Individual variation creates diverse migratory portfolios in native populations of a mountain ungulate

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Abstract. Ecological theory and empirical studies have demonstrated population-level demographic benefits resulting from a diversity of migratory behaviors with important implications for ecology, conservation, and evolution of migratory organisms. Nevertheless, evaluation of migratory portfolios (i.e., the variation in migratory behaviors across space and time among individuals within populations) has received relatively little attention in migratory ungulates, where research has focused largely on the dichotomous behaviors (e.g., resident and migrant) of partially migratory populations. Using GPS data from 361 female bighorn sheep (*Ovis canadensis*) across 17 (4 restored, 6 augmented, 7 native) populations in Montana and Wyoming, USA, we (1) characterized migratory portfolios based on behavioral and spatial migratory characteristics and (2) evaluated the relative influence of landscape attributes and management histories on migratory diversity. Native populations, which had been extant on the landscape for many generations, had more diverse migratory portfolios, higher behavioral switching rates, reduced seasonal range fidelity, and broad dispersion of individuals across summer and winter ranges. In contrast, restored populations with an abbreviated history on the landscape were largely non-migratory with a narrow portfolio of migratory behaviors, less behavioral switching, higher fidelity to seasonal ranges, and less dispersion on summer and winter ranges. Augmented populations were more variable and contained characteristics of both native and restored populations. Differences in migratory diversity among populations were associated with management histories (e.g., restored, augmented, or native). Landscape characteristics such as the duration and regularity of green-up, human landscape alterations, topography, and snow gradients were not strongly associated with migratory diversity. We suggest a two-pronged approach to restoring migratory portfolios in ungulates that first develops behavior-specific habitat models and then places individuals with known migratory behaviors into unoccupied areas in an effort to bolster migratory portfolios in restored populations, potentially with synergistic benefits associated with variation among individuals and resulting portfolio effects. Management efforts to restore diverse migratory portfolios may increase the abundance, resilience, and long-term viability of ungulate populations.

Key words: bighorn sheep; green wave; individual heterogeneity; migration; migratory diversity; mountain ungulate; Ovis canadensis; portfolio effects; restoration; Yellowstone.

Introduction

Migration is one of the most inspiring aspects of animal behavior and ecology. Advances in GPS technology have enhanced our ability to track animal movements over fine temporal and expansive spatial scales and highlighted broad differences between species and populations, as well as differences among individuals within a population (Dingle and Drake 2007, Cagnacci et al. 2011, Mueller et al. 2011, Singh et al. 2012). Characterizing and understanding individual variation in migratory behaviors has important implications for the ecology, conservation, and evolution of migratory organisms. Consequently, biologists have used numerous metrics to

describe and quantify individual variation within populations and the potential demographic benefits to migratory organisms. For example, asynchronous runs of sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska, USA are an aggregate of several hundred discrete life histories. While the return numbers of any single life history are inherently volatile, the complementary dynamics among life histories when viewed in aggregate can dampen variability and result in more stable growth over time (Schindler et al. 2010), akin to the buffering effects of diversified financial portfolios (Markowitz 1952).

Similar demographic benefits of migratory portfolios have been described for birds. For example, as detailed by Gilroy et al. (2016), avian species with low migratory diversity (i.e., a population with all migrant or all resident individuals) and restricted winter ranges over a small geographic area, were more likely to experience population declines. In contrast, partially migratory species that occupied multiple winter ranges over a large area were more resilient to anthropogenic habitat loss, likely driven by the diverse migratory network and broad population spread resulting in expansive winter ranges (Gilroy et al. 2016). Similarly, the term migratory connectivity has been used to describe the extent to which individuals share seasonal ranges (Webster et al. 2002, Webster and Marra 2005). The diversity in individual ranges associated with weak migratory connectivity, i.e., when individuals from a single summer range migrate to multiple winter ranges, 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).

Research on migratory ungulates has focused largely on classifying the resident and migrant components of partially migratory species with less emphasis on characterizing individual variation among migrants in a population (Hebblewhite and Merrill 2009, Middleton et al. 2013, Eggeman et al. 2016, Rolandsen et al. 2016, Spitz et al. 2018). However, in addition to describing broad variation in migratory behaviors and patterns between populations (Mueller et al. 2011), more recent efforts have described the presence and benefits of individual variation within populations (Cagnacci et al. 2011, Singh et al. 2012). For example, Lowrey et al. (2019) characterized migratory patterns of female bighorn sheep (*Ovis canadensis*) over elevation and geographic continuums and found notable differences in the variation among individuals within restored, augmented, and native populations but did not classify migratory behaviors. In addition, three distinct migratory behaviors (short, moderate, and long-distance) 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). Last, Barker et al. (2018) documented a continuum of individual migratory behaviors from resident to migrant elk

(*Cervus canadensis*) in western Montana, with important implications for nutritional availability, which decreased along the resident–migrant continuum. These studies indicate the importance of broadening the study of individual variation in migratory ungulates. Moreover, implementing metrics used to characterize individual variation in migratory behaviors in other taxa may support our understanding of ungulate demography, disease transmission, inter- and intraspecific competition, and connectivity (Morrison et al. 2016, Sawyer et al. 2016, Barker et al. 2018, Lowrey et al. 2019) and are increasingly relevant as the use of GPS collars continues to result in large data sets over broad spatial scales.

With widespread anthropogenic landscape alteration and degradation resulting in broad-scale reductions in migration (Wilcove and Wikelski 2008), understanding sources of variation in migratory diversity is a critical component to developing and implementing conservation strategies for migratory organisms (Mueller et al. 2011, Martin et al. 2018, Tucker et al. 2018). For example, within the context of migration being a learned behavior in ungulates, the period of time over which a population has developed "knowledge" of the spatial and temporal characteristics of a landscape may influence not only the proportion of migrants in a population (Jesmer et al. 2018), but the diversity of migratory behaviors (Lowrey et al. 2019). Additionally, landscape characteristics such as phenological timing and regularity (Fryxell and Sinclair 1988, Mueller et al. 2011, Merkle et al. 2016, Aikens et al. 2017, Rickbeil et al. 2019), topographic relief (Monteith et al. 2018), winter severity (Hsiung et al. 2018), and anthropogenic factors such as roads, development, and irrigated agriculture (Middleton et al. 2013, Wilson et al. 2016, Tucker et al. 2018, Barker et al. 2019) are known to influence migration in ungulates, but have an unknown association with migratory diversity.

