



Original Research Article

Prioritizing seasonal habitats for comprehensive conservation of a partially migratory species

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ABSTRACT

For conservation reserves to protect habitat to support viable populations, they must be effective in protecting all vital requirements; yet, it is unclear the extent that conservationists need to prioritize seasonal habitats when delineating reserves for partially migratory species. Identifying the similarity among seasonal habitats will assist conservationists in prioritizing specific requirements. Habitat similarity presumably falls along a gradient depending on the degree to which a species is migratory. How migratory a population is may even vary considerably within a species. A partially migratory species of conservation concern is the greater sage-grouse (*Centrocercus urophasianus*), where breeding habitat has been prioritized. Our goal was to determine if a more migratory sage-grouse population required a different habitat conservation strategy to meet its comprehensive requirements than a less migratory population. Firstly, even though our study populations differed in behavior they both reflected what was expected for partially migratory populations with seasonal habitats that on average had a moderate degree of similarity. This suggests that prioritizing the conservation of one seasonal habitat will result in partly protecting other seasonal requirements but not completely meet all requirements. Secondly, for both populations, prioritization of breeding habitat was justified because breeding habitat was most like other seasonal requirements. Thirdly, information specific to each study population was necessary to identify the importance of prioritizing additional seasonal habitat with a greater need to include summer and winter habitat for the more migratory population. We created a cumulative habitat prediction map that depicts comprehensive habitat requirements to help guide reserve delineation. This process can be used to delineate priority areas for conservation reserves for other partially migratory species.

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1. Introduction

Habitat loss and fragmentation from anthropogenic land-use changes is a cause of population decline for many species. Therefore, habitat conservation has been an utmost concern for conservation biologists as the world's human population increases. One factor that can complicate habitat conservation is migration behavior. Species with multiple and unique seasonal habitat requirements can only be adequately protected if all annual requirements meeting their life history needs are addressed. The relevance of conserving all seasonal habitat requirements was made apparent when New-World Nearctic-

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Neotropical birds continued to decline when only breeding habitat was investigated and conserved, while winter habitat was ignored (Robbins et al., 1989; Faaborg et al., 2010). It is now understood that disregard for landscape requirements for a migratory species' breeding range, winter range, or even migratory habitat connecting these seasonal ranges may result in population decline (Sherry and Holmes, 1995; Faaborg et al., 2010). It is also deducible that conservation of landscapes for resident species would meet all the annual requirements because habitat use during different seasons overlaps. However, it is more difficult to determine the level of conservation required to meet the annual habitat requirements of partially migratory species, which fall along a continuum between fully migratory and fully resident (Cagnacci et al., 2011). When delineating conservation reserves for landscape habitat protection, are partially migratory species more like migratory species in that all seasonal requirements must be prioritized, or are they more like resident species in that prioritizing one seasonal requirement is adequate because conserving it will indirectly protect other seasonal requirements? It is argued that the most widespread form of migration is partial migration, so this question is relevant for many species of conservation concern worldwide (Chapman et al., 2011).

One such partially migratory species, the greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse'), proves an excellent example of a species that falls between the opposing ends of the migration behavior spectrum. Not only are sage-grouse a partially migratory species, but individuals and populations exhibit considerable variation in the distances of migrations between seasonal habitats (Fedy et al., 2012). Sage-grouse populations also generally have three distinct seasonal habitat requirements (breeding, summer, and winter) with any combination of one to three seasonal ranges for individuals to meet those requirements (Connelly et al., 2000; Connelly et al., 2011). Therefore, there are also potentially three inter-seasonal migratory habitat requirements. In addition, it is possible for residents and migrants to share any of the three seasonal ranges (Pratt, 2017). The variety of behavior and requirements complicates what seasonal habitats sage-grouse conservation strategies should prioritize.

The sage-grouse is a species of conservation concern because it has undergone significant range contractions and long-term population declines (Schroeder et al., 2004; Western Association of Fish and Wildlife Agencies, 2015) resulting in several petitions for listing under the Endangered Species Act (Stiver, 2011). The unifying factor in these petitions was threats of habitat loss and fragmentation from land surface disturbances (U. S. Fish and Wildlife Service, 2010). Owing to the history of these petitions, management agencies started implementing more intensive habitat conservation actions through regulatory mechanisms that limit the amount and timing of disturbance. One prominent example is the Wyoming Governor's Executive Order for Greater Sage-Grouse Core Area Protection (hereafter Core Area Strategy; State of Wyoming, 2015).

