To select an appropriate landscape extent for each population, we calculated a population centroid, which we then buffered by 30 km. The 30 km buffer approximated the 95 percent quantile distribution of migration distances between seasonal home range centroids and provided the most relevant landscape extent given our seasonal scale of interest. Moreover, the method allowed us to avoid the use of hunt units, which often extend far beyond the known distributions of bighorn sheep, and also avoid the use of GPS locations, which would provide a limited characterization of the 'available' landscape for resident populations. Within each population extent we generated three metrics of landscape heterogeneity - the mean elevation (± the 25th and 75th percent quantiles), the total range of elevation (i.e. the max – min), and lastly, to use a measure of elevational difference that was less sensitive to extremes, the difference between the 95th and 5th percent quantiles. We used NDVI amplitude and time-integrated NDVI to index forage production and phenology during the growing seasons from 2003 to 2017 and estimated a mean value for each metric and year.

We plotted the landscape heterogeneity and phenology metrics against migratory diversity and found no obvious differences between restored, augmented, or native herds. There was a general positive correlation between migratory diversity and the three landscape heterogeneity metrics suggesting higher and more heterogeneous landscapes were associated with migratory diversity (Figure S5.3.2). There was a general negative correlation between both NDVI metrics and migratory diversity (Figure S5.3.3). Nonetheless, these patterns were consistent across all herd types and indicate that our comparisons across management histories were not cofounded by local heterogeneity or phenology.

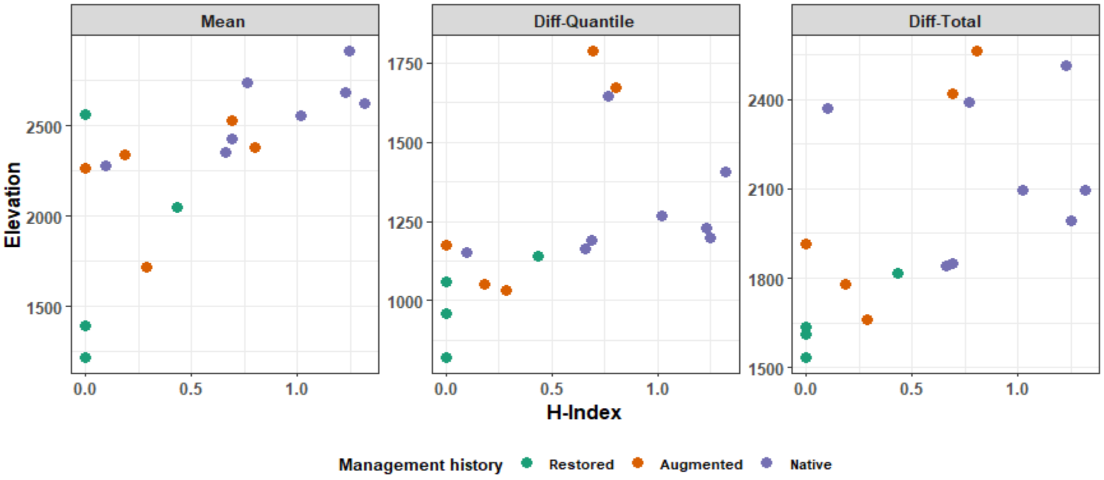

Figure S5.3.2 Elevation metrics plotted against Shannon's H-index for the 17 populations of restored, augmented, and native bighorn sheep. The panels show the mean elevation, the difference between the 95th and 5th percent quantiles, and the total difference in elevation, respectively.