We used 629 seasonal migrations from 361 female bighorn sheep across 17 (4 restored, 6 augmented, 7 native) populations in western Montana and Wyoming, USA to address two research objectives. Our first objective was to characterize population-level migratory portfolios. We used the term migratory portfolio to describe variation in migratory behaviors across space and time among individuals within populations. We predicted native populations, with a long and uninhibited history on the landscape, would have diverse migratory portfolios resulting in a broad distribution of individual ranges (i.e., population spread). In contrast, we expected restored populations, which did not have historical (i.e., pre-extirpation) knowledge of the landscape, to be characterized by a limited migratory portfolio resulting in short distances between individual home ranges and minimal population spread. Recognizing the large losses of the native component that prompted the translocations into augmented populations, we predicted that metrics of individual variation in augmented populations would

mirror restored populations. Our second objective was to understand the relative influence of landscape attributes and management histories (i.e., restored, augmented, or native) on migratory diversity (i.e., the proportion of migratory behaviors within a population). We predicted that a population's management history and therefore the degree of herd knowledge regarding spatial and temporal characteristics of a landscape that had developed through their consistent presence on the landscape would be most strongly associated with migratory diversity.

METHODS

Study areas

Our study populations were distributed broadly across the northern Rocky Mountains in western Montana and Wyoming, USA (Fig. 1), with a continuum of management histories and population characteristics (Table 1). We used winter capture locations and GPS location data to group female bighorn sheep into populations following regional management units (i.e., state hunting districts or national park boundaries; Appendix S1). We defined native populations as those never extirpated or augmented, with a continuous 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 historical bighorn sheep range but reestablished through translocations after population extirpation. The number of translocation events in each restored or augmented population ranged from 1 to 7 (mean = 3.6, SD = 2.19) with a total number of translocated animals ranging from 7 to 165 (mean = 51.8, SD = 68.52, Appendix S2).

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. High elevations contained alpine and sub-alpine flora, mid-elevations were characterized by mixed coniferous forests, and low elevations consisted of a mosaic of shrub communities and agriculture production. All populations were located in areas with a suite of native carnivore species, including black bears (*Ursus americanus*), wolves (*Canis lupus*), coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and Golden Eagles (*Aquila chrysaetos*). Grizzly bears (*Ursus arctos*) were also present, except in the Petty Creek and Lost Creek areas of Montana. Most populations of bighorn sheep were sympatric with one or more additional ungulates, including mule deer, white-tailed deer (*Odocoileus virginianus*), elk, and mountain goats (*Oreamnos americanus*). A subset of the study populations were also described in Lowrey et al. (2019).

Animal capture and data collection

Animal captures 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. Our capture efforts targeted most known winter ranges for each population. Biologists fitted animals with store-on-board or remote-download GPS collars programmed to record locations at varied intervals ranging from one to 13 h. Where the GPS collar manufacturer provided metrics, we censored GPS locations with an HDOP >10 (D'Eon and Delparte 2005) and a horizontal error >100 m (Lowrey et al. 2018).

Seasonal periods and migratory behavior classification

The use of nonlinear 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. 2016, Eggeman et al. 2016). While NSD has been expanded to incorporate metrics of elevation in delineating migratory behavior (Spitz et al. 2017), it is not possible to characterize migratory behaviors with respect to elevation and geographic metrics simultaneously. However, within complex mountain landscapes, elevation and geography can function independently along a migration route, and be equally important in classifying migratory behaviors (Lowrey et al. 2019). As an alternative to the delineation of migratory behaviors using NSD, we implemented *k*-means clustering, one of the most widely used clustering techniques (Jain 2010). Although 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). Following Lowrey et al. (2019), we characterized migratory patterns between core seasonal ranges, which we defined using no more than the first 60 d of GPS locations between 1 January and 10 May for winter, and 1 July and 31 August for summer. Use of data from these core periods ensured individuals would be within the respective seasonal range and accommodated the varied capture schedules across populations. While the 10 May cutoff for winter was relatively late, biologists captured the majority of individuals in January–March. Moreover, the few individuals captured in early May were on known winter ranges prior to spring migration. We censored individual years with fewer than 10 d of monitoring within either core seasonal period.