The Core Area Strategy was a method to create conservation reserves designed to protect vital habitat that would support viable populations. For these conservation reserves to fulfill their purpose they must be effective in protecting all vital habitat requirements. Sage-grouse habitat conservation has focused on breeding habitat because of its importance for reproduction and the Core Area Strategy was based on sage-grouse breeding densities (State of Wyoming, 2008; Doherty et al., 2011). The Core Area Strategy treated sage-grouse as a resident species in the sense that conservation of one seasonal requirement should adequately conserve all seasonal requirements. Even though the Core Area Strategy suggests it incorporates non-breeding season habitat (State of Wyoming, 2015) there are concerns whether the strategy captures all annual habitat requirements (Fedy et al., 2012; Smith et al., 2016). There has been increased recent interest in quantifying all the seasonal requirements for sage-grouse, but none have explicitly incorporated migratory habitat which connects seasonal ranges (e.g., Fedy et al., 2012, 2014; Walker et al., 2016).

Our overall goal was to determine if a more migratory sage-grouse population required a different habitat conservation strategy to meet its comprehensive requirements than a less migratory population. To address this goal, we developed three specific objectives. Our first objective was to describe the degree of migratory behavior for our two study populations by documenting the proportion of the population exhibiting migratory behavior and the distances of migration events. Our second objective was to determine if habitat requirements for each of our study populations were more like migratory populations with seasonal habitats that are dissimilar, or if they were more like resident populations with seasonal habitats that are similar to each other. We measured how similar the landscapes were that support the annual requirements for our partially migratory populations by predicting seasonal habitat with resource selection models. We did this for the three main seasons: breeding, summer, and winter. Breeding habitat was sagebrush (*Artemisia* spp.) dominated areas that supported pre-nesting, nesting, and early brood-rearing; summer habitat was more mesic sites that supported late-brood rearing and provided herbaceous forage during drier summer conditions; with winter habitat providing sagebrush forage above snow (Connelly et al., 2011). We also predicted habitat selection for the three inter-seasonal periods: summer transition (breeding to summer range), fall transition (summer to winter range), and spring transition (winter to breeding range). Our third objective was to identify which seasonal habitats conservation actions should prioritize for our two study populations. The seasonal habitat that should first be prioritized is that which is most like all other seasons because conserving landscapes that protect it will also conserve the most habitat for other seasonal requirements. After the first season is prioritized, the next logical step is to identify what habitat requirements are not being met and then prioritize those. Predicted resource selection maps that guide conservation are usually based on habitat use for a single season, but as an outcome of our analysis we created a habitat map depicting the cumulative relative probability of selection for year-long habitat requirements.

2. Methods

2.1. Study areas

Our study was based on observations of sage-grouse from two study areas in the sagebrush-steppe of central Wyoming and the Bighorn Basin of north-central Wyoming and extreme south-central Montana, USA (Fig. 1). The Bighorn Basin study area was a collection of three smaller research sites that represented relatively distinct populations (i.e., no documented mixing of radio-marked grouse) along the eastern and northern edges of the larger Bighorn Basin. Both study areas were composed of Wyoming big sagebrush (*A. tridentata wyomingensis*) at lower elevations and mountain big sagebrush (*A. t. vaseyana*) at higher elevations. Black sagebrush (*A. nova*) was abundant in localized areas. There was a gradient in temperature and precipitation with elevation, especially in the Bighorn Basin (Pratt et al., 2017). Grouse locations in the Bighorn Basin study area ranged in elevation from ~1180 m to ~2880 m and in the Central Wyoming study area ranged from ~1560 m to ~2750 m. Because of the larger range in elevation, the Bighorn Basin varied more in plant community diversity. The sagebrush-steppe ecosystem in the Bighorn Basin occurred at moderate elevations between Gardner's saltbush (*Atriplex gardneri*) desert below and coniferous forest above, squeezed to its narrowest extent along the northeastern edge of the basin coinciding with the location of our research sites. Therefore, our grouse sample in the Bighorn Basin was from smaller, more isolated populations on the edge of its natural distribution (Fig. 1). In contrast, our Central Wyoming sample was from a larger contiguous population. There was little anthropogenic disturbance in both study areas and existing disturbance was localized. However, both study areas have the potential for increased disturbance in the future, namely, bentonite mining in the Bighorn Basin, and uranium mining in Central Wyoming.