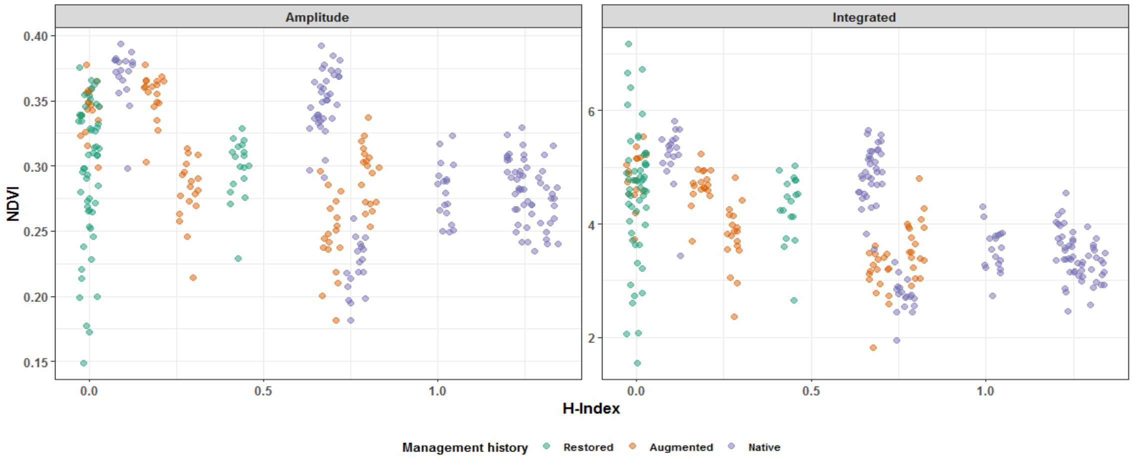

Figure S5.3.3 Mean NDVI amplitude and time-intrigued NDVI vales from 2003 to 2017 plotted against Shannon's H-index for the 17 populations of restored, augmented, and native bighorn sheep. The H-index values were plotted with additional jitter to reduce overlapping points.

Appendix S5.4: Monitoring periods in relation to the core winter start and end dates

While our 10-May winter cut-off date was relatively late in the winter period, the large majority of individuals were captured between January and March, well before the 10-May termination date (Figure S5.4.1).

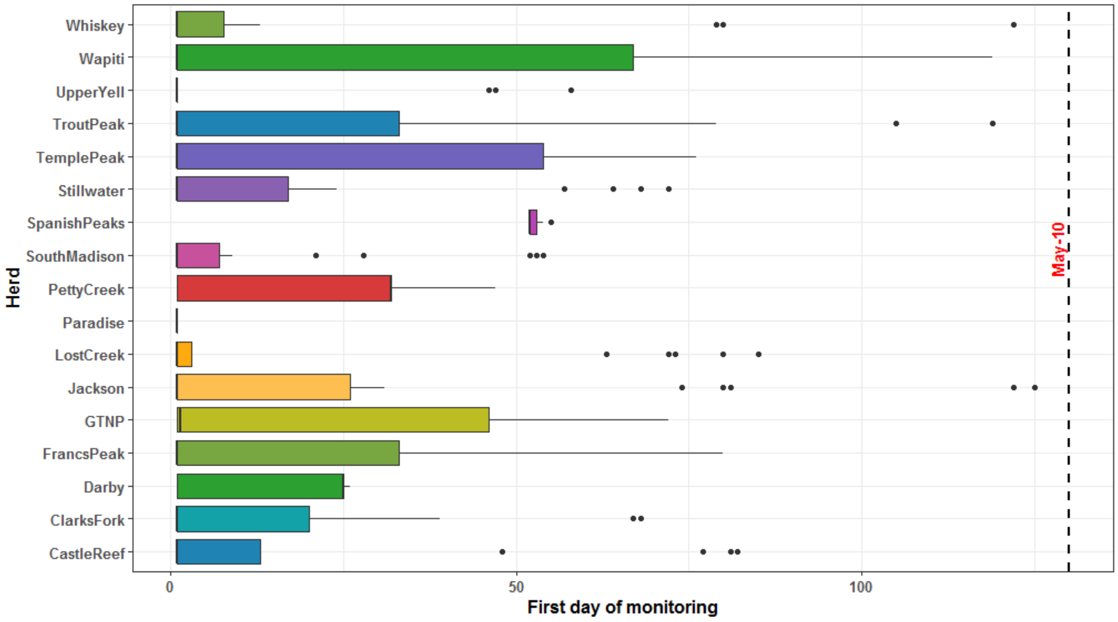

Figure S5.4.1 Box plots characterizing the distribution of monitoring start dates in winter for female bighorn sheep, Montana and Wyoming, USA, 2008 – 2018. All captures occurred on known winter ranges prior to spring migration.