For each animal-year, we estimated geographic and elevational distance indices between summer and winter ranges, which were based on the GPS locations within the respective season. We characterized geographic distance by measuring the Euclidian distance between seasonal range centroids and characterized elevational
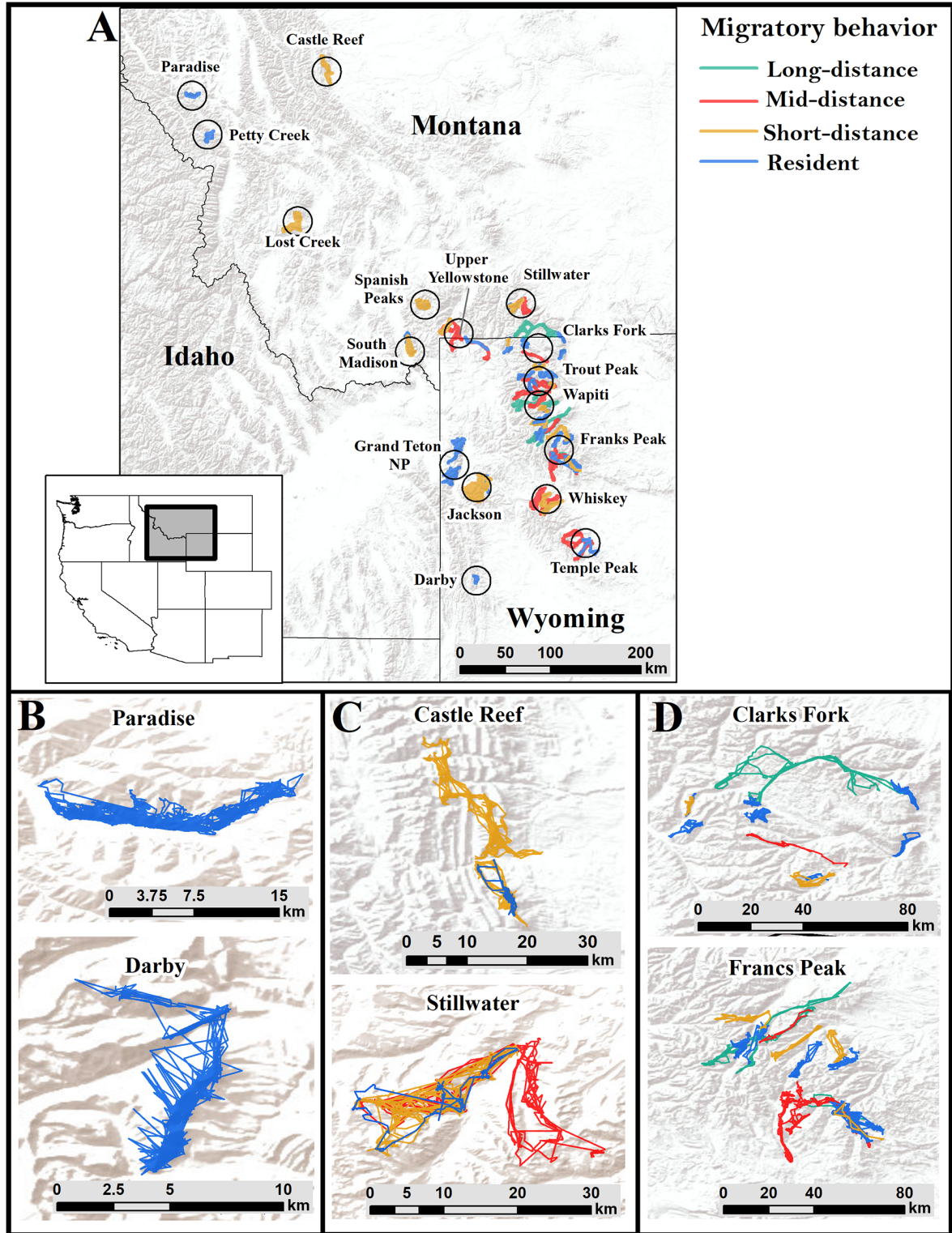
FIG. 1. (A) Locations of the 17 bighorn sheep study populations across Montana and Wyoming, USA, 2008–2018. Population polygons represent the population available extent generated by buffering the centroid by 15.8 km. Paths are shown for long- (green), mid- (red), and short-distance (yellow) migrants. 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 migration, 21 May to 16 June; fall migration, 26 September to 28 October). Panels B–D show two detailed examples of all individuals within two restored, augmented, and native populations, respectively. Note the different scales between panels A–D.

TABLE 1. Management histories and population abundance estimates for 17 populations of bighorn sheep in Montana and Wyoming, USA, 2008–2018.

State and name	Number collared	Management units†	Population estimate‡	Management history
Montana				
South Madison	39	HD-302	280	Augmented
Lost Creek	24	HD-213	100	Restored
Paradise	21	HD-124	352	Restored
Petty Creek	14	HD-203	160	Restored
Spanish Peaks	11	HD-301	172	Augmented
Stillwater	18	HD-501, 502	75	Augmented
Castle Reef	16	HD-422, 424	150	Augmented
Upper Yellowstone	10	HD-305, northwest YNP	320	Native
Clark's Fork	20	HD-1, northeast YNP	600	Native
Darby Mountain	5	HD-24	60	Restored
Franc's Peak	28	HD-5, 22	840	Native
Wyoming				
Grand Teton NP§	23	GTNP, HD-6	100	Native
Jackson	35	HD-7	450	Native
Temple Peak¶	21	–	50–75	Augmented
Trout Peak	16	HD-2	700	Native
Wapiti Ridge	37	HD-3	850	Native
Whiskey Mountain	23	HD-9, 10	850	Native

†The aggregation of management units within each herd unit is further described in Appendix S1.
‡Estimates were provided by area biologists and determined from local knowledge, minimum counts, and recent trends within the five most recent years of the study period.
§Population spans Grand Teton National Park (GTNP; non-hunted) and HD-6 in Wyoming where hunting is allowed.
¶Non-hunted population without a management unit.

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. 2019). While this approach was used by Lowrey et al. (2019) to characterize migratory patterns, they did not classify migratory behaviors. Building from Lowrey et al. (2019) we then used k-means clustering of the elevation and geographic distances to classify migratory behaviors. More specifically, we scaled and centered the distances using the mean and one standard deviation, then assessed the similarity across all animal-years and selected an optimal number of k migratory behaviors (i.e., groups) such that the total within-group sum of squares was minimized and distances between groups were maximized. The k-means approach was advantageous compared with the NSD approach because it did not rely on a pre-defined set of migratory behaviors and enabled us to classify migratory metrics using both elevation and geographic distances simultaneously.

Characterizing migratory portfolios

To meet our first objective of characterizing population-level migratory portfolios, we used two metrics that focused on variation of migratory behaviors within populations and two additional metrics that focused on individual variation across space. With respect to migratory behaviors, we defined migratory diversity as the relative proportion of migratory behaviors (defined using the k-means clustering) in each population (Gilroy et al.

2016). To account for the presence of multiple migrations for some individuals, we randomly selected a single migration from each individual and calculated the relative proportion of behaviors in each population. We repeated this process 500 times and reported the mean proportion (±SE) of each behavior from the 500 iterations as a metric of migratory diversity. Next, because individuals switching between migratory behaviors can further diversify population-level migratory portfolios, we calculated behavioral switching rates for each population as the proportion of individuals with ≥ 2 yr of monitoring that switched behaviors in consecutive years and summarized the behaviors between which switching occurred (Eggeman et al. 2016).

To characterize individual variation across space, we estimated spatial fidelity among years as the Euclidian distance between consecutive seasonal ranges for each individual (i.e. we compared winter range to winter range distance and summer range to summer range distance). We summarized seasonal fidelity separately between years with a consistent migratory behavior and for years in which a behavioral switch occurred. Second, we characterized among-individual seasonal spread (i.e., dispersion) within years by calculating the pairwise distances between all individual seasonal range centroids (Gilroy et al. 2016).

Modeling migratory diversity within populations

To evaluate the importance of landscape characteristics and management histories on migratory diversity

TABLE 2. Candidate model set representing eight hypotheses of the potential influences of management and landscape characteristics on migratory diversity of bighorn sheep populations across Montana and Wyoming, USA, 2008–2018.