2.2. Migration and season classification

We captured female sage-grouse and equipped them with Global Positioning System (GPS) transmitters during 2011–2014 in Bighorn Basin and 2012–2014 in Central Wyoming (see Pratt et al., 2017). Grouse capture and monitoring were approved by University of Wyoming Animal Care and Use Committee (protocols 03142011, 03132011, 20140228JB00065, and 20140128JB0059) and completed under permits from Wyoming Game and Fish Department (Chapter 33 Permits 800 and 801) and Montana Department of Fish, Wildlife and Parks (Scientific Collector's Permits, 2013–072, 2014–037, and 2015–76). We defined a grouse as migratory if it demonstrated use of seasonally-dependent non-overlapping ranges. We delineated

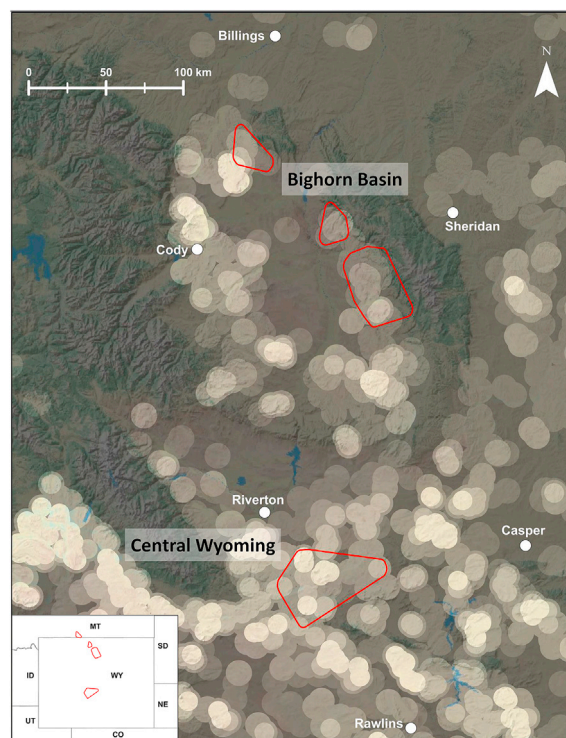


Fig. 1. Minimum convex polygons (red polygons) of greater sage-grouse capture locations in Bighorn Basin and Central Wyoming, USA, 2011–2014. Regions increasingly highlighted represent increasing breeding kernel density (100%, 75%, 50%, and 25%; from Doherty et al., 2011) of sage-grouse. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

seasonal ranges and migration events (see Pratt et al., 2017) based on a 95% utilization distribution calculated, over the life of each individual, from a dynamic Brownian bridge movement model (Kranstauber et al., 2012; move R package, Smolla and Kranstauber, 2016; R version 3.2.4, R Core Team, 2016). For most grouse, there was fidelity in migratory behavior and in the location of seasonal ranges from year to year, but with a few exceptions, we allowed for an annual shift in delineations of seasonal range if they did not overlap with previous years. We uniquely defined seasonal arrival and departure dates for every migratory grouse and each seasonal transition as the threshold between spending more time within a seasonal range than outside of that seasonal range. For example, the departure date for the breeding season was the day a grouse left breeding range and then spent more time away than any return trips back into breeding range. The timing of presence within these seasons is described in Pratt et al. (2017). We then classified grouse locations to the appropriate main season (breeding, summer, winter) if they were between the arrival and departure dates for that season and not part of a migration event. We classified grouse locations to the appropriate inter-seasonal period (summer transition, fall transition, spring transition) if they were outside seasonal range and part of a migration event. We assigned locations of non-migratory grouse to season based on the study area specific mid-point between the median arrival and departure dates of migratory grouse. We calculated distances between seasonal ranges as the Euclidean distance between centers of mass of the seasonal utilization distributions.

2.3. Seasonal resource selection and habitat similarity

To measure seasonal habitat similarity, we first predicted habitat for our study area by measuring population-level resource selection for each season and inter-seasonal period with grouse-use locations compared to available locations (Manly et al., 2002). We pooled grouse-use locations for each study area and defined habitat availability to the extent of the study area (second-order selection; Johnson, 1980). In the Bighorn Basin, we restricted habitat availability to each individual research site. We generated 20 times the number of available locations as seasonal grouse-use locations within our study area extents which we delineated by accumulating 95% utilization distributions for every grouse-season-year. We did not allow available locations to occur in non-habitat (closed canopy, developed, or non-terrestrial land covers; 2011 National Land Cover Database; Homer et al., 2015). This design helped highlight resource selection for one season compared to other seasons by eliminating larger regions of non-habitat. We modeled the relative probability of selection for each season and inter-seasonal period with generalized estimating equations (PROC GENMOD, SAS 9.4, SAS Institute Inc, 2012), by assigning available locations in proportion to use locations, to form clusters and account for repeated observations of the same individual (with independent or compound-symmetric correlation structure; Koper and Manseau, 2009; Fieberg et al., 2010).

