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EXECUTIVE SUMMARY

Pratt, Aaron, C., Partial Migration, Habitat Selection, and the Conservation of Greater Sage-Grouse in the Bighorn Basin of Montana and Wyoming, Ph.D., Ecosystem Science and Management, December, 2017.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') has undergone range contractions and population declines largely due to habitat loss, fragmentation, and degradation of remaining habitat. These declines have resulted in unprecedented conservation actions designed to reduce these threats. We investigated partial migration and maladaptive habitat selection, two phenomena that could complicate sage-grouse habitat conservation and hinder the effectiveness of these actions. My dissertation is organized into an Introduction of these concepts, followed by three empirical chapters that provide greater understanding of partial migration and the consequences of habitat selection in sage-grouse populations. My dissertation focused on data collected in the Bighorn Basin as well as in central Wyoming, near Jeffrey City. In Chapter One, our primary objective was to investigate what influenced sage-grouse when deciding to migrate between seasonal ranges and if there was variation in environmental conditions that explained why only some individuals migrated. Sage-grouse interpreted direct indicators of resource quality, especially temperature, when timing movements between seasonal ranges. For summer and fall transitions migratory grouse experienced more migration cues and were likely avoiding more rapid plant desiccation in warmer breeding ranges and avoiding higher snow accumulation in colder summer ranges with more precipitation. Conservationists must prioritize seasonal habitats when delineating

reserves designed to protect partially-migratory species. In Chapter Two, our primary objective was to evaluate whether a more migratory sage-grouse population required a different habitat conservation strategy relative to seasonal requirements than a less migratory population. For both populations, prioritization of breeding habitat was justified because breeding habitat was most like other seasonal requirements and it had the greatest estimated contribution to population change. However, information specific to each 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. Sage-grouse conservation could be hindered by maladaptive habitat selection, where individuals select habitat where their fitness is lower or avoid habitat where they would perform better. Thus, in Chapter Three our objective was to evaluate whether sage-grouse selected habitat relative to habitat quality (survival), and identify any characteristics where they were not matching selection with apparent survival and reproductive costs or benefits. We only measured a positive relationship between habitat selection and survival during winter and we found evidence for a negative selection relationship relative to several habitat characteristics. In this analysis we evaluated whether bentonite mining, an important source of disturbance in our study, was a cause of maladaptive selection. We found evidence that bentonite mining had negative effects on brood and adult survival, but grouse were responding adaptively by avoiding mining during these same seasons. Our research has identified areas that warrant further investigation relative to potential mechanisms of maladaptive habitat selection in sage-grouse or possible secondary benefits of risky habitats.

PARTIAL MIGRATION, HABITAT SELECTION, AND THE CONSERVATION OF GREATER SAGE-GROUSE IN THE BIGHORN BASIN OF MONTANA AND WYOMING

by

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DEDICATION PAGE

I first dedicate my dissertation to the memory of Tom Easterly, Wyoming Game and Fish Department biologist in Greybull who died in 2014. Tom was very instrumental in helping the Bighorn Basin study get off the ground. He worked tirelessly for the wildlife, including sage-grouse, and people of the Bighorn Basin.

Secondly, I dedicate this dissertation to my family. I thank the fellow members of Grace Baptist Church of Greybull and Trinity Baptist Church of Laramie for their spiritual support and for many opportunities to serve. My parents, Duane and Sandra, have always been supportive throughout my educational and professional endeavors. I have special gratitude towards my wife Tamara, and daughters Evelynn, Taylen, and Abigail for being my family, though not all necessarily by choice. Finally, any good thing I may have accomplished was not possible without my Lord and Savior, Jesus Christ.

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INTRODUCTION

Greater Sage-Grouse Conservation

The greater sage-grouse (*Centrocercus urophasianus*) was once commonly found across the sagebrush (*Artemisia* spp.) biome, but has lost approximately 40% of its historic range (Schroeder et al. 2004) and has experienced long-term population declines (0.83% per year decline from 1965–2015; WAFWA 2015). Since 2002, the United States Fish and Wildlife Service (USFWS) has received several petitions to list the greater sage-grouse under the U.S. Endangered Species Act (ESA) of 1973 (Stiver 2011). Subsequently, in 2010, the USFWS finding was that greater sage-grouse were warranted for protection range-wide, but were precluded from ESA listing because other species were under more severe threat of extinction (USFWS 2010). In 2010, the greater sage-grouse was considered warranted for listing because of 2 of 5 potential factors that can qualify a species: (1) present or threatened destruction, modification, or curtailment of habitat or range, and (2) inadequacy of existing regulatory mechanisms (USFWS 2010). The primary threat to sage-grouse habitat loss and fragmentation are from land surface disturbances such as agricultural development (Swenson et al. 1987, Smith et al. 2016a), energy development (Doherty et al. 2008; 2011, Harju et al. 2010, Gregory and Beck 2014, LeBeau et al. 2014, Kirol et al. 2015), residential development (Connelly et al. 2004), livestock grazing (Beck and Mitchell 2000, Boyd et al. 2014), and fire (Connelly et al. 2000a, Blomberg et al. 2012, Lockyer et al. 2015).

Based on previous decisions by USFWS relative to listing greater sage-grouse and the 2010 finding, state and federal agencies across the species range started implementing more intensive habitat monitoring and conservation actions through regulatory mechanisms that limit the amount and timing of disturbance. Due to increased regulatory mechanisms implemented in states after 2010, many of which followed the 2008 Wyoming Governor's Executive Order for Greater Sage-Grouse Core Area Protection (State of Wyoming 2015) as an example, in 2015, the USFWS found that the greater sage-grouse was no longer warranted for listing under the Endangered Species Act; citing that the collection of these plans "reduce threats on approximately 90 percent of the breeding habitat across the species' range (USFWS 2015)." The Wyoming 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 intended purpose, which was to prevent listing of greater sage-grouse as an endangered species, they must be effective in protecting vital sage-grouse habitat requirements. We investigated 2 phenomena that could complicate greater sage-grouse (hereafter, 'sage-grouse') habitat conservation and hinder the effectiveness of these conservation actions: partial migration and maladaptive habitat selection.

Partial Migration

Migration is a behavioral adaptation in animals faced with selecting heterogeneous resources (Dingle and Drake 2007). These resources need to be predictable both spatially and temporally to create a life history strategy of to-and-fro migration (see Dingle and Drake 2007 for definitions of types of migration). The migrant leaves its seasonal range where resource conditions are waning to seek new seasonal ranges where conditions are stable or improving. Examples of motivations for migration include accessing higher forage quality by red deer

(*Cervus elaphus*; Albon and Langvatn 1992) and avoiding severe storms that limit foraging by white-ruffed manakins (*Corapipo altera*; Boyle et al. 2010). The concept of migration includes movement that is undistracted, straightened out, and on a larger scale than normal daily activities (Dingle and Drake 2007). Populations can be partially migratory if there are residents and migrants in the population. Examples of species with populations of partial migrants include elk (*Cervus elaphus*; Hebblewhite and Merrill 2009) and blue tits (*Cyanistes caeruleus*; Nilsson et al. 2010).