Suite and model	Description	Hypothesized relationship with migratory diversity	Citation
Management			
Management history (restored, augmented, native)	Three-level factor specifying the management history of each population	restored − augmented − native +	Lowrey et al. (2019)
Phenology			
Green wave duration	Difference between the day of maximum NDVI amplitude between high- and low-elevation areas	+	Merkle et al. (2016) and Aikens et al. (2017)
Phenology regularity	The mean standard deviation of NDVI amplitude across all pixels from 2001 to 2017	+	Mueller et al. (2011) and Barker et al. (2019)
Topography			
Topographic relief	Range in elevation between the low and high elevation areas	+	Monteith et al. (2018) and Tucker et al. (2018)
Anthropogenic landscape alteration			
Road density	Road density of major federal, state and county roads	−	Wilson et al. (2016) and Tucker et al. (2018)
Urban areas	Amount of developed areas according to National Land Cover database classifications	−	Tucker et al. (2018)
Irrigated agriculture	Amount of agriculture areas according to National Land Cover database classifications	−	Barker et al. (2019)
Climate (snow)			
Snow gradient	The difference in winter snow water equivalent between high and low elevation areas	+	Hsiung et al. (2018)

Note: The + refers to a positive hypothesized relationship while the refers to a negative hypothesized relationship.

within populations, we 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 as defined by *k*-means clustering, and p_i was the proportion of each migratory behavior *i* in a given population (Krebs 1999). The result provided a quantitative measure of the relative diversity of migratory behaviors within each population. We used the result as a response variable in a suite of eight univariate linear models to evaluate the relative strength of association between migratory diversity, landscape characteristics and management histories, which we evaluated using an information criterion (AIC; Table 2; Burnham and Anderson 2002). As a population-level attribute, our sample size of measures of migratory diversity was reduced from the number of individuals to the number of populations (i.e., *n* = 17). Consequently, to evaluate the relative importance of landscape attributes and management histories and their correlation with population-level migratory diversity, we considered only a modest set of simple, non-interactive models with clear hypotheses related to the migratory diversity of populations (Table 2).

We defined a consistent available landscape extent for each population based on observed movement metrics rather than relying on hunt units, which often extend far beyond the known distributions of bighorn sheep, or landscape extents determined from GPS locations (i.e., minimum convex polygons), which would have provided a limited characterization of the "available" landscape for resident populations. More specifically, we buffered the centroids of each study population by 15.8 km. This distance represented the 75% distribution quantile of migration distances among all pooled individuals and provided a consistent delineation of the available landscapes across the continuum of migratory behaviors (Fig. 1; Appendix S3).

Within each population extent, we characterized landscape characteristics hypothesized to influence migratory diversity (Table 2). We used 2016 land cover data from the National Land Cover Database (NLCD; Yang et al. 2018) to quantify the amount of anthropogenic development (including low, medium, and high classifications) and irrigated agriculture (including hay/pasture and cultivated crop classifications). We estimated road density using Montana and Wyoming Department of Transportation geospatial data, which we subset to include only major federal, state, and county roads. We characterized the topographic relief in each study area

using a 30-m digital elevation model to determine the difference between the 90% and 10% quantiles. The 90% and 10% quantiles helped to buffer our calculation of relief from the maximum and minimum elevation values with limited distribution across the landscape. To relate migratory diversity to differences in snow amounts along the elevation gradient, we calculated the mean difference in winter (1 October to 30 April) snow water equivalent (SWE, NOHRSC 2004) between the high and low elevation areas (i.e., ≤10% and ≥90% quantiles, respectively) from 2008 to 2017. This provided a single measure of the difference in SWE across the elevation gradient in each study population.

We characterized landscape phenology using normalized difference vegetation index (NDVI) derived from 8-d surface reflectance images with 250-m resolution from moderate resolution imaging spectroradiometer (MODIS) Terra satellites (MODIS product MOD09Q1). We calculated NDVI values on a per-pixel basis within each study population's extent and through time, and derived NDVI amplitude for each year, which represents the magnitude of change in NDVI over the course of the growing season for each pixel. We characterized the duration of spring green-up (i.e., the green wave; Bischof et al. 2012) along the elevation gradient in each study population following similar methods used to calculate elevational differences in SWE described above. We first derived the day of the year that recorded the maximum NDVI amplitude, then calculated an average day of max NDVI amplitude for the low and high elevation areas, and averaged the difference between the high and low elevation day of max NDVI amplitude among years (Lowrey et al. 2019). Additionally, because the tendency to migrate is linked with not only the presence of green waves, but their predictability (Fryxell 1991), we calculated the variation in green wave timing as the standard deviation in NDVI amplitude for each pixel from a longer time series spanning 2001–2017. We then calculated the mean standard deviation for each study population (Mueller et al. 2011, Barker et al. 2019). To reduce the influence of changes in agriculture irrigation on the variation in NDVI amplitude through time, we excluded low elevation areas ≤10% elevation quantile and areas defined as hay/pasture or cultivated crop according to the 2016 NLCD land cover layer (Yang et al. 2018).

We conducted all analyses in the R environment for statistical computing (R Core Team 2018) in combination with the sf (Pebesma 2018) and raster (Hijmans 2017) packages for spatial analysis, and the factoextra (Kassambara and Mundt 2017) and stats (R Core Team 2018) packages for k-means clustering.

RESULTS

Captures and classified migratory behaviors

We recovered GPS location data from 361 individuals across 17 populations (4 restored, 6 augmented, 7 native) in Montana and Wyoming. From this sample, we characterized 629 migrations with a mean of 1.74 migrations (range 1–4) for each individual. Individuals were monitored for an average of 529 (SD = 298) days. An optimal value of $k = 4$ groups of migratory behaviors provided the best balance between minimizing the within-group distances and maximizing among-group distances (Appendix S4). The four migratory behaviors 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 (Fig. 2). Resident behavior was common across all management histories and tended to occur at low elevations in restored populations and at both high and low elevations in native populations. Short-distance seasonal movements of 5–20 km between seasonal ranges 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. Long-distance migrants were only present in native populations and moved 30–50 km between seasonal ranges. Many of the long-distance migrations were between high-elevation summer and winter ranges with little difference in elevation.