Appendix S5.5: Selecting an optimal *k* groups

We selected an optimal number of *k* groups that balanced minimizing the within group and maximizing between group sum of squared Euclidian distances. Within group distance began to stabilize at four groups (Figure S5.5.1). Between group distances were less clear with little difference between two to five groups (Figure S5.5.2). As a result, we selected *k* = 4 as the best balance between the two metrics. In addition, relative to three groups, four groups resulted in less overlap between group polygons (Figures S5.5.3 and S5.4).

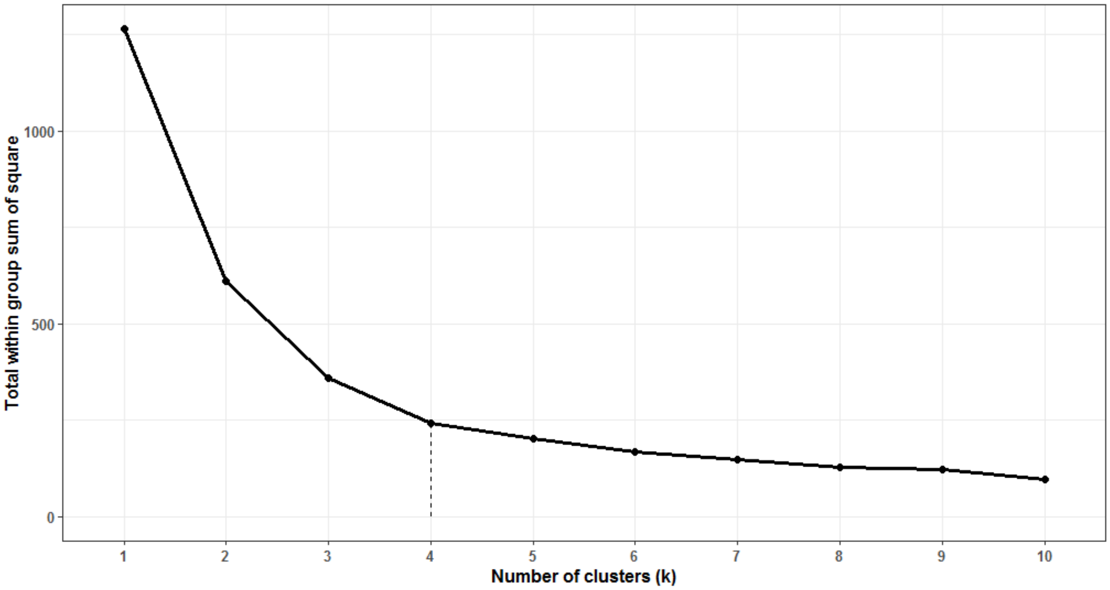

Figure S5.5.1 Total within group sum of squares for *k* = 1 – 10.