In birds there has been a long history of study on latitudinal migrations. Altitudinal migrations also have been documented in several tropical birds (Loiselle and Blake 1991, Johnson and Maclean 1994), in addition to, temperate birds such as American dippers (*Cinclus mexicanus*; Morrissey 2004), dark-eyed juncos (*Junco hyemalis*; Rabenold and Rabenold 1985), dusky grouse (*Dendragapus obscurus*; Cade and Hoffman 1993), mountain chickadees (*Parus gambeli*; Dixon and Gilbert 1964), and spotted owls (*Strix occidentalis*; Laymon 1989). However, little work has been done on the essential factors influencing avian altitudinal migration in temperate regions. Facultative and partial migration appears to be the norm for altitudinal bird migrants (Rabenold and Rabenold 1985, Hahn et al. 2004, Morrissey 2004). The sage-grouse is a temperate species where many populations exhibit altitudinal movements between seasonal ranges (e.g., Dalke et al. 1963, Klebenow and Gray 1968, Fischer et al. 1997, Beck et al. 2006, Caudill et al. 2016). Sage-grouse access different habitats throughout the annual cycle resulting in distinct breeding, summer, and winter seasons (Connelly et al. 2011). Sage-grouse can be nonmigratory, have two unique seasonal ranges (to-and-fro migration), or have three unique seasonal ranges (round-trip migration;

Connelly et al. 2000b). In Chapter One we set out to learn more about what influenced sage-grouse when deciding when to migrate between seasonal ranges and if there was any variation in environmental conditions that explained why only some individuals were migratory.

Species with multiple and unique seasonal habitat requirements cannot be adequately protected if not all annual requirements meeting their life history needs are addressed. The relevancy of conserving all seasonal habitat requirements was made apparent when New-World Nearctic-Neotropical avian migrants continued to decline when only breeding habitat was investigated, while ignoring winter habitat (Robbins et al. 1989, Faaborg et al. 2010). It is now simple to understand that disregard for landscape requirements of migrants for either 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 easily deducible that conservation of landscapes for residents would meet all the annual requirements because habitat use during different seasons overlaps. However, it is less apparent when determining seasonal habitat requirements of partial migrants which fall along a continuum between migrants and residents (Cagnacci et al. 2011). The sage-grouse proves an excellent example of a species that falls within the opposing ends of the migration behavior spectrum. Not only are sage-grouse a partially-migrant species, but individual populations exhibit considerable variation in their migratory strategies (Fedy et al. 2012). This complicates what seasonal habitat sage-grouse conservation strategies should prioritize. In Chapter Two our goal was to evaluate whether a more migratory population required a different habitat conservation strategy, relative to prioritizing seasonal habitat requirements, than a less migratory population.

Habitat Selection

The classic model of animal distribution assumes variability in habitat quality will lead individual animals to choose the best unoccupied site (Pulliam and Danielson 1991). The assumption that individuals will select habitat that maximizes their fitness is reasonable if habitat selection is adaptive, and they are capable of investigating and choosing from a large number of sites when deciding where to live. Stated another way, high-quality habitat, or habitat that supports greater fitness, should have a higher probability of use than lower-quality habitat, or habitat that supports lower fitness. If individuals are to select the highest-quality habitat available then they must identify cues for necessary resources to support successful reproduction and reduce risk of mortality (Williams and Nichols 1984, Kristan 2003). Situations where animals are not able to properly identify these features can result in an ecological trap (first identified by Dwernychuk and Boag 1972). An ecological trap occurs where an individual preferentially selects habitat that reduces its fitness (Robertson and Hutto 2006). More recently, the concept of a perceived trap has been described (Patten and Kelly 2010). Perceived traps are scenarios where an individual preferentially avoids habitat that would increase its fitness. A central concept to these ideas is the misperception by the animal of the habitat features that influence fitness (Schlaepfer et al. 2002, Robertson and Hutto 2006). Animals cannot directly observe the fitness consequences of their selection decisions but can only observe the physical characteristics of their environment. This maladaptive selection of habitat features distinguishes these concepts from source-sink habitats. Source-sink theory does not include a misperception by the animal but an increase in use of sink habitat when source habitat is close to capacity (Pulliam 1988). Populations under source-sink dynamics demonstrate adaptive habitat selection when individuals select high-quality habitat or avoid low-quality habitat (Figure 1A; Patten and Kelly 2010).

Anthropogenic disturbance is expected to be the main cause of ecological and perceptual traps because of its effects on habitat selection and fitness (Remes 2000, Battin 2004, Bock and Jones 2004, Robertson and Hutto 2006, Patten and Kelly 2010). Examples of ecological traps include Bell's sparrows (*Artemisiospiza belli*) that selected undisturbed habitats having lower nest success (Misenhelter and Rotenberry 2000) and indigo buntings (*Passerine cyanea*) attracted to artificial forest edges having lower reproductive success (Weldon and Haddad 2005). Examples of perceptual traps include shorebirds (suborder Charadrii) avoiding nesting near man-made structures even though there was no effect on nest success (Wallander et al. 2006) and lesser prairie-chickens (*Tympanuchus pallidicinctus*) avoiding powerlines and highways where there was no effect on nest success (Pruett et al. 2009). Even though there are many examples of negative impacts from anthropogenic disturbance causing traps there also are cases where environmental features appear to cause traps. Two examples include black-throated sparrows (*Amphispiza bilineata*) nesting more frequently in shrub communities where nest success was lower (Pidgeon et al. 2003) and lesser prairie-chickens avoiding areas of low shrub density where nest success was no different than areas with high shrub density (Patten and Kelly 2010).

Considering previous research summarized above, a population can demonstrate a strong positive selection for higher-quality habitat (Figure 1B). It also could demonstrate a poor or a strong negative selection for higher-quality habitat if it is influenced by ecological or perceptual traps. A population in a source-sink dynamic should remain stable unless the amount of source habitat is very limited (solid line in Figure 1B; Pulliam and Danielson 1991). In contrast, a population under the influence of ecological and perceptual traps will tend toward extinction unless the population can adapt fast enough (dashed line in Figure 1B; Donovan and Thompson 2001, Kokko and Sutherland 2001). Therefore, there are potentially serious consequences for population persistence if the dynamic under which a population operates is not identified. The sage-grouse is already vulnerable from habitat loss and fragmentation so the addition of ecological or perceptual traps would exacerbate its vulnerability. There have been recent studies that have identified possible scenarios where sage-grouse do better or worse in terms of habitat selection and fitness choices (Aldridge and Boyce 2007, Atamian et al. 2010, Dzialak et al. 2011, Smith et al. 2014, Kirol et al. 2015, Gibson et al. 2016). Therefore, the objective of Chapter Three was to evaluate whether sage-grouse selected habitat relative to habitat quality for the combination of the most critical demographic rates and seasonal habitat requirements (i.e., nest, brood, adult breeding, adult summer, and adult winter survival; Connelly et al. 2011, Taylor et al. 2012), and to identify any habitat characteristics that were being selected contrary to the apparent costs or benefits associated with those characteristics.

An economically important source of surface disturbance in our study area was derived from bentonite mining. Wyoming contains 70% of the world’s bentonite clay deposits, and mines in the region where our study was located produce >50% of Wyoming’s annual supply (Wyoming Mining Association 2016). Bentonite clay extraction is carried out by shallow open-pit mining that leads to loss of sagebrush habitat. To date, most bentonite mining has occurred in areas dominated by salt desert shrub communities, but plans call for mining operations to increase in sagebrush communities, which are occupied by sage-grouse. Since anthropogenic disturbance is expected to be the main cause of maladaptive habitat selection and bentonite mining is a growing source of surface disturbance, we specifically evaluated whether mining was a cause of sage-grouse not matching selection with apparent costs or benefits from mining activity in Chapter Three.