Characterizing migratory portfolios

Our metrics of behavioral diversity contained calculations of migratory diversity and behavioral switching. On average, migratory diversity increased along the continuum from restored to native populations (Fig. 3), with the exception of Grand Teton National Park, which is a native population currently characterized by high-elevation residents. There were 224 individuals with at least two years of monitoring that we included in the characterizations of switching among years. Across all management types, 9% 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. The majority of the observed switches (n = 18, 58%) occurred between resident and migrant behaviors. The remaining switches (n = 13, 42%) were between the short-, mid-, and long-distance migratory behaviors.

Our characterizations of individual variation in space use contained descriptions of fidelity to seasonal ranges and population spread. Across years without a change in migratory behavior, there was generally high fidelity to consecutive seasonal ranges across all management histories with mean elevation and geographic differences of 70 m (SD = 72 m) and 1.4 km (SD = 1.7 km) between ranges, respectively (Fig. 4). Not surprisingly, there was less fidelity during years with a behavioral change. In native and augmented populations, increased switching rates between resident and migratory
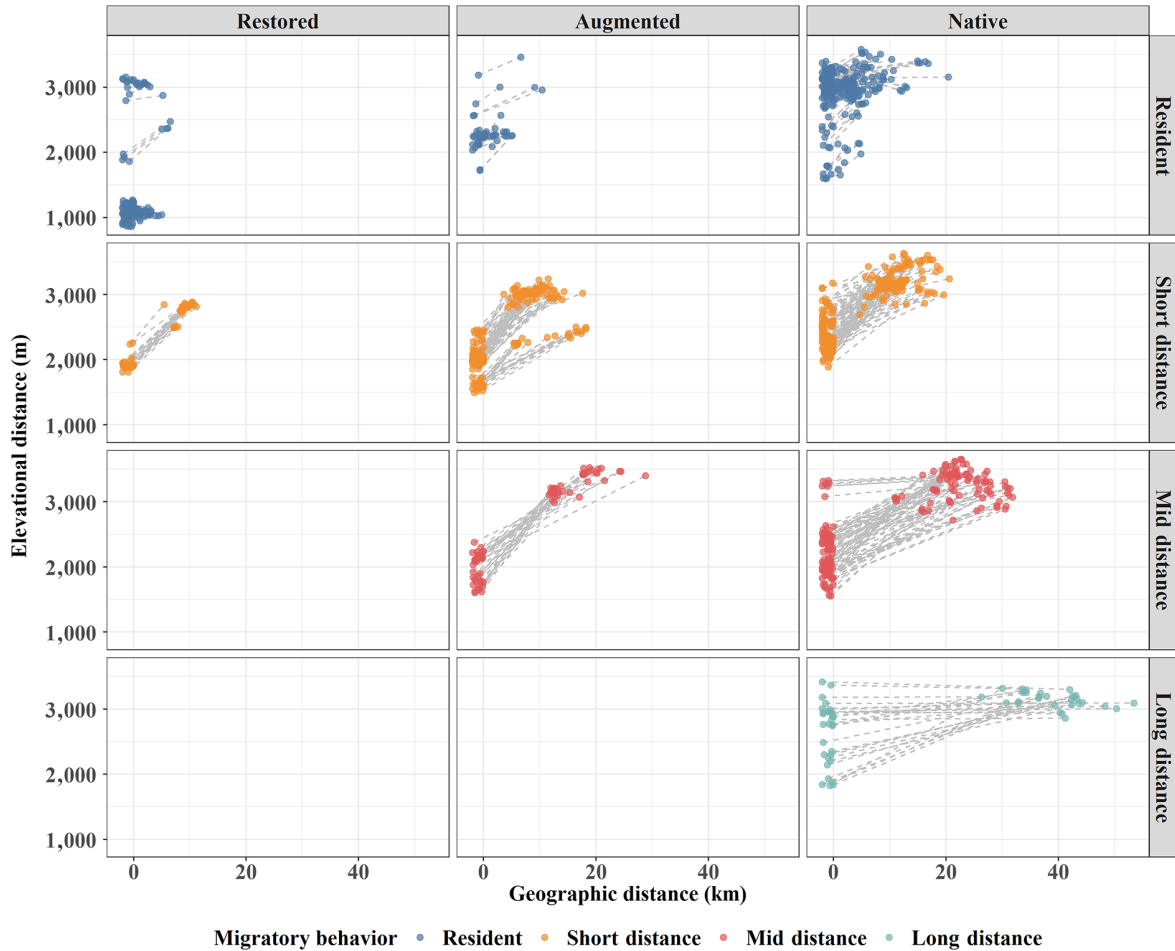
Fig. 2. Seasonal movement portfolios of female bighorn sheep as characterized by elevational and geographic distances between winter and summer home range centroids, in 17 native, augmented, and restored populations Montana and Wyoming, USA 2008–2018. Resident, short-, mid-, and long-distance migratory behaviors are separated by rows, while columns separate native, augmented, and restored populations. 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 (gray lines).

behaviors resulted in an average elevational difference of 182 m (SD = 225 m) and 271 m (SD = 302 m), and an average geographic difference of 4.2 km (SD = 7.5 km) and 3.6 km (SD = 4.7 km), respectively. With respect to population spread, individuals within restored populations were largely concentrated on a single range with an average of <3 km between individual seasonal home ranges centroids (Fig. 5). Augmented populations had slightly more spread with an average of 8.1 and 4.3 km individual home range centroids in summer and winter, respectively. In contrast, native populations were spread diffusely across the landscape with an average 18 and 19.7 km between individual home range centroids in summer and winter, respectively.