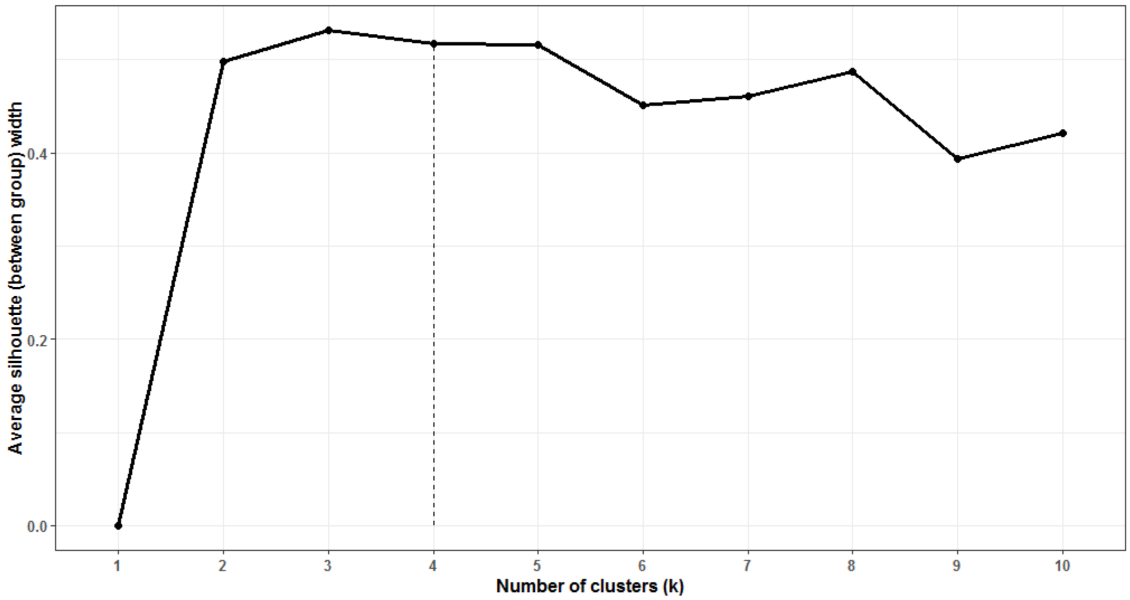

Figure S5.5.2 Total between group sum of squares for *k* = 1 – 10.

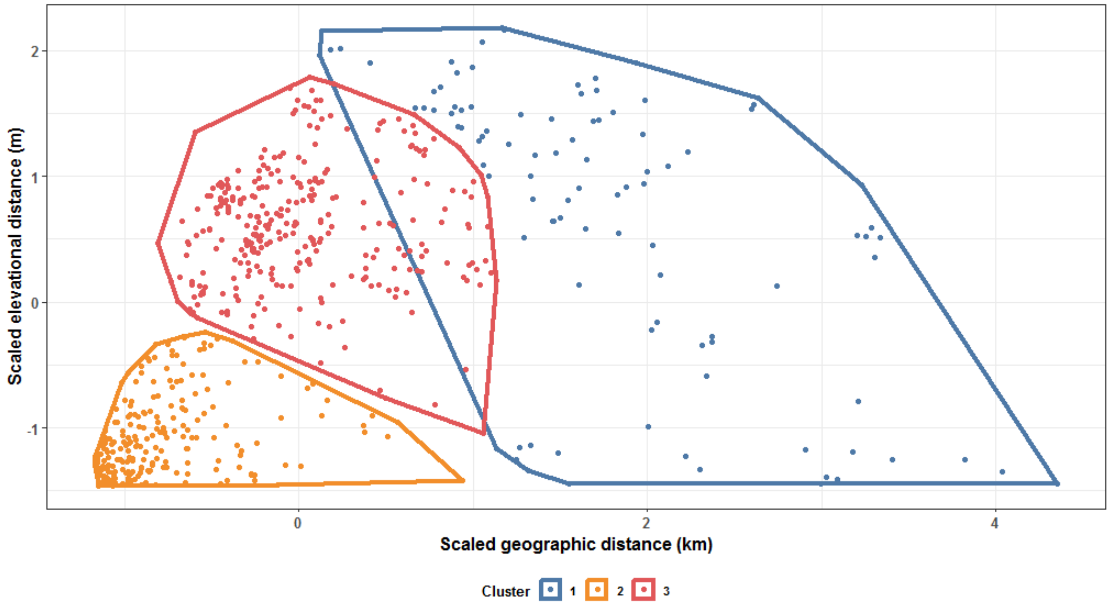

Figure S5.5.3 Group polygons for *k* = 3.