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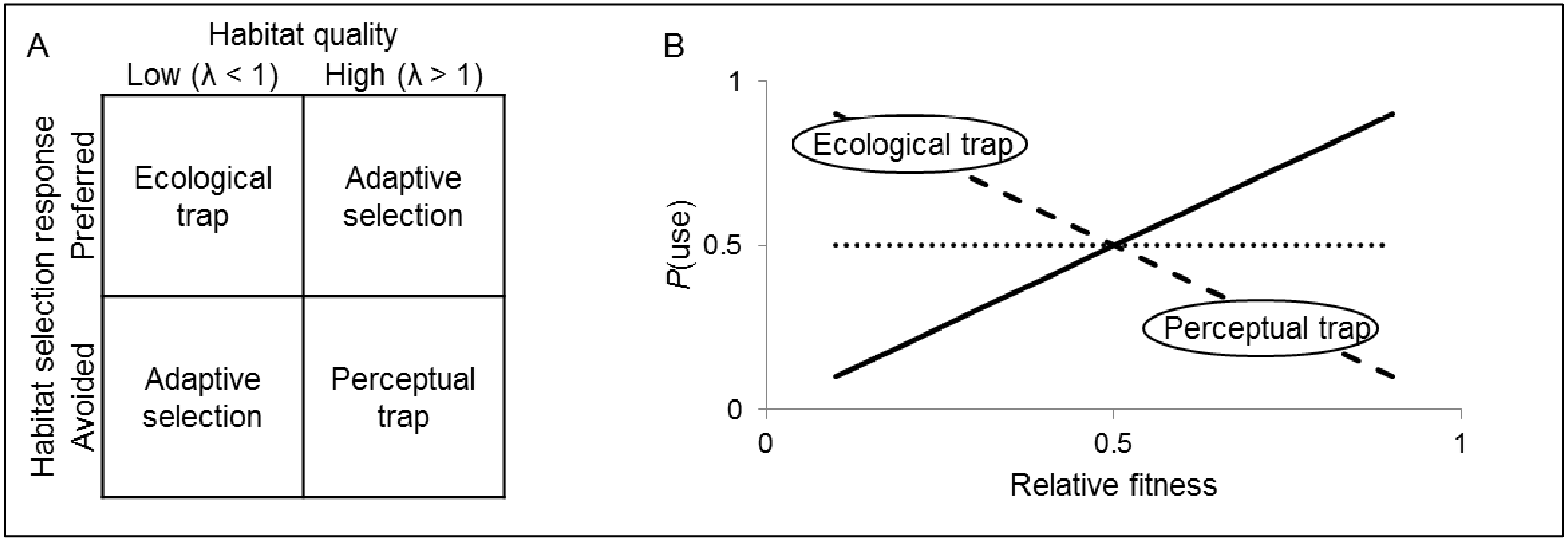

Figure 1. (A) Conceptual diagram of scenarios of habitat selection relative to quality resulting in adaptive selection, ecological traps, and perceptual traps (Patten and Kelly 2010). (B) Populations can represent a strong positive ability (solid line), no ability (dotted line), or strong negative ability (dashed line) to match selection to fitness.

CHAPTER ONE

Environmental Cues Used by Greater Sage-Grouse to Initiate Altitudinal Migration

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ABSTRACT

Migration is a behavioral strategy to access resources that change across a landscape. Animals must ultimately interpret cues to properly time movements that match changing resource quality. Many animals do this by responding primarily to indirect indicators of resource quality such as an internal biological clock or photoperiod. Others are heavily dependent on more direct indicators such as weather or plant phenology. Timing of movement also can be modified by factors specific to individuals. We used time-to-event models for Greater Sage-Grouse (*Centrocercus urophasianus*) to investigate whether an altitudinal avian migrant was influenced by direct indicators of resource quality when timing migration, and whether timing was influenced by individual characteristics, during the spring (winter to breeding range), summer (breeding to summer range), and fall (summer to winter range) transitional seasons. Greater Sage-Grouse interpreted direct indicators of resource quality, especially temperature,

when timing movements between seasonal ranges. Timing was also dependent on individual characteristics including location, reproductive status, and habitat use. After we identified which migration cues were important, we evaluated if migratory and non-migratory individuals were experiencing similar environmental conditions, which may partly explain why there are different behaviors in a partially-migrant population. For the summer and fall transitions, migratory grouse experienced more stimulatory migration cues because of differences in elevation of seasonal ranges. Migratory birds were likely avoiding more rapid plant desiccation in warmer breeding ranges and avoiding higher snow accumulation in colder summer ranges with more precipitation. Altitudinal migrants are likely to use direct indicator cues because they have great utility when migration distances are relatively short. In addition, landscapes with altitudinal migrants have sharp environmental gradients creating conditions conducive for partially-migratory behavior in a population.

INTRODUCTION

Migration is a behavioral adaptation used by many animals when faced with selecting heterogeneous resources (Dingle and Drake 2007). Resources need to be predictable both spatially and temporally to create a life history strategy of annual to-and-fro or round-trip migration (see Dingle and Drake 2007 for definitions of types of migration). Migrants leave their seasonal range where resource conditions are usually waning to seek new seasonal ranges where conditions are stable or improving. Migrating individuals must ultimately interpret internal or environmental cues to initiate movements that will properly time arrival on stopover sites or the next season’s range. Mismatching arrival and optimal resource conditions could result in negative fitness consequences such as reduced survival or reproductive success (McNamara et al. 2011). Some species, such as many mid- to long-distance latitudinal migrants, use internal biological clocks (circannual rhythms) and/or photoperiod to initiate migratory movements (e.g., Gwinner 1996, Meunier et al. 2008). Both internal biological clocks and photoperiod should be relatively easy for an individual to interpret because of no yearly variation in the cue; however, they will not consistently be well correlated with changes in the timing of resource quality on the next season's range, which can have significant yearly variation (Bradshaw and Holzapfel 2007). Therefore, internal biological clocks and photoperiod are deemed indirect indicators of resource quality. Other species, such as mule deer (*Odocoileus hemionus*), an altitudinal migrant, also use more direct indicators of resource quality such as weather or plant phenology (Monteith et al. 2011). Direct indicators can be useful if they reflect changes in the environment of the current range that are consistent with changes occurring on the next season's range. However, direct indicators may be more difficult to interpret if they vary considerably from day to day. Thus, the utility of migration timing cues can depend on how interpretable they are and how well they track environmental changes of destinations. Though research has been done on latitudinal avian migrants and non-avian altitudinal migrants, little work has been conducted on altitudinal avian seasonal migrations (but see Hahn et al. 2004, Boyle et al. 2010, and Boyle 2011).

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') is a temperate species where many populations exhibit altitudinal movements between seasonal ranges (e.g., Dalke et al. 1963, Klebenow and Gray 1968, Fischer et al. 1997, Beck et al.

2006, Caudill et al. 2016), as well as, at least one population with relatively short-distance latitudinal migrations (Tack et al. 2012, Smith 2013). Sage-grouse access different habitats throughout the annual cycle resulting in distinct breeding, summer, and winter seasons (Connelly et al. 2011). Sage-grouse can be non-migratory, have 2 unique seasonal ranges (to-and-fro migration), or have 3 unique seasonal ranges (round-trip migration; Connelly et al. 2000). Breeding habitat generally includes large areas of sagebrush-dominated (*Artemisia* spp.) plant communities in the vicinity of leks that also include an herbaceous layer (Holloran 1999, Connelly et al. 2000, Holloran and Anderson 2005, Hagen et al. 2007, Connelly et al. 2011). Summer habitat can include a wide-variety of plant communities within sagebrush-dominated landscapes that have areas with a greater source of moisture that keeps plants from desiccating (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 sagebrush-dominated plant communities, where sagebrush plants provide food and cover, particularly in areas where tall sagebrush or topography permit sagebrush to extend above snow (Beck 1977, Remington and Braun 1985, Connelly et al. 2000, Connelly et al. 2011). Seasonal movements for sage-grouse are presumed to be tied to forage quality and availability. Sage-grouse appear to depart their breeding range because of decreased forage quality when plants desiccate, depart their summer range because of decreased forage quantity when snow limits availability, and depart their winter range to return to breeding range under favorable conditions (i.e. spring green-up; Dalke et al. 1963, Berry and Eng 1985, Dunn and Braun 1986, Connelly et al. 1988, Fischer et al. 1996).