We based landscape predictor variables on climate (temperature [PRISM Climate Group, 2016], snow depth [Liston and Elder, 2006]), distance to active leks, topography (compound topographic index [Gessler et al., 1995], heat load index [McCune and Keon, 2002], slope, vector ruggedness measure [Sappington et al., 2007]), and vegetation (see Pratt, 2017 for details). Vegetation metrics included variables of percent cover representing bare ground, herbaceous (annual grass and herbaceous cover), and shrub layers (big sagebrush [*Artemisia tridentata*], non-sagebrush [not *Artemisia* spp.], and total shrub cover). We also utilized shrub height; probability of black sagebrush (*A. nova*) and juniper (*Juniperus* spp.) presence; agriculture, forest, and wetland land cover (Homer et al., 2015); and the soil-adjusted vegetation index (Qi et al., 1994), which represents vegetation 'greenness.' We wanted to be comprehensive, so we included many biologically-meaningful variables, including variables used in other sage-grouse resource selection studies (e.g., Fedy et al., 2014; Smith et al., 2016; Walker et al., 2016). We measured the topographic and vegetation variables (mean, standard deviation, and/or proportion) at multiple spatial scales (circular analysis regions with 0.05, 0.1, 0.2, 0.4, 0.8, 1.6, and 3.2 km radii). Because many of these variables were highly correlated, we implemented principal component analysis to reduce these variables into independent components that explained the environmental variation important to sage-grouse in our study areas. We inspected scree plots, which suggested that approximately nine components were enough to explain much of the variation (~70%) in our landscape predictor variables. We then used all nine components as the explanatory variables in our seasonal resource selection models.

We validated the predictive performance of our seasonal resource selection models using five-fold cross-validation (Johnson et al., 2006). For each season, we randomly created five independent folds by estimating parameter coefficients from 80% of the locations of each individual (Koper and Manseau, 2009). We retained 80% of the locations of each individual, instead of 80% of individuals, because the highly variable number of locations per individual during the transitional seasons would create highly variable sizes in the folds. We then mapped (30-m resolution) the predicted resource selection function based on the retained data into five quantile bins and regressed the observed number of withheld test locations to the expected number in each bin, expecting intercepts = 0, slopes = 1, and high coefficient of determination (r^2) values (Johnson et al., 2006).

To ascertain seasonal habitat similarity, we calculated Hellinger distance (HD) based on all pairwise combinations of seasonal habitat selection maps. The HD measure has been used to compare prediction maps in the field of ecological niche and species distribution modeling (Warren et al., 2008; Wilson, 2011). Before calculating HD , we created habitat prediction rasters (30-m resolution) from our resource selection functions and normalized the cell values for each raster to sum to 1. We rescaled the HD measure to range from 0 (perfect negative correspondence between habitat predictions) to 1 (perfect positive correspondence). We interpreted $HD \geq 0.85$ as both habitats having high similarity, $0.65 \leq HD < 0.85$ as moderately high similarity, $0.35 < HD < 0.65$ as moderate similarity, $0.15 < HD \leq 0.35$ as moderately high dissimilarity, and $HD \leq 0.15$ as high dissimilarity. We also interpreted $HD \leq 0.35$ as suggesting that a habitat conservation strategy required for a migratory

population (i.e., all seasonal requirements must be prioritized) would be necessary. Likewise, we interpreted $HD \geq 0.65$ as suggesting that a habitat conservation strategy for a resident population (i.e., only one seasonal requirement needs to be prioritized) would be adequate. We expected seasonal habitats for a partially migratory population to have HD values close to 0.5 with smaller values suggesting a greater need to prioritize more seasonal requirements. We also interpreted that the main season (breeding, summer, or winter) that had the highest average HD value would be the season that should be prioritized first because conserving it would simultaneously conserve more of the other seasonal requirements. Then, the seasons least like the first prioritized season would be the next seasonal requirements that should be prioritized.