Modeling migratory diversity among populations

Our migratory diversity index for populations increased along the continuum from restored to native

populations with average values of 0.11 (SD = 0.22), 0.39 (SD = 0.34), and 0.87 (SD = 0.41) for restored, augmented, and native populations respectively, mirroring the diversity of individual migratory behaviors within each population and management history (Fig. 3). The management history hypothesis had the most support for explaining variation in population-level migratory diversity, with 59% of the model weight and an R^2 value of 0.49. The green wave duration hypothesis ranked second (ΔAIC_c = 3.28, R^2 = 0.25); however, counter to our hypotheses there was a negative relationship between green wave duration and migratory diversity, with populations experiencing shorter green wave duration (i.e., faster green-up rates) being more likely to migrate. Urban areas, irrigated agriculture, and road density all had negative relationships with migratory diversity, but were poorly ranked among the model set and explained little variation in migratory diversity. Similarly, topographic relief, snow gradient, and
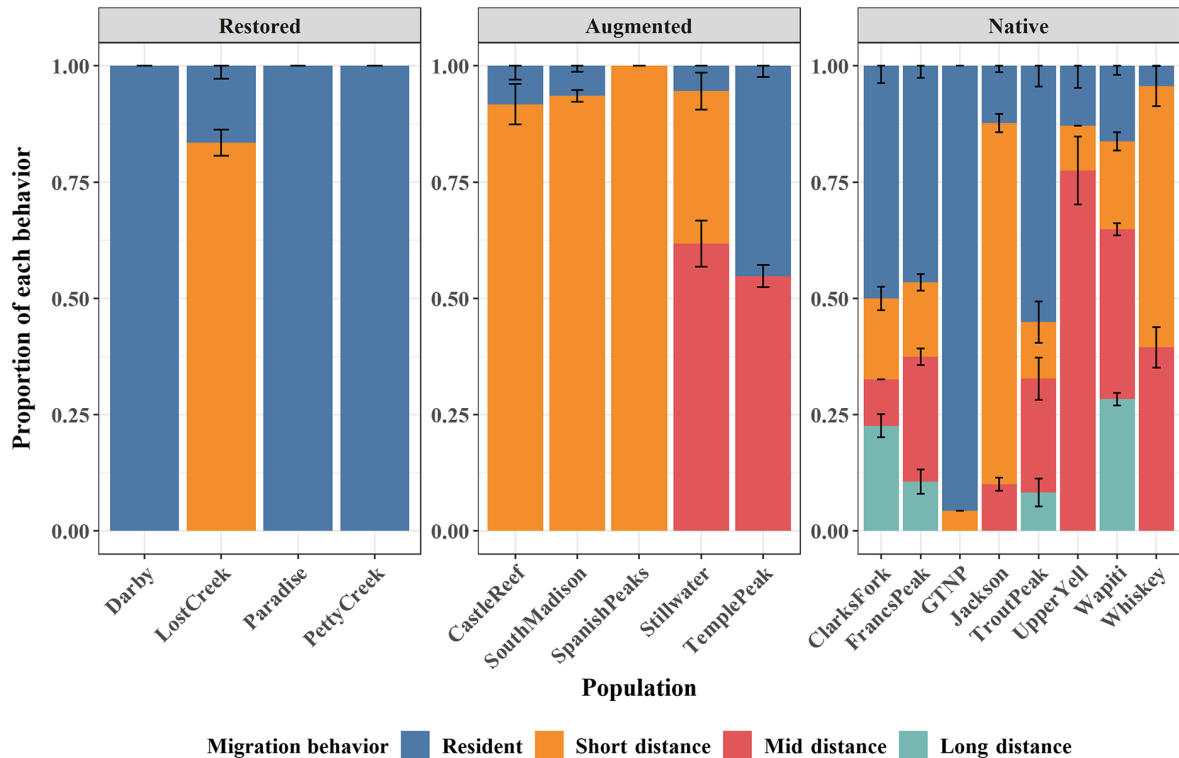
Fig. 3. The mean proportion of resident, short-distance, mid-distance, and long-distance migratory behaviors for restored, augmented, and native bighorn sheep populations, Montana and Wyoming, USA 2008–2018. Standard error bars pertain to the lower behavior (i.e., color) at each boundary.

phenology regularity ranked low and correlated weakly with migratory diversity.

DISCUSSION

The presence of diverse migratory portfolios in native bighorn sheep populations suggests each migratory behavior has sufficient demographic benefits to persist over time. The populations in our study occupied rugged and heterogeneous mountain landscapes where plant phenology is characterized by the complex interaction of both broad- and fine-scale patterns. Rather than develop a single migratory behavior, it appears migratory behaviors of native bighorn sheep reflect the complexity of their mountain environment and exploit multiple landscape patterns across varied spatial scales. Akin to the findings in other migratory taxa (Schindler et al. 2010, Gilroy et al. 2016), we expect that within-population variation in migratory behaviors and spatial patterns may buffer populations from the effects of interannual variation in environmental conditions and other perturbations that may differentially affect the fitness of one migratory behavior vs. another and result in more stable demographic performance over time.

Native populations contained a diverse structure in which a single population was characterized by an aggregation of many groups of animals (i.e., subpopulations),

often with multiple migratory behaviors, that were broadly distributed over the population range. A single high-elevation range could contain residents as well as multiple migrant behaviors in winter, and also serve as the summer range for individuals migrating upward from low-elevation winter ranges. In this way, a single range could be occupied year-round, but by different groups of animals depending on the season and their migratory behaviors. Moreover, the increased switching rates and reduced fidelity to seasonal ranges observed in native populations resulted in migratory portfolio dynamics that changed through time. Indeed, the plasticity of migratory behaviors further diversified the migratory portfolios of native populations. In contrast, restored populations were often characterized by a single seasonal range as indicated by the minimal population spread, with most animals being resident or exhibiting the same migratory behavior, which was consistent among years.