Timing of migration also has been shown to be influenced by individual characteristics such as reproductive status or distance of migration events (Yong et al. 1998, Mitrus 2007, Monteith et al. 2011, Lendrum et al. 2013). For example, an individual with dependent young offspring may delay migration (Schroeder and Braun 1993, Fischer et al. 1996), or those that travel farther may advance migration timing. Our first objective was to evaluate whether Greater Sage-Grouse were influenced by direct indicators of resource quality and whether they also were influenced by individual characteristics when timing migration during the spring (winter to breeding range), summer (breeding to summer range), and fall (summer to winter range) transitional seasons. We thus examined 3 hypotheses that represented: H_1) grouse only using indirect indicators of resource quality, H_2) grouse using direct indicators of resource quality, and H_3) grouse using direct indicators and influenced by individual characteristics. Altitudinal migrations are shorter than mid- to long-range latitudinal migrations and environmental changes at seasonal ranges closer together are more likely to be correlated (Tombre et al. 2008); therefore, we predicted sage-grouse would use direct indicators of resource quality. For sage-grouse, distances travelled are likely short enough that correlated environmental changes between seasonal ranges will provide added utility over the easily-interpretable nature of indirect indicators of resource quality. This is consistent with research that determined summer and fall movements of sage-grouse were influenced by vegetal moisture and precipitation, respectively (Fischer et al. 1996, Caudill et al. 2016). We built on this research by completing a more precise and comprehensive analysis investigating all seasons with more variables and with daily observations.

Partial migration, where some individuals in a population are migratory, has been argued to be the most widespread form of migration found in all major taxa, including sage-grouse (Chapman et al. 2011, Fedy et al. 2012). A popular question is why only some of the individuals are migratory, which has been explained in 2 ways. First, migration may be condition-dependent, based on age, sex, physical condition, or dominance. Chapman et al. (2011) contend that the bulk of the documented evidence for partial migration is from species with condition-dependent migration. The second possibility is that there are differences in behavior amongst individuals that are determined through their genetic make-up or learned behaviors during ontogeny (Sweanor and Sandegren 1988, Pulido et al. 1996, Nelson 1998). The latter seems more likely with sage-grouse because of consistency in behavior for individuals from year to year (Berry and Eng 1985). What is not frequently addressed is the landscape context that these individuals are in; specifically, what environmental changes they are exposed to. This is not necessarily mutually exclusive of the 2 proposed answers but could add qualification to them. The variation in environmental conditions individuals are exposed to may influence whether they exhibit migratory behavior (Cagnacci et al. 2011). Thus, our second objective, after identifying which migration cues sage-grouse use, was to determine whether migratory and non-migratory individuals experienced different environmental conditions that could explain variation in their behavior. Because migratory and non-migratory individuals in our study population were intermixed spatially we predicted that they would experience the same environmental changes.

METHODS

Study Area

We obtained field data from 2 study areas located across sagebrush-steppe landscapes (Knight et al. 2014) of central Wyoming and the Bighorn Basin of north-central Wyoming and extreme south-central Montana (Figure 1). Both areas were composed of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) at lower elevations with mountain big sagebrush (*A. t. vaseyana*) occurring at higher elevations. Black sagebrush (*A. nova*) was abundant in localized areas.

Bighorn Basin. The 30-year (1981–2010) normal average annual precipitation and temperature were 31 cm and 7.0 °C, respectively (PRISM Climate Group 2016). There was a strong gradient in temperature and precipitation with elevation (Figure 2). At low elevations the sagebrush-steppe transitioned to Gardner's saltbush (*Atriplex gardneri*) desert and at high elevations it transitioned to coniferous forest. The Bighorn Basin study area was further split into 3 research sites that represented relatively distinct populations (i.e. no documented mixing of radio-tagged grouse), topographies, and available summer habitat (Figure 1). The Carbon site (45.1°N, 108.7°W) ranged in elevation from ~1,210 m to ~2,660 m. Summer habitat included riparian areas and irrigated hayfields/pastures at lower elevations and high-elevation montane meadows. Elevation at the Shell site (44.7°N, 108.0°W) was ~1,220 m to ~1,940 m. Summer habitat included irrigated hayfields/pastures and relatively low-elevation montane sagebrush. Hyattville (44.2°N, 107.7°W) ranged in elevation from ~1,180 m to ~2,880 m and summer habitat included irrigated hayfields/pastures and mid- to high-elevation montane sagebrush.

Central Wyoming. The Central Wyoming study area (42.6°N, 107.9°W) varied less in elevation (~1,560 m to ~2,750 m) and vegetation diversity compared to the Bighorn Basin study area. Average annual 30-year normal precipitation and temperature were 26 cm and 6.1 °C, respectively (Prism Climate Group 2016). Summer habitat included riparian areas and mid-elevation montane sagebrush.

Data Collection

Sage-grouse were captured by spotlighting and hoop netting (Giesen et al. 1982, Wakkinen et al. 1992) near leks during spring 2011–2014 in Shell and Hyattville, 2012–2014 in Central Wyoming, and 2013 and 2014 in Carbon. Additional grouse were located and captured during summer at night-roosting locations of previously tagged birds. Grouse were tagged with Global Positioning System (GPS) equipped Platform Transmitter Terminals (22-g Solar Argos/GPS PTT-100 [~ 32 g with harness; Microwave Telemetry, Columbia, Maryland, USA] or Model 22 GPS PTT [North Star Science and Technology, King George, Virginia, USA]). Transmitters were rump-mounted, solar-powered, and uploaded GPS locations (± ~20-m error) to satellites used by the Argos system (CLS America, Largo, Maryland, USA) every 3 days. They were programmed to acquire 3 locations per day from November 1–March 14 (at 0900, 1200, and 1500), 4 locations per day from March 15–April 30 and August 25–October 30 (at 0700, 1000, 1300, 1600), and 5 locations per day from May 1–August 24 (at 0600, 0900, 1200, 1500, 1800). This schedule included locations on a 3-hour interval during daytime hours with first locations recorded at about 1–1.5 hours after sunrise to about 2 hours before sunset. Transmitters also were programmed to include a location at midnight (2400).

Migration Identification

We defined a grouse as migratory if it demonstrated use of seasonally-dependent non-overlapping ranges. We believe this definition encapsulates the 2 most important aspects of migration outlined in Dingle and Drake (2007), though we propose sage-grouse as an excellent example of how migratory and resident behavior fall along a continuous gradient (Cagnacci et al. 2011, Fedy et al. 2012). Non-overlapping ranges represented infrequent movements on a greater spatial scale connecting distinct areas of frequent, smaller scale movements termed ‘station-keeping’ activities. In addition, the use of these ranges corresponded with the periodicity of seasonal habitat use on the annual cycle, which is one of the longest timescales experienced by an animal. We identified seasonal ranges using a combination of contour levels of a utilization distribution and by calculating displacement. We calculated a 95% utilization level to identify and delineate large concentrations of use, for the lifespan of each individual, from a dynamic Brownian bridge movement model with a moving window size of 9 locations and a margin of 3 locations (move R package, R version 3.2.4, R Core Team 2016; Kranstauber et al. 2012). We evaluated several different combinations of window sizes and margins and all produced similar results for the extent of the 95% contour level. This combination was reasonable given our location fix rate relative to the type of changes in movement we could detect. We evaluated different contour levels relative to their ability to distinguish seasonal ranges. Contour levels above 95% tended to include all grouse locations, even for those that were obviously migratory, while contour levels below 95% created too many polygons. In 24% of instances, we used a 90% contour level if the only grouse locations included within the 95% level and not the 90% level were initiations or completions of migration events. To guide determining whether non-overlapping polygons delineated by the utilization distribution were seasonally dependent we visually inspected a plot of net-squared displacement (adehabitatLT R package; Bunnefeld et al. 2011) looking for characteristic 'plateaus' (i.e. displacement was larger between seasonal ranges than within seasonal ranges). Breeding range, as defined for females, was focused around the concentration of locations from the pre-egg-laying, nesting, and early-brood-rearing periods.