To demonstrate how predicted resource selection maps that guide conservation can be modified to include comprehensive year-long habitat requirements we created a cumulative relative probability of selection map. We first binned each of our predicted seasonal resource selection rasters (30-m resolution) into five quantiles (1–5 from lowest to highest relative probability of selection). We then weighted each season equally by summing the binned selection values for all six seasons. This resulted in a map with possible values from six (low probability of selection for all seasons) to 30 (high probability of selection for all seasons).

3. Results and discussion

3.1. Migration

We utilized 108,523 locations from 81 female grouse for all seasons in the Bighorn Basin (2011–2015) and 55,165 locations from 52 female grouse in Central Wyoming (2012–2015). Our first objective was to describe the degree of migratory behavior for our two study populations. A greater percentage of grouse in the Bighorn Basin were migratory for the summer transition (Bighorn Basin: 79% migratory [$n = 58$]; Central Wyoming: 50% migratory [$n = 24$]), the fall transition (Bighorn Basin: 84% migratory [$n = 49$]; Central Wyoming: 66% migratory [$n = 41$]), and the spring transition (Bighorn Basin: 63% migratory [$n = 43$]; Central Wyoming: 44% migratory [$n = 32$]). Average migration distances were 1.7-times farther in the Bighorn Basin for the summer transition and 1.8-times farther for the fall transition (Table 1). On average, migration distances were larger in Central Wyoming for the spring transition, but the maximum observed distance was substantially larger in the Bighorn Basin (Table 1). The Bighorn Basin population was more migratory, having a greater proportion (~75% on average) of migratory individuals during all three seasons and greater migration distances during two of the seasons. Central Wyoming had on average about 50% of individuals that exhibited migratory behavior between each seasonal range. Partial migration has been argued to develop as a strategy to release populations from density-dependent effects during non-shared seasons (Griswold et al., 2011). Sage-grouse have been shown to demonstrate a wide variety of migration behavior, but partial migration appears to be the norm, at least in Wyoming (Fedy et al., 2012). We did not calculate migration distances in the same manner as Fedy et al. (2012), but an approximate comparison suggests that Bighorn Basin and Central Wyoming populations are near maximum and near average of inter-seasonal distances observed in Wyoming, respectively. Other predominately migratory populations in Wyoming have landscapes more like the Bighorn Basin in elevational gradient, which is conducive for sage-grouse migration (Pratt et al., 2017). Theory suggests that these predominately migratory populations would be larger if the landscape could support a greater proportion of residents (Griswold et al., 2011).

3.2. Seasonal habitat similarity

Our second objective was to develop seasonal habitat predictions using resource selection models to determine whether our sage-grouse study populations had similar seasonal habitats like resident populations or dissimilar habitats like migratory populations. Validation of the ability of the seasonal resource selection models to predict withheld data, by regressing the observed number of withheld test locations to the expected number in each of five quantile bins, included high r^2 values (mean $r^2 = 0.97 \pm 0.005$ SE) and 52 of 60 (87%) of the cross-validations meeting all standards (intercept = 0,

Table 1

Greater sage-grouse migration distances (km; Euclidean distance between centers of mass of seasonal utilization distributions) observed for summer transition (breeding–summer), fall transition (summer–winter), and spring transition (winter–breeding) in Bighorn Basin and Central Wyoming, USA, 2011–2015.

Season	<i>n</i>	Min.	25th quart.	Median	75th quart.	Max.
Study area						
Summer transition						
Bighorn Basin	59	2.5	7.9	13.0	16.8	33.8
Central Wyoming	14	4.6	6.2	7.5	9.9	12.0
Fall transition						
Bighorn Basin	52	4.7	19.1	19.1	25.8	92.3
Central Wyoming	28	5.7	7.8	10.4	15.8	46.7
Spring transition						
Bighorn Basin	35	3.0	7.6	11.4	17.0	85.9
Central Wyoming	17	7.1	9.8	15.6	21.0	40.8