While phenological patterns and tracking green waves of newly emergent vegetation (i.e., surfing the green wave) has recently become a focus of migration studies (Bischof et al. 2012, Merkle et al. 2016, Aikens et al. 2017, Middleton et al. 2018), a diversity of migratory behaviors may aid in the long-term persistence of native populations. In addition to elevational migrants that likely followed green waves of newly emergent vegetation
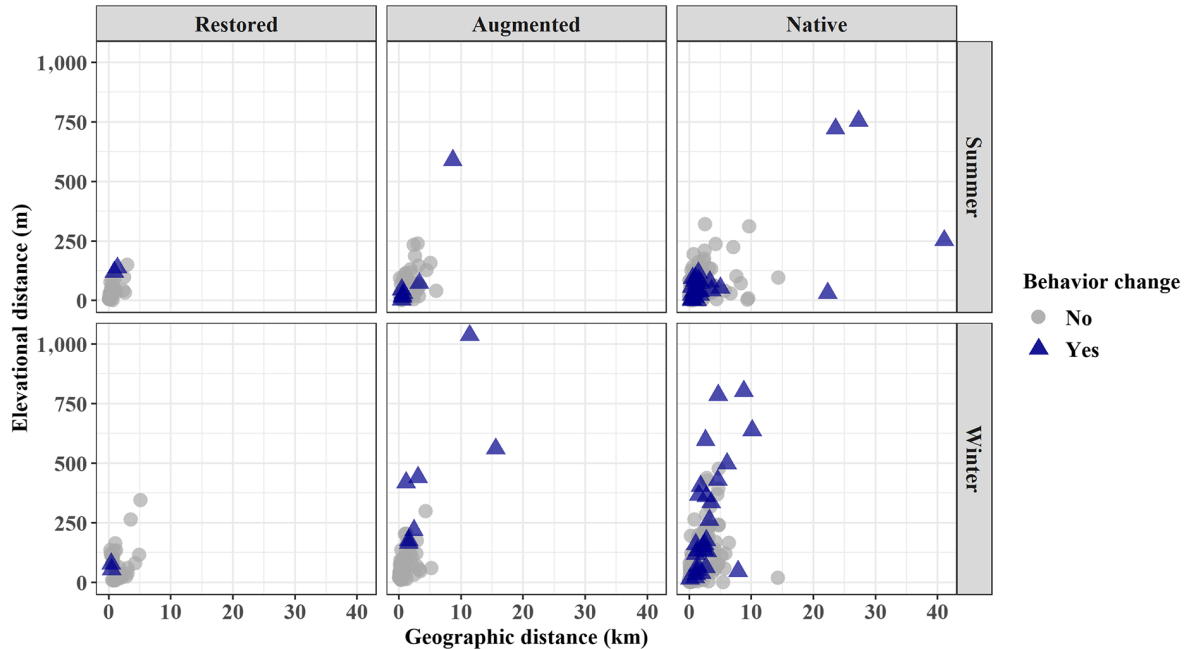
Fig. 4. Individual bighorn sheep fidelity to consecutive seasonal home ranges for restored, augmented, and native populations in Montana and Wyoming, USA, 2008–2018. Summer and winter seasons are shown in the top and bottom row, respectively, while restored, augmented, and native management histories are shown in separate columns. Each point represents the elevation and geographic distance between individuals' consecutive seasonal ranges (i.e., winter range to winter range distance and summer range to summer range distance) for years with consistent migratory behaviors (gray circles) and years where a behavioral switch occurred (blue triangles). The blue triangles close to 0, 0 (i.e., little change in both axes) were from behavioral changes between short-, mid-, or long-distance migrants with little difference in seasonal ranges.
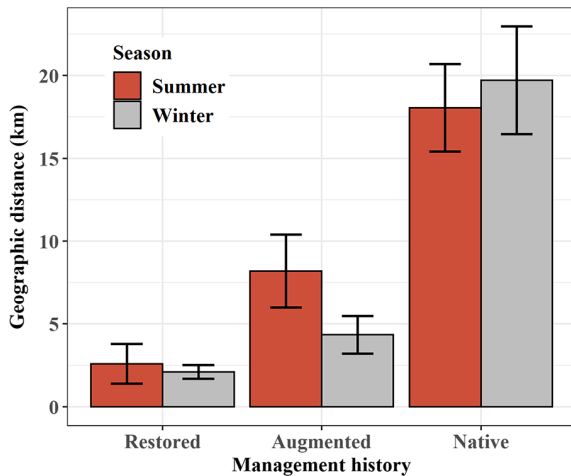

Fig. 5. Bar plots describing the average (±SE) pairwise distances between female bighorn sheep individual home range centroids in summer (red) and winter (gray) seasons for 17 restored, augmented, and native populations in Montana and Wyoming, USA, 2008–2018.

from low-elevation winter ranges to high-elevation summer ranges, native populations also contained high- and low-elevation residents as well as long-distance migrations between two distinct high-elevation ranges with little difference in elevation. The occurrence of multiple migratory behaviors with varied spatial patterns suggests the presence of alternative foraging strategies that are less reliant on phenological patterns along an elevation gradient (Sawyer et al. 2016, Courtemanch et al. 2017). Thus, while surfing the green wave is a nutritionally advantageous strategy for some individuals in some landscapes, our results suggest this strategy is one of several migratory behaviors maintained in native populations with a collective knowledge of the landscape.

Additionally, a diverse migratory portfolio may serve to buffer a population against the effects of disease epizootics. Bighorn sheep are highly vulnerable to pneumonia epizootics that can result in sharp population declines and poor lamb recruitment (Cassirer et al. 2017). Across our study region, recent work has indicated a broad occurrence of respiratory pathogens in all bighorn sheep populations (Butler et al. 2018) and many populations in our study area have suffered pneumonia epizootics (Appendix S2). Moreover, 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 migratory portfolios of native populations may help to minimize pathogen transmission among individuals and reduce the severity of pneumonia epizootics through reducing transmission rates and

lowering densities across multiple seasonal ranges. In contrast, the lack of multiple seasonal ranges and population spread in restored populations creates a population-wide vulnerability to pneumonia epizootics as all or most individuals share a common range and are more densely aggregated.

Disease epizootics that occurred in the past may have affected the contemporary migratory portfolios observed in this study. Similar to other disturbances to migratory populations such as anthropogenic barriers, overhunting, etc., a disease epizootic that disproportionately affects one segment of a population could cause a migratory behavior to disappear. Of the four native populations without long-distance migrations, three (Jackson, Upper Yellowstone, and Whiskey Mountain) had experienced disease epizootics with mortality estimates up to 80 percent of the population (Appendix S2). While the migratory behaviors of the lost population components are unknown, it seems possible that large mortality events could result in the loss of specific migratory behaviors.