A migration initiation event was recorded on the day a grouse left the extent of its current seasonal range and met at least 1 of 2 criteria: 1) approached closer to the next seasonal range than its current seasonal range, or 2) moved in the direction of its next seasonal range (i.e. distance to next seasonal range was less than any portion of its current seasonal range) and did not return for >1 day. Under this definition an individual could have multiple events for each season-year. We included all departure events because we presumed that grouse were deciding when to leave based on conditions of the current range, but could ultimately decide to return after acquiring additional information of conditions along the migration route or at the next seasonal range. Once an individual was spending more time inside the next seasonal range than outside, it was considered no longer able to initiate migration even if it did happen to make a return trip into its first seasonal range. If there were continuous missed location fixes for >72 hours, then observations on that bird were censored after the last known day it remained completely in a seasonal range. The start and end of a transitional season was the earliest and latest ordinal date that migration events were observed, respectively. An individual was considered available for migration if the date was within the defined transitional season, the bird was present in seasonal range, and it was not incubating a nest. We visually inspected boxplots of migration event dates for each season to identify potential outliers. Leaving winter range was slightly skewed early and leaving summer range was slightly skewed late but no recorded events were considered significant outliers.

Data Analysis

We used mixed-effects Cox proportional hazards regression models (coxme R package; Cox 1972) to relate migration events for the 3 transitional periods per our 3 hypotheses represented by applicable daily-dependent predictor variables. We developed and compared the best models to represent each hypothesis using second-order Akaike's information criterion corrected for small sample sizes (AICc; AICcmodavg and MuMIn R packages; Burnham and Anderson 2002).

Modulating variables. We included variables that we considered to have a modulating effect on migration timing (Table 1.1). We expect these variables do not determine migration at the seasonal scale, but can modulate timing by a few days. These variables included wind speed, precipitation (sum of rain and snow), and change in atmospheric pressure. We hypothesized that migration would be avoided during days of high wind speed or precipitation even if other cues were encouraging migration. We predicted that migration may be encouraged or discouraged if grouse can forecast weather patterns by interpreting changes in atmospheric pressure. For example, a grouse may want to leave summer range in advance of stormy weather as indicated by dropping atmospheric pressure. Change in atmospheric pressure was the difference in daily average pressure (measured at nearest weather station; NCEI 2016) of the current day from the previous day. We also considered change in atmospheric pressure in its quadratic form to evaluate whether grouse were selecting for unchanging conditions. Modulating variables could compete in all 3 hypotheses. We utilized raster data for wind speed, precipitation (rain and snow), and snow depth (described as a Direct indicator below) with 750-m resolution. These data were obtained from a meteorological distribution model (MicroMet; Liston and Elder 2006b) and a snow-evolution model (SnowModel; Liston and Elder 2006a). These models have been implemented and validated in several landscapes in the western USA and other countries (e.g., Hiemstra et al. 2002, Liston and Hiemstra 2011).

Indirect indicator. If grouse solely use an indirect indicator of resource quality, such as an internal biological clock or photoperiod, then migration timing should not significantly vary from year to year. In addition, direct indicators, which do vary from year to year, should not explain any significant variation in the observations. Therefore, the indirect-indicator hypothesis was simply represented by a null model.

Direct indicators. The direct indicators of resource quality we considered included temperature, rain precipitation, snow precipitation, snow depth, and plant phenology (Table 1.1). Because organisms likely interpret environmental changes over a time period greater than one day we calculated all direct indicator variables (as well as change in atmospheric pressure) with a ‘linear predictor’ that included α as a weighting factor of the current-day’s value relative to previous-days’ values (Gienapp et al. 2005). As α approached 1, the current day’s value had increasing influence over previous days’ values (see figure 1 in Gienapp et al. 2005). When $\alpha = 1$ it was equivalent to the current day’s value. When α was small it acted like a smoothing parameter that represented a trend over the entire season. We considered values for α in increments of 0.01 from 0.01 to 0.1 and in increments of 0.05 from 0.1 to 1. We started calculations from 30 days prior to the first day of each season and the value on day 0 was the average of those first 30 days. This was to prevent extreme starting values having undue influence over the calculations when α was small.

We considered temperature (4-km resolution; PRISM Climate Group 2016) as a minimum, mean, or maximum daily measurement as grouse could interpret temperature in any of the 3 forms, but we only selected 1 because they were all highly correlated. Because we considered precipitation events, on the day of, as a modulating variable we considered rain and snow with lag effects and trends as direct indicators, which may have an opposite effect on migration initiation (Caudill et al. 2016). For example, increasing snow fall may encourage migrating from summer range but grouse may not leave on the day of precipitation. We only considered rain and snow accumulation variables with an α lower than that which was not correlated ($|r| < 0.6$) with precipitation of the current day. We considered lag effects for daily rain and snow amounts from 1 to 7 days. Snow depth was a variable that could increase probability of migration from summer range and decrease probability from winter range. Plant phenology was represented by the modified soil-adjusted vegetation index (SAVI; Qi et al. 1994), a vegetation greenness index, in 2 different forms based on MODIS MOD09Q1 surface reflectance data available at 8-day intervals (250-m resolution; LP DAAC 2016). The first plant phenology variable was the normalized SAVI values. Normalized SAVI was calculated in several steps: 1) obtaining data for 1 year centered on the season in question, 2) setting negative values (i.e. snow) to no data, 3) setting all values below the 0.025 quantile, and no data, as 0 (to represent no vegetation activity during winter), 4) applying a 3-

observation moving median filter, 5) rescaling the values between 0 and 1, and 6) linearly interpolating values within the 8-day data acquisition window (Bischof et al. 2012). The second plant phenology variable was the change in SAVI measured by the slope between the previous and next observation for every normalized 8-day observation. The measured slopes were also linearly interpolated between observations to obtain daily values.

All variables, except atmospheric pressure, were calculated based on a weighted average of the utilization distribution for the departure seasonal range in question. For example, the value for snow depth for a given day-bird-year combination for the spring transition (leaving winter range) was the weighted average snow depth for that day based on the utilization distribution for that bird-year's winter range. The final utilization distribution for each bird-season-year was based on non-migratory locations bookended by arrival and departure dates. We defined the seasonal arrival date as the day the bird started spending more time within the seasonal range than migrating from or in its previous season, and the seasonal departure date was the day the bird started spending more time outside the seasonal range than within.

Individual characteristics. The individual characteristics we considered included location, summer range type, elevation of next seasonal range, distance to next seasonal range, days since nest fate, and whether the bird was brood rearing (Table 1.1). These are individual-specific characteristics that could encourage a grouse to advance or delay departure compared to other individuals. We also considered interactions between the individual characteristic variables and the direct indicator variables. Location could be important because of behavioral differences among populations or different landscape contexts.