slope = 1; Johnson et al., 2006). The main seasons (breeding, summer, and winter) were less similar in the Bighorn Basin than in Central Wyoming (Table 2). The mean *HD* of all pairwise combinations for the three main seasons was 0.44 (range: 0.35–0.52) suggesting main seasonal habitat had moderate similarity in the Bighorn Basin and 0.70 (range: 0.60–0.76) suggesting habitat had moderately high similarity in Central Wyoming. This was expected because migration behavior should be connecting less similar seasonal habitats. We believe that the Bighorn Basin population was more migratory because of the larger elevational gradient with low-elevation (i.e., warmer and drier) areas suitable for breeding/winter, but not for summer, and high-elevation areas (i.e., colder and wetter) suitable for breeding/summer, but not for winter (Pratt et al., 2017). Summer and winter habitat were the two main seasons most unlike each other for both study areas, which coincided with the fall transition having the greatest proportion of migrants. Summer habitat for sage-grouse can be provided by a variety of plant communities if there is a source of moisture that delays plant desiccation (e.g., riparian, montane sagebrush, wet meadows, and irrigated hayfields or pastures; Klebenow and Gray, 1968; Wallestad, 1971; Fischer et al., 1996; Connelly et al., 2011). Winter habitat occurs in areas where sagebrush provides food and cover in snow (Beck, 1977; Remington and Braun, 1985; Connelly et al., 2000; Connelly et al., 2011). In the Bighorn Basin, there were also areas of stark habitat edges that can provide for one seasonal requirement, but not for multiple seasons, such as agricultural lands (irrigated hayfields and pastures) used during summer. Agricultural lands were frequently used during summer in the Bighorn Basin but were mostly absent from Central Wyoming where breeding and summer habitat were quite similar. The shorter minimum migration distances (Table 1) in the Bighorn Basin further highlights the contrast between seasonal habitats where Bighorn Basin sage-grouse were sometimes selecting seasonal ranges that were separate but in close proximity.

Conversely, migratory habitat was slightly more like the main seasons in the Bighorn Basin than in Central Wyoming (Table 2). The mean *HD* of all pairwise combinations between inter-seasonal periods and the main seasons was 0.54 (range: 0.27–0.77) for Bighorn Basin and 0.48 (range: 0.15–0.66) for Central Wyoming. Migratory habitat in the Bighorn Basin was less unique and it was most like breeding habitat, even for the fall transition, which connects summer and winter range (Table 2). This was also a function of the elevational gradient across the landscape: winter range occurred mostly in lower elevation areas to the southwest, while summer range was often in higher elevations to the northeast, with migrations through breeding habitat in between. In contrast, habitat use during the summer transitional season was most unique from other seasonal habitats in Central Wyoming.

Sixteen of all 30 (53%) pairwise *HD* measures suggested moderate similarity ($0.35 < HD < 0.65$) between seasonal habitat for both populations (10 of 15 [67%] for Bighorn Basin and 6 of 15 [40%] for Central Wyoming; Table 2). Of the remaining 14 pairwise measures they were approximately equally distributed between similar (3 of 15 [20%] for Bighorn Basin and 4 of 15 [27%] for Central Wyoming) and dissimilar values (2 of 15 [13%] for Bighorn Basin and 5 of 15 [33%] for Central Wyoming). These observations were anticipated given that our study populations were partially migratory, neither fully like migratory populations or resident populations; however, on average, the more migratory Bighorn Basin population was comparable to Central Wyoming. Theoretically, a migratory species' seasonal habitats should be dissimilar while a resident species' seasonal habitats should be similar. Having seasonal habitats that are at least moderately similar is desirable for conservation because it is not necessary to prioritize every season when delineating reserves to protect habitat. Therefore, reserve delineations can be based on less information and by conserving requirements for one season, the requirements for other seasons will be partly protected as well. This was the case when the Core Area Strategy used lek locations, which are at the core of breeding range, as the basis for protection (State of Wyoming, 2008; Doherty et al., 2011). Some of our monitored migratory grouse whose breeding and winter ranges were not near each other would still winter in areas near leks.

Though this investigation did not intend to directly evaluate the delineations of the Core Area Strategy, some of our conclusions are consistent with a prior analysis that evaluated Core Area Strategy delineations relative to protecting winter habitat (Smith et al., 2016). One conclusion in Smith et al. (2016) was that core areas associated with smaller populations are less likely to capture winter habitat use. We provide further refinement of this conclusion in that smaller core areas associated with more migratory populations are less likely to capture winter habitat use. In contrast, small core areas delineated for less migratory populations may provide adequate protection. We feel this conclusion can be expanded to include summer habitat for populations that exhibit migratory behavior between breeding and summer range. These observations highlight the need for understanding the movement behavior of local populations when delineating conservation reserves.

Table 2

Hellinger distance representing similarity (ranges from 0 for perfectly dissimilar to 1 for perfectly similar) between greater sage-grouse seasonal habitat predicted from resource selection functions in Bighorn Basin (to upper-right of diagonal) and Central Wyoming (to lower-left of diagonal), USA, 2011–2015.