Migratory behaviors in ungulates often reflect a trade-off between forage quality and predation risk (Hebblewhite and Merrill 2009, White et al. 2014). As a consequence, predation maybe be an additional factor that can influence migratory diversity. However, the effect of predation is influenced by a number of local attributes, for example the degree of spatial overlap between prey species that share a common predator through apparent competition (DeCesare et al. 2009, Johnson et al. 2013) or the presence of specialist individuals that disproportionately prey on a single species (Festa-Bianchet et al. 2006, Elbroch and Wittmer 2013). These interspecific dynamics are complex and difficult to characterize over broad spatial scales with varied predator guilds, prey composition, and terrain attributes. Moreover, predation can also interact with management histories and have a stronger effect in restored or translocated populations, which are often small and isolated (Berger 1990, Rominger et al. 2004). In these instances, although predation may serve as a proximate cause influencing migratory behaviors, the ultimate cause may be the initial extirpation and subsequent loss of knowledge regarding the spatial and temporal landscape patterns needed to sustain migration (Jesmer et al. 2018, Lowrey et al. 2019). While we recognize predation as an important driver of migration in ungulates, developing a covariate that accurately described the complex local factors influencing population-level predation was not possible within our broad comparative analysis across Montana and Wyoming.

An exception among native populations was Grand Teton National Park, which had a relatively limited migratory portfolio. Bighorn sheep in this population remain on high-elevation, windswept ridgelines for most of the year, but descend 500 m in spring to gain access to forage approximately 30 d before spring green up on the high-elevation ranges (Courtemanch et al. 2017).

While the contemporary population consists of mostly high-elevation residents, historical migration patterns were known to contain elevational migrations between the current year-round ranges and low-elevation winter ranges in the surrounding valleys (Whitfield 1983). Courtemanch et al. (2017) suggested that the remnant bighorn sheep persisted by adopting a high-elevation resident strategy. Nevertheless, within the context of the migratory diversity observed in other native populations throughout the region, an alternative explanation is that both strategies existed historically and that the migrant component was unable to persist with the loss of low elevation winter ranges caused by anthropogenic development. Although likely reduced from historical abundances before the loss of elevational migrations, the historical portfolio of migratory behaviors has allowed the population to persist, albeit with reduced distribution and abundance.

Among restored populations, Darby Mountain in western Wyoming was unique in that resident bighorn sheep occupied high-elevation year-round ranges akin to the resident behaviors observed in native populations. Biologists relocated 35 individuals (20 female, 15 male) from Whiskey Mountain, a partially migratory population, during winter in 1981 to start the Darby Mountain population. Helicopters transported animals in wood crates to historical high-elevation winter ranges (WYGF 1980). Although sourced from low- to mid-elevation ranges, the resident behavior appears to be transferable to high elevations where the population has remained stable, albeit at low abundance (Table 1). The restoration of the Darby Mountain population indicates that alternative approaches to bighorn sheep restoration, including establishing release sites in high-elevation winter ranges, may help to diversify migratory portfolios through adding high-elevation resident populations where they do not currently exist.

Historical population declines are not unique to bighorn sheep. However early management interventions focused on translocation, harvest regulation, and habitat protection that were successful in restoring elk, mule deer, and pronghorn (*Antilocapra americana*) did not afford bighorn sheep comparable levels of recovery. The increases in abundances of other ungulate species may have helped to diversify their migratory portfolios through increases in density (Mysterud et al. 2011). For example, restored populations of elk in southwest Montana that were established in the 1940s have continued to rebound to levels that are above population objectives in many areas and contain a range of migratory behaviors along the resident-migrant continuum (Barker et al. 2018, 2019). While we recognize density can be an important attribute influencing animal migration (Mysterud et al. 2011), we were not able to evaluate the relationship between population-level density and migratory diversity beyond measures of population spread. For example, population-level density (i.e., number of individuals per unit area) had little relevance given the

subpopulation structure of native bighorn sheep populations. Moreover, although native populations were more abundant, they often had larger population units than restored or augmented populations. Although bighorn sheep can occupy a diversity of rugged landscapes, their limited population recovery relative to other ungulates may contribute to, or result from, their reduced behavioral tendency to colonize areas of unoccupied habitat (Geist 1971; Lula et al., *in press*). Nonetheless, the limited success of past management actions to increase bighorn sheep abundance and distribution or bolster migratory diversity through translocations (Lowrey et al. 2019) emphasizes the importance of preserving native systems with intact migratory portfolios where they have persisted.

Our work further describes the presence of migratory portfolios in native bighorn sheep populations and contributes to a growing body of literature emphasizing the importance of the long-term development of knowledge and memory in ungulate migration (Jesmer et al. 2018, Jakopak et al. 2019, Merkle et al. 2019). Building from the theoretical and empirical evidence indicating the benefits of individual variation in migratory behaviors across taxa, we encourage future work that links demography with population-level migratory diversity in ungulates. As migration continues to decline globally, relating migratory portfolios to vital rates is an important next step to help inform the management and conservation of migratory ungulates.

In addition, we suggest incorporating migratory diversity into ungulate restoration through the development of behavior-specific habitat models (e.g., separate migrant and resident models). For example, when multiple migratory behaviors (e.g., low- and high-elevation residents) are included in a single model, the result would represent an average migratory behavior and not accurately predict any single behavior. We suggest a two-pronged approach that first creates behavior-specific habitat models to identify the habitats for each migratory and resident behavior. Secondly, we suggest placing animals with known migratory behaviors into unoccupied habitats identified by the habitat models that match their respective migratory behavior. These steps may serve as an alternative restoration approach to efficiently build diverse migratory portfolios in restored populations, potentially with synergistic benefits associated with variation among individuals and resulting portfolio effects. While individual migratory behaviors may not be known prior to translocation, knowledge of general migrant or resident population classifications can be used to translocate residents to resident habitats and migrants to migrant habitats identified from behavior-specific habitat models (Lowrey et al. 2019). Expanding existing bighorn sheep populations within contiguous mountain ranges helps to mirror the diffuse population spread observed in native herds with reduced chances of introducing novel pathogens, and has shown positive results in Montana (MTFWP 2013, Lula et al., *in press*)

and California (U.S. Fish and Wildlife Service 2007, Johnson et al. 2011). Behavior-specific habitat models could help inform these translocation efforts, especially at high-elevations. Maintenance of a diverse migratory portfolio can functionally increase the forage available to a population through increasing access to and use of more seasonal ranges across the landscape, and help to maintain a more abundant population (Sawyer et al. 2016). Indeed, we assert that identifying and maintaining diverse migratory portfolios may buffer populations from disturbances, resulting in long-term resilience and persistence.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2106/full

Data Availability

Data supporting the findings of this study are available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.80gb5mknj