Location was represented by study area (Bighorn Basin or Central Wyoming) or research site (Carbon, Shell, Hyattville, or Central Wyoming). Artificially-maintained water sources in irrigated hayfields and pastures could influence migration timing to and from summer range so each grouse was assigned to a categorical summer range type of irrigated hayfield/pasture or a summer range absent of artificial water sources. A grouse's prior knowledge of the variation in timing of environmental changes based from elevational gradients could explain differences among individuals with destinations at different elevations. For example, a grouse whose breeding range was at a high elevation, with a persistent snow pack, may have left winter range later than another grouse whose breeding range occurred at lower elevation. We naturally expected that individuals who travel farther would leave sooner than those closer to the next seasonal range. Reproductive activity could place restraints on how an individual can respond to migration cues when leaving breeding range. Days since nest fate was the number of days since a grouse's nest was depredated or hatched. For males and females who did not incubate a nest, days since nest fate were set equal to the incubating female with the earliest nest fate that year. The brood female variable was categorically dependent on whether the bird was a female with a successful nest.

Variable screening and sequential modeling. First, we investigated whether to use sex and/or individual as random effects. A null model with individual and not sex was the top-performing model for all seasons so all models for remaining analysis steps included individual as a random effect. This accounted for non-independence of multiple events from an individual within and among years. We then compared single-variable models with AICc to select the most supported α value for linear predictors or lag amounts. In addition, we assessed whether the linear or quadratic form of atmospheric pressure was most supported, assessed temperature variables (minimum, mean, or maximum), and determined if study area or site were more predictive. We carried forward the most predictive variable within each variable class. We assessed correlation of remaining variables and did not allow correlated ($|r| \geq 0.6$) variables to compete in the same models. Variables that failed to meet the proportional hazards assumption as demonstrated by a non-zero slope for the Schoenfeld residuals were excluded from analysis (Schoenfeld 1982). The variables considered within each hypothesis were as follows: H_1) a null model with modulating variables for the indirect-indicator-only hypothesis, H_2) modulating variables and direct indicators for the direct-indicators hypothesis, and H_3) modulating variables, direct indicators, and individual characteristics for the direct-indicators-plus-individual-characteristics hypothesis. We compared all possible combinations of the appropriate variables to create the most parsimonious model to represent each hypothesis and then compared the 3 hypotheses using AICc. We only present individual variable results ($\beta \pm$ SE) from significant variables ($P < 0.1$) in the top Cox proportional hazards regression model.

Migratory vs. non-migratory. Only data from migratory individuals were used to identify migration timing cues. After we identified which cues determined timing, we calculated the relevant environmental conditions experienced by migratory and non-migratory grouse to investigate whether differences in environmental conditions could help explain partial-migratory behavior in sage-grouse. Seasonal bounding dates for non-migratory grouse were the mid-points between seasonal departure and arrival dates calculated from migratory birds. Seasonal utilization distributions were then calculated based on locations within these bounding dates. We calculated the average environmental conditions over the total length of each transitional season for every individual's departing seasonal range. We then compared average conditions (mean ± SE) experienced between migratory and non-migratory individuals with a 2-sample *t*-test (2-tailed).

RESULTS

We observed 67 migration initiation events (mean = March 17, range: January 20–May 3) from 43 GPS-tagged grouse during 2011–2015 for the spring transition season (winter to breeding range; Table 1.2). We censored 1 event due to poor fix rate and 2 events because of unknown location of breeding range. The model representing direct indicator cues with individual characteristics (H_3) had overwhelming model support (model weight of evidence, $w_i = 0.99$) and significant variables included 1 modulating variable (prec), 2 direct indicators (tmin, savi), and 2 individual characteristics (area, elev; Table 1.3). There was convincing evidence that grouse were not initiating migration on days with precipitation ($\beta = -12.6 \pm 4.7$, $P = 0.007$). There also was evidence that grouse in Central Wyoming were migrating earlier ($\beta = 1.58 \pm 0.62$, $P = 0.01$) and grouse whose breeding ranges were at higher elevations were migrating later ($\beta = -1.44\times10^{-3} \pm 0.83\times10^{-3}$, $P = 0.08$). Timing of migration away from winter range was determined by increasing recent ($\alpha = 0.95$) minimum temperature and a moderate accumulation ($\alpha = 0.25$) of increasing SAVI (Table 1.4 and Figure 1.3A). In our study areas, 55% ($n = 77$) of the monitored population were migratory between winter and breeding range.

Migratory and non-migratory grouse experienced the same temperatures and SAVI levels during the spring transition (Table 1.4 and Figure 1.3A).

We observed 101 migration initiation events (mean = June 16, range: May 13–August 3) from 73 GPS-tagged grouse for the summer transition season (breeding to summer range; Table 1.2). We censored 1 event due to poor fix rate, 4 events because of unknown location of summer range, and 2 events from a female that was an inconsistent incubator during hot and dry conditions. Like the spring transition, the model representing direct indicator cues with individual characteristics (H_3) for the summer transition had overwhelming model support (w_i = 1.00; Table 1.3). Significant variables in this model included no modulating variables, 1 direct indicator cue (tmax), 4 individual characteristics (brod, styp, area, dist), and 1 interaction (savi × area). Brood-rearing grouse (β = -0.994 ± 0.266, $P < 0.001$), grouse whose summer range included artificial water sources (β = -0.969 ± 0.321, $P = 0.003$), and grouse that traveled farther ($\beta = -3.79\times10^{-2} \pm 2.15\times10^{-2}$, $P = 0.08$) all initiated migration at a slower rate relative to when they could migrate (i.e. no longer incubating a nest). There also was evidence that Central Wyoming grouse initiated migration quicker relative to when they could migrate (β = 10.1 ± 4.7, $P = 0.03$) and they were more influenced by decreasing SAVI (β = -12.4 ± 5.6, $P = 0.03$) than Bighorn Basin grouse. Timing of migration away from breeding range was determined by the trend (α = 0.02) of increasing maximum temperatures (Table 1.4 and Figure 1.3B). In our study areas, 73% ($n = 92$) of the monitored population were migratory between breeding and summer range. Migratory individuals experienced 6% warmer temperatures than non-migratory individuals (Table 1.4). Specifically, breeding seasonal ranges of migratory birds had the same trend, but warmer accumulated maximum temperature than non-migrant breeding ranges during the summer transition (Figure 1.3B).

We observed 124 migration initiation events (mean = October 12, range: August 12–January 8) from 84 GPS-equipped grouse for the fall transition season (summer to winter range; Table 1.2). We censored 1 event due to poor fix rate and 11 events because of unknown location of winter range. Consistent with previous seasons, the direct indicators with individual characteristics (H_3) was the best supported ($w_i = 1.00$; Table 1.3) hypothesis. Significant variables included no modulating variables, 4 direct indicator cues (tmax, spre, rlag, rpre), 1 individual characteristic (styp), and 1 interaction (spre × area). Grouse whose summer range had an artificial water source were leaving sooner ($\beta = 1.36 \pm 0.39$, $P < 0.001$). Timing of migration away from summer range was determined by decreasing recent ($\alpha = 0.65$) maximum temperature, moderate accumulation ($\alpha = 0.3$) of increasing snow, and increasing rain with a lag effect ($\alpha = 1$, lag = 3 days) and rain trend ($\alpha = 0.06$; Table 4 and Figure 1.3C). There also was suggestive evidence that Central Wyoming grouse were reacting differently to snow than Bighorn Basin grouse ($\beta = -13.0 \pm 6.6$, $P = 0.05$) in that they were initiating migration during relatively snow-free periods. In our study areas, 75% ($n = 92$) of the monitored population migrated between summer and winter range. Migratory and non-migratory grouse experienced the same average rain amounts measured by daily values with lag effect and as a trend (Table 1.4). However, summer seasonal ranges of migratory grouse had 13% colder temperatures and 52% more snow during the fall transitional season (Table 1.4 and Figure 1.3C).