Season	Breeding	Summer transition	Summer	Fall transition	Winter	Spring transition
				Bighorn Basin		
Breeding		0.52	0.45	0.77	0.52	0.69
Summer transition	0.18		0.57	0.58	0.27	0.44
Summer	0.76	0.25		0.50	0.35	0.37
Fall transition	0.66	0.15	0.62		0.58	0.71
Winter	0.73	0.15	0.60	0.61		0.58
Spring transition	0.64	0.12	0.54	0.58	0.66	
			Central Wyoming			

3.3. Prioritization of seasonal habitat

Our third objective was to identify whether the seasonal habitats that should be prioritized for conservation differed between our more and less migratory populations. Breeding habitat was the main seasonal habitat that was most like all other seasonal habitats in both study areas. The mean *HD* of all combinations with breeding habitat was 0.59 for Bighorn Basin and 0.59 for Central Wyoming (Table 2). Therefore, the habitat conservation strategy that would maximize protecting habitat requirements should prioritize breeding habitat first. We feel that this conclusion is likely applicable to most sage-grouse populations because characteristics of what is suitable for breeding habitat is less restrictive than for either summer or winter (Connelly et al., 2011). Additionally, the characteristics that make habitat suitable during summer (herbaceous forage available during dry months) can contradict the characteristics that make habitat suitable during winter (sagebrush forage available during months with snow) in some landscapes (Pratt et al., 2017). Prioritizing one seasonal requirement may be a justifiable first step for conservation of many partially migratory species because it will be easier to establish reserves based on only one season with a smaller footprint. This also will allow for establishing reserves based on less information. For sage-grouse, this was accomplished by using lek locations, which was the basis of information pertaining to sage-grouse distribution and habitat requirements, as a surrogate when reserves were established in the Core Area Strategy (State of Wyoming, 2008; Doherty et al., 2011).

After breeding habitat is prioritized, the next conservation step is to identify what seasonal habitat requirements are not being met because conservation of breeding habitat would meet these other seasonal needs the least. In the Bighorn Basin, it would be a greater priority to also target conservation of the other main seasons ($HD = 0.45$ between breeding and summer, $HD = 0.52$ between breeding and winter) because they are most unlike breeding habitat. In Central Wyoming, it would be a greater priority to also target transitional habitat ($HD = 0.31$ between breeding and summer transition, $HD = 0.64$ between breeding and spring transition). However, it can be argued that transitional seasonal habitat warrants less priority because it was used by a smaller proportion of the population and it may be less responsible for population change because it was used over a shorter time and supported reproductive activities to a lesser degree than main seasonal habitat (Taylor et al., 2012; Pratt, 2017). Further study of sage-grouse seasonal space use, such as that conducted by Smith et al. (2016), may be warranted for populations where local experts do not have the knowledge to evaluate to what degree current Core Area Strategy delineations meet habitat requirements outside the breeding season.

This analysis assumed equal threats to each season; if one season has a much higher magnitude of threats that would contribute to habitat loss or fragmentation then that season should obviously be prioritized. An additional assumption was that protecting a parcel of land for one season would also protect it for another season. Some conservation actions such as disturbance timing stipulations, which may limit human activity during the breeding season but not during the winter season, were not addressed here (State of Wyoming, 2015).

Our overall goal was to determine if a partially migratory species that exhibited a variety of migratory behavior would require a different strategy to conserve its comprehensive habitat requirements for different populations. Though limited, our observations suggest that is not the case for initial habitat conservation actions that can be implemented range-wide such as prioritizing breeding habitat for sage-grouse. However, local information is required to determine the effectiveness of these initial actions and determine what secondary habitat conservation actions may be required. This conclusion may be true for other partially migratory species of conservation concern if their patterns of migration and habitat use are similar. For conservation reserves to fulfill their intended purpose, which is to protect habitat to support viable populations, they must be effective in protecting all vital requirements. We mapped the cumulative relative probability of selection of our study area landscapes, based on the relative probability of resource use (i.e., raster cells) for all seasons (weighting each season equally), which can be used by conservationists when initially delineating reserves designed to capture the most of the all-year habitat requirements (Fig. 2). When creating a map of comprehensive habitat requirements each season could be weighted based on the proportion of the population using the seasonal habitat, the contribution of each season to population growth, or some other criteria (Pratt, 2017). This process can be used to delineate priority areas for reserves for other partially migratory species of conservation concern. Because sage-grouse require large landscapes to meet multiple seasonal requirements, its conservation is frequently described as an umbrella effect (Rowland et al., 2006; Hanser and Knick, 2011; Gamo et al., 2013; Carlisle et al., 2017). Conservationists delineating habitat conservation reserves that actively address comprehensive, year-long requirements for sage-grouse will be creating a larger umbrella that will protect more species than if only one seasonal requirement is addressed (Carlisle et al., 2018). This would also be the case for many similar species of conservation concern worldwide because partial migration is the most widespread form of migration behavior (Chapman et al., 2011).