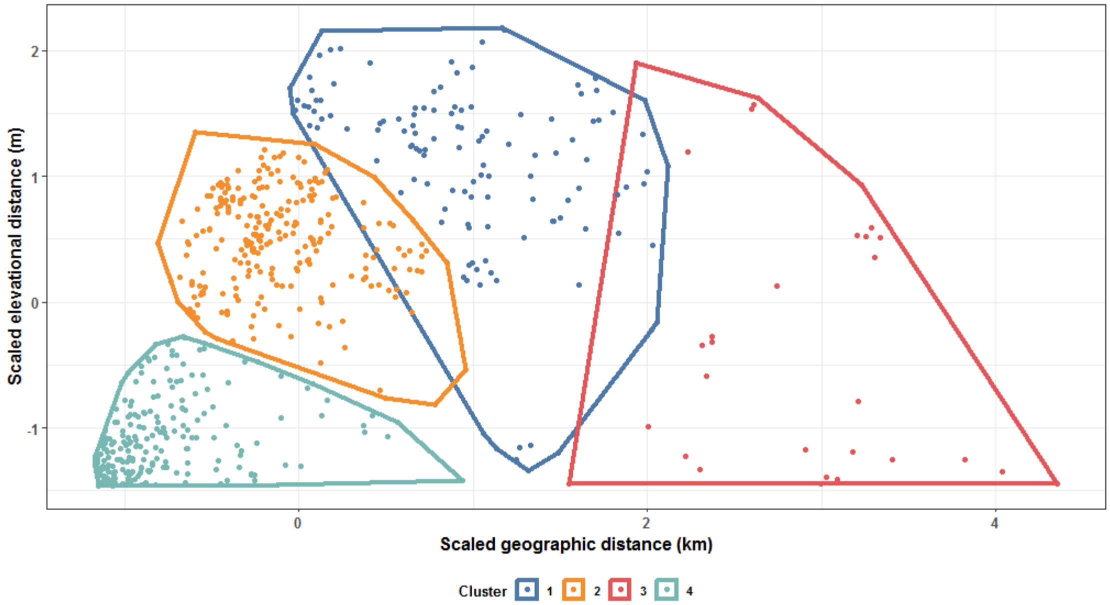

Figure S5.5.4 Group polygons for *k* = 4.

CHAPTER SIX

CONCLUSION TO THE DISSERTATION

Synthesis

The broad-scale and integrated approach of the Greater Yellowstone Area Mountain Ungulate Project and the State-wide Bighorn Sheep Research Initiative have provided an extensive dataset to address applied research questions pertaining to the spatial ecology of bighorn sheep (Ovis canadensis) and mountain goats (Oreamnos americanus) in the northern Rocky Mountains. By working across ecosystems in diverse ecological settings with a wide array of populations, we were able to draw conclusions from comparative studies with broad relevance across the region. Building from an increasingly large dataset as animals were continually instrumented and GPS collars recovered, we addressed progressively more complex topics pertaining to range expansion of introduced mountain goats, niche overlap with native bighorn sheep, and bighorn sheep migratory portfolios.

In Chapter Two, our work detailed the habitat characteristics of mountain goats in the southwest Greater Yellowstone Area (GYA) and their potential expansion throughout the region (Lowrey et al. 2017). Interpreting our results as well as those from other studies with different methodological approaches, there is general agreement that suitable habitats will not limit the expansion of introduced mountain goats (DeVoe et al. 2015, Lowrey et al. 2017). This issue has garnered much attention as the continued colonization of Grand Teton National Park (GTNP) has coincided with a decline in native bighorn sheep, which are now estimated to be equally abundant as mountain goats with minimum counts of around 80 individuals for each species. The bighorn sheep in GTNP are a small and isolated population, and while it is unknown if the decline is linked with mountain goats, the expansion of an introduced species into GTNP has prompted great public interest and highlighted the urgency for a finalized mountain goat management plan for GTNP, which is expected before the end of 2018. Moreover, the suspected source population of mountain goats (GTNP unpublished data) have tested positive for all the major pathogens associated with respiratory disease in mountain ungulates (Lowrey et al. 2018a). Our habitat models from Chapter 2 have been well received by regional managers who have incorporated our findings into the management plan for GTNP, as well as extrapolated habitat models throughout Idaho to assist Idaho Game and Fish with state-wide habitat mapping.

The observed expansion of mountain goats prompted concerns over competition and overlap with native bighorn sheep. In Chapter Three, we employed a niche-based view of habitat and used novel approaches to estimate seasonal niche overlap on shared ranges in the northeast GYA (Lowrey et al. 2018b). While we predicted strong overlap in summer, the large degree of overlap in both seasons was a surprising result. Regional state and federal wildlife agencies have worked diligently to restore bighorn sheep for the last half century and prioritize the wellbeing of native bighorn sheep over introduced mountain goats, especially in bighorn sheep core native ranges, which are a management priority throughout Wyoming. Our work on niche overlap as well as related work on disease (Butler et al. 2017, Lowrey et al. 2018a, Butler et al. In press), has helped to inform decisions pertaining to the management of introduced mountain goats. As of November 2018, the Wyoming Game and Fish commission had approved an unlimited hunting season on mountain goats in the northern Absaroka Mountains. Local biologists are now working to design and implement the new strategy with the expressed intent of limiting mountain goat expansion into native bighorn sheep range and reducing or maintaining densities of mountain goats where the two species are sympatric.