DISCUSSION

We found strong evidence that sage-grouse use direct indicators of resource quality when deciding when to initiate migration, and are also influenced by individual characteristics, regardless of season. The timing of sage-grouse spring migrations were determined by increasing temperatures and advancing spring green-up, were modulated by not departing on days with precipitation, and also were dependent on location and breeding range elevation. Summer migrations were determined by increasing temperatures and were dependent on location, reproductive status, summer range type, and migration distance. Timing for fall migrations were determined by decreasing temperatures, increasing rain trends, increasing snow trends, and were dependent on location and summer range type. The closer an individual's seasonal range is to the next season's range the more correlated the environmental changes will be and the greater utility a direct indicator of resource quality should have (Tombre et al. 2008). Because altitudinal migrants are relatively short-distance migrants, they are likely to use direct indicators of resource quality. This has been demonstrated by research on a temperate ungulate migrant (Monteith et al. 2011) and by preliminary research on Greater Sage-Grouse, a temperate avian migrant (Fischer et al. 1996, Caudill et al. 2016). We were able to further elucidate the relationship between sage-grouse migration timing and direct indicator cues, beyond this preliminary research, because of our more precise (daily observations) and comprehensive (all seasons and additional variables) analysis. This use of direct indicators is also consistent with anecdotal evidence found in tropical avian migrants (Boyle et al. 2010, Boyle 2011). Pink-footed Geese (*Anser brachyrhynchus*) have been described using both direct (temperature) and indirect (photoperiod) indicators depending on where they were along their migration routes and how correlated their location was with the next stopover (Bauer et al. 2008, Duriez et al. 2009).

Temperature was consistently the most significant variable but whether it was maximum or minimum and whether it was accumulated over short or longer time periods depended on the season. Temperature has been documented to be a significant cue for migration in a variety of taxa (e.g., Bauer et al. 2008, Keefer et al. 2009, Monteith et al. 2011), as well as, a cue for other avian activities (e.g., Gienapp et al. 2005, Visser et al. 2009). We expected a greater influence from those variables (savi, sslo) directly representing plant phenology as sage-grouse are presumed to change seasonal ranges because of growth and senescence of plants, at least for the spring and summer transitions (Fischer et al. 1996). Plant phenology has been proposed as the driving force for other altitudinal migrants (Bischof et al. 2012, Merkle et al. 2016). Migration timing did correlate well with expected grouse responses to plant phenology. Spring migration occurred during peak green-up, summer migration occurred when plants started desiccating, and fall migration occurred shortly before the onset of winter (Figure 1.4). SAVI did contribute to timing during the spring transition and the change in SAVI was correlated (but less predictive) with temperature during the summer transition. Plant phenology not playing a significant role during the fall transition is consistent with senescence of plants not being the reason grouse leave summer range, but the presence of snow limiting forage availability (Dunn and Braun 1986). Dingle and Drake (2007) stated that preemption, or when habitats are abandoned before quality has appreciably declined, is a key component of migration and that preemption cannot rely on proximate cues but on surrogates that forecast habitat deterioration. This is consistent with the apparent secondary role of plant phenology in promoting grouse to leave breeding range. Temperature could be the surrogate forecasting a state where plant desiccation becomes too extreme. Temperature, rain, and snow precipitation could also be playing this role forecasting conditions of decreased forage availability at the end of the summer season. Caudill et al. (2016) also documented precipitation as a significant driver of juvenile sage-grouse leaving summer range in Utah, USA. Red deer (*Cervus elaphus*) were described as exhibiting risk-averse behavior by leaving summer range before the onset of winter (Rivrud et al. 2016). For the spring transition, preemptive departure decisions are attempting to predict improving conditions on breeding range, not escaping deteriorating conditions, unless migratory birds are avoiding increased breeding competition on winter range (Kokko and Lundberg 2001, Gillis et al. 2008).

Even though we found evidence that sage-grouse were heavily influenced by direct indicator cues there could still have been an internal clock or photoperiod foundation that limited the extents of migratory seasons (Bradshaw and Holzapfel 2007). However, there is no question that direct indicators were used by sage-grouse to appropriately time movement within a transitional season according to environmental gradients in time and space. The advantage of internal biological clocks or photoperiod is that they do not vary from day to day or year to year so they should be easier to interpret than direct indicator cues, which can vary considerably (Bradshaw and Holzapfel 2007). Therefore, it would make sense that animals using direct indicator cues would interpret them accumulated over a longer period (i.e. low α). Bauer et al. (2008) determined the most predictive α level for temperature along 3 stages of geese migration was ≤ 0.03. We found grouse interpreting cues over a range of time periods (α

= 0.02–0.95). Interpreting temperature over a short time frame for the spring and fall transitions may reflect a greater chance for an individual to initiate movement prematurely than during the summer transition when temperature was interpreted over a longer time frame. However, this is contradicted by the consistency in the proportion of grouse with multiple events in a year for spring (18%, n = 65), summer (19%, n = 97), and fall (21%, n = 113). These cues accumulated over a shorter time frame appear to be as dependable, as evidenced by the consistency in premature migrations, which is not consistent with simulations described in Duriez et al. (2009) with Pink-footed Geese. This study argues that if geese initiate spring migrations based on recent temperatures there would be too many premature departures. However, a possible explanation is that these cues become dependable by moderation from additional cues including plant greenness and rain/snow precipitation for spring and fall, respectively (Duriez et al. 2009, McNamara et al. 2011).

Not surprisingly, individual characteristics influenced migration timing in all 3 seasons (Fischer et al. 1996, Schroeder and Braun 1993). We found variations in sage-grouse behavior between Bighorn Basin and Central Wyoming suggesting effects from differences in topographies, underlying gene pool, or other population-specific factors. Identifying the timing of migratory movements has much conservation value for a species of concern such as sage-grouse whose range and abundance has declined drastically (Schroeder et al. 2004, WAFWA 2015) and whose conservation is dependent on regulatory mechanisms (USFWS 2015). Land-surface disturbance is temporally regulated via timing stipulations in Wyoming (State of Wyoming 2015) and Montana (State of Montana 2015) to minimize negative impacts on sage-grouse. However, our observations demonstrate that seasonal timing is location specific and local information is usually lacking (Appendix A Figures 1.6 and 1.7). Migratory behavior also was influenced by presence of offspring, summer habitat use, and spatial and topographic characteristics of the destination seasonal range. Research on mule deer demonstrated that they are also influenced by individual characteristics such as age, body condition, migration distance, location, and anthropogenic disturbance (Monteith et al. 2011, Lendrum et al. 2013). Though body condition has been documented as influential on migratory behavior in birds (e.g., Yong et al. 1998, Mitrus 2007) we were not able to investigate this factor for sage-grouse.