4. Conclusion

The Bighorn Basin population had 27–58% more grouse migrating between seasonal ranges and its breeding, summer, and winter seasonal habitats were about 37% less similar than in Central Wyoming. However, its transitional habitats were less unique because most migrations were through breeding range. In contrast, migratory grouse in Central Wyoming during the summer transitional season were using unique areas compared to non-migratory grouse. Even though our study populations differed in behavior they both reflected what was expected for a partially migratory population with seasonal habitats that on average were moderately similar. This suggests that the conservation of one seasonal habitat will result in partly protecting other seasonal requirements but not completely meet all requirements. Comprehensive habitat conservation strategies

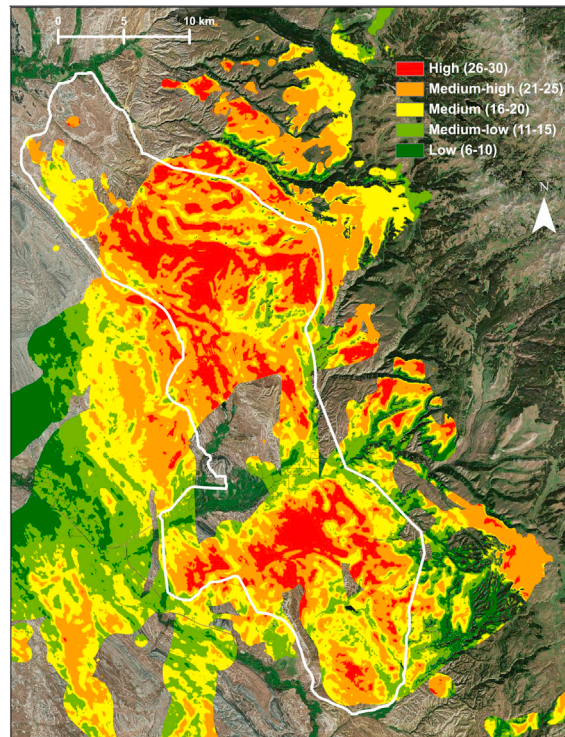


Fig. 2. Example map of cumulative relative probability of selection for year-long (i.e., three main seasons and three transitional seasons) greater sage-grouse habitat requirements for part of the Bighorn Basin study area, USA. Prediction mapped to the extent of available habitat defined by combined grouse utilization distributions. White outline delineates area under current protection through the Core Area Strategy, which was based on breeding habitat.

should take the same initial approach for both our study populations. Conservationists should prioritize breeding habitat first because it was the seasonal habitat that was the most like all other seasons; therefore, conserving landscapes to protect breeding habitat will also protect the most other seasonal requirements. This provides justification for the initial approach taken by the Core Area Strategy. After prioritizing breeding habitat, optimal conservation strategies differed between the two study populations. Because the Bighorn Basin population was more migratory, the main seasonal habitats were less similar; therefore, it is more important to also prioritize areas of summer and winter habitat that are unlike breeding habitat. In Central Wyoming, some migratory habitat was the most unique seasonal habitat.

Strategies to delineate conservation reserves designed to protect vital habitat must meet all seasonal requirements to protect species from habitat loss and fragmentation. If conservation reserves are based on only a specific seasonal requirement they need to identify if they also meet any other seasonal requirements that are different from the prioritized season. For a migratory species, all seasonal requirements should be equally prioritized for protection, while for a resident species, conserving a landscape based on one seasonal requirement will also conserve other seasonal requirements. For partially migratory species, our study highlights the need for local information on behavior and habitat use to identify the amount each seasonal habitat needs to be addressed by conservation. Even though the initial approach of delineating reserves based on breeding range taken by the Core Area Strategy is justified, only knowing the approximate extent of comprehensive habitat requirements based on lek locations without knowing the migratory behavior of the population does not provide any information on whether additional seasonal habitats need to be prioritized.

Declarations of interest

None.

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