In Chapter Four we expanded beyond the sympatric ranges of bighorn sheep and mountain goats and examined individual variation in bighorn sheep seasonal movement strategies across restored, augmented and native populations within Montana, Wyoming, Idaho, and Colorado (Lowrey et al. In review). Building from recent work that describes migration along a continuum rather than dichotomous behaviors (i.e. resident and migrant), we characterized migratory movements along geographic and elevational gradients, and showed that native herds had longer migrations on average and significantly more variation among individuals (Lowrey et al. In review). This work provided the foundation for Chapter Five which characterized population-level migratory portfolios with respect to categorized migratory behaviors, behavioral placidity, seasonal fidelity, and population spread. The enhanced individual variation in native populations resulted in diverse portfolios of migratory behaviors, including newly documented high elevation long-distance migrants, increased switching rates between migratory behaviors, and sub-populations that were diffusely spread across both summer and winter ranges. In contrast, restored populations had limited individual variation, were largely non-migratory, had less switching between years, and were generally concentrated on both summer and winter ranges. In addition to increasing the abundance and distribution of bighorn sheep on the landscape, we suggest there may be value in simultaneously increasing the diversity of seasonal movement strategies, and in so doing, building resilience to future perturbations and disease, and mirroring the movement portfolios observed in native populations of bighorn sheep.

Directions for Future Research

Within the integrated research approach, future directions are abundant with the opportunity to link spatial ecology with demography, disease, or genetics. Building from the portfolio ideas discussed in Chapters Four and Five, there are two exciting research directions linking spatial ecology and demography. First, testing for demographic portfolio effects through linking migratory diversity with demographic trends is an exciting area of research. As described in anadromous fishes, asynchronous vital rates among subpopulations, although inherently volatile, can result in relatively stable population-level abundances over time when viewed in aggregate (Schindler et al. 2015). While the benefits of a portfolio of migratory behaviors and seasonal ranges is intuitive and supported by theoretical ecology and empirical results from other migratory taxa, we have yet to link migratory diversity in ungulates to demography beyond the dichotomous classifications of partially migratory populations (e.g., Hebblewhite and Merrill 2011). Where available, comparing the correlation between vital-rate time series for different migratory behaviors within a population may help to explain observed abundance through time and identify possible portfolio effects. Where vital rates are not available at the sub-population level, a coefficient of variation of population-level abundance through time may correlate with migratory diversity. For example, populations with a diverse migratory portfolio are expected to have more stable abundances through time, resulting in a lower coefficient of variation relative to populations with a limited migratory portfolio.

Additionally, as discussed in Chapter Five, future efforts to create specific habitat models for each migratory behavior will produce a portfolio of seasonal habitats that can be targeted in restoration efforts. For example, rather than aggregate all migratory behaviors (i.e., high- and low-elevation residents, as well as shot-, mid- and long-distant migrants) to create an ‘average’ population model that will likely produce suboptimum predictions for each behavioral component, generating unique models for each behavior will result in a portfolio of seasonal habitats, each with optimal predictions for the respective behavior. As large aggregates of GPS data continue to reveal a multitude of movement behaviors, such insights can be used to update habitat models to reflect increasingly diverse migratory behaviors. In addition, by comparing seasonal habitats across migratory behaviors, future work could address questions regarding range similarity and the potential benefits (i.e., increased forage or reduced predation) of one behavior over another.

Lastly, although Chapters One and Two have contributed to an increased understanding of the habitat characteristics of mountain goats in the GYA, there is still scant literature describing their migration patterns. Mountain goat movements are difficult to delineate into seasons because of the large degree of individual variation in response to seasonal environmental conditions (Rice 2008), yet a better understanding of migratory and dispersal movements has important implications for disease spread and range expansion. Applying some of the novel tools used for bighorn sheep in Chapters Four and Five to mountain goats would help to better describe their migratory behaviors, distances, and timing.

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