We found mixed results as to whether migratory individuals were experiencing more stimulatory cues compared to non-migratory individuals. There were no differences in environmental conditions for the spring transition. However, temperatures were warmer for migratory grouse during the summer transition and there were colder temperatures with more snow during the fall transition. The trends in these cues were the same between ranges of migratory and non-migratory grouse, but the average levels were different. The differences in the average environmental conditions suggest that these migrations were facultative (Fischer et al. 1996, Dingle and Drake 2007). That is, if migratory grouse were moved to a different location where environmental conditions are different, or if there was an abnormal year where environmental conditions did not worsen to the normal extent, they may no longer exhibit migratory behavior (Skov et al. 2010). Changes in temperature and precipitation along an elevation gradient appeared to be the major drivers of what environmental conditions grouse experienced, especially in the Bighorn Basin (Figures 1.2 and 1.5). The pattern was similar in Central Wyoming, but on a much narrower scale because the range of elevations in Central

Wyoming was much smaller. For the summer transition, migratory grouse breeding ranges were, on average, at lower elevations which were warmer and would have plants that desiccated faster than higher elevations. During fall, migratory grouse summer ranges were, on average, at higher elevations, which were colder with more snow. However, for the spring transition, the effects from elevational differences between migratory and non-migratory grouse were not significant. Most winter ranges were at lower elevations and were used by both migratory and non-migratory individuals. Many of these winter ranges were also used for breeding ranges so we suspect that migratory individuals were dispersing themselves amongst more abundant breeding habitat. These results are consistent with the presumed notion that migrant sage-grouse avoid higher plant desiccation during summer and higher snow accumulation during winter, but are just returning to their respective breeding ranges during spring (Dalke et al. 1963, Berry and Eng 1985, Dunn and Braun 1986, Connelly et al. 1988, Fischer et al. 1996).

Differences in environmental conditions between migratory and non-migratory sage-grouse seasonal ranges demonstrate that there is a landscape context to migratory behavior. Some individuals migrate because they are experiencing different environmental conditions. There has been documentation of changes in the level of partial migration when the environment changes temporally (e.g., Fieberg et al. 2008), but less so if the change is spatial. One notable exception is Cagnacci et al. (2011) who showed that an interaction between snow and topography explained variation in levels of partial migration for roe deer (*Capreolus capreolus*) at a continental scale. Our research suggests that environmental gradients can explain partial migration at a population scale. This effect is more likely where the environmental gradient is sharp and the scale of migration is small compared to the geographic range of the population, which typifies sage-grouse range in the western USA. Partially-migratory populations are increasingly recognized as more common than originally thought (Chapman et al. 2011). The landscape context of individuals may have significant influence on their behavior and could be a major contributing cause of why partially-migratory species are so prevalent.

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Game and Fish Department (Chapter 33 Permits 800 and 801) and Montana Fish, Wildlife and Parks (Scientific Collector's Permits 2013-072, 2014-037, and 2015-76).

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Table 1.1. Predictor variables used to investigate timing of Greater Sage-Grouse migration during the spring, summer, and fall transitional seasons in Bighorn Basin and Central Wyoming, USA, 2011–2015.

Variable	Description
Modulating variables	
prec	daily total precipitation (rain + snow, water equivalent, cm)
wspd	daily average wind speed (m s^{-1})
atmp[ab]	atmospheric pressure trend (current day mean minus previous day mean, mmHg)
Direct indicators	
tmin[a]	daily minimum temperature (°C)
tmea[a]	daily average temperature (°C)
tmax[a]	daily maximum temperature (°C)
rpre[a]	daily total rain precipitation (cm)
rlag[a]	rain precipitation with lag effect of 1-7 days (cm)
spre[ac]	daily total snow precipitation (water equivalent, cm)
slag[ac]	snow precipitation with lag effect of 1-7 days (water equivalent, cm)
snod[ac]	snow depth at beginning of day (cm)
savi[a]	vegetation ‘greenness’ index (0-1)
sslo[a]	daily change in ‘greenness’ index (slope)
Individual characteristics	
area	location (Bighorn Basin[d], Central Wyoming)
site	location (Carbon, Shell, Hyattville[d], Central Wyoming)
styp[e]	summer range type (presence of artificial water)[d]
elev	elevation of destination (m)
dist	distance to destination (km)
nfat[f]	days since nest fate
brod[f]	brood rearing[d]

[a] considered different levels of temporal-weighting (α)

[b] considered quadratic form

[c] only relevant for spring and fall transition

[d] Bighorn Basin, Hyattville, summer range without artificial water, and grouse without broods were the reference categories

[e] only relevant for summer and fall transition

[f] only relevant for summer transition

Table 1.2. Number of migration events observed during the spring, summer, and fall transitional seasons from GPS-tagged Greater Sage-Grouse in Bighorn Basin and Central Wyoming, USA, 2011–2015.

	Bighorn Basin						Central Wyoming		Total	
	Carbon		Shell		Hyattville					
Season	events	grouse	events	grouse	events	grouse	events	grouse	events	grouse
Spring	5	3	1	1	41	25	20	14	67[a]	43[a]
Summer	14	9	17	11	54	43	16	10	101[bc]	73[b]
Fall	11	6	16	6	61	45	36	27	124[de]	84[d]

[a] 1 event from a male grouse

[b] 11 events from 9 male grouse

[c] 35% brood rearing and 28% summer range with artificial water

[d] 5 events from a male grouse

[e] 23% summer range with artificial water

Table 1.3. Top models representing the 3 migration-cues hypotheses for the 3 transitional seasons for Greater Sage-Grouse in Bighorn Basin and Central Wyoming, USA, 2011–2015. Model selection statistics include number of model parameters (*K*), difference in AICc between model and top model (ΔAICc), and model weight of evidence (w_i).

Season	Model statistics		
Hypothesis (variables)	*K*	ΔAICc	w_i
Spring transition			
H_3: Dir ind + ind cha (prec + tmin + savi + rlag + area + elev + tmin × area)	8	0.00[a]	0.99
H_2: Dir ind (prec + tmin + savi + rlag + snod)	6	8.59	0.01
H_1: Ind ind (prec + wspd)	3	24.86	0.00
Summer transition			
H_3: Dir ind + ind cha (tmax + savi + brod + styp + area + dist + savi × area)	8	0.00[b]	1.00
H_2: Dir ind (atmp + tmax + savi)	4	16.72	0.00
H_1: Ind ind (atmp + atmp^2)	3	59.72	0.00
Fall transition			
H_3: Dir ind + ind cha (tmax + spre + rlag + rpre + styp + area + tmax × area + spre × area)	9	0.00[c]	1.00
H_2: Dir ind (tmax + spre + rlag + rpre)	5	11.85	0.00
H_1: Ind ind (prec + atmp + atmp^2)	4	75.05	0.00

[a] AICc = 293.30

[b] AICc = 527.00

[c] AICc = 674.25

Table 1.4. Variable coefficients (β) and the comparisons between migratory and non-migratory Greater Sage-Grouse for significant direct indicator cues in top models for each of the 3 transitional seasons in Bighorn Basin and Central Wyoming, USA, 2011–2015.

Season	Variable coefficient			Migratory			Non-migratory			*t*-test		
Variable	β	SE	*P*	Mean	SE	*n*	Mean	SE	*n*	*t*	df	*P*
Spring												
tmin	0.222	0.060	<0.001	-5.53	0.26	42	-5.66	0.26	35	0.3	74	0.74
savi	1.81	0.95	0.06	0.506	0.025	42	0.495	0.024	35	0.3	75	0.76
Summer												
tmax	0.483	0.079	<0.001	18.5	0.3	67	17.4	0.4	25	2.3	49	0.03
Fall												
tmax	-0.155	0.027	<0.001	10.6	0.3	69	12.2	0.3	23	-3.9	71	<0.001
spre	3.20	0.82	<0.001	2.95[a]	0.24[a]	69	1.94[a]	0.30[a]	23	2.6	53	0.01
rlag	1.24	0.42	0.003	5.58[a]	0.34[a]	69	5.14[a]	0.55[a]	23	0.7	40	0.49
rpre	2.94	1.27	0.02	6.01[a]	0.35[a]	69	5.56[a]	0.59[a]	23	0.7	38	0.51

[a] ×10^{-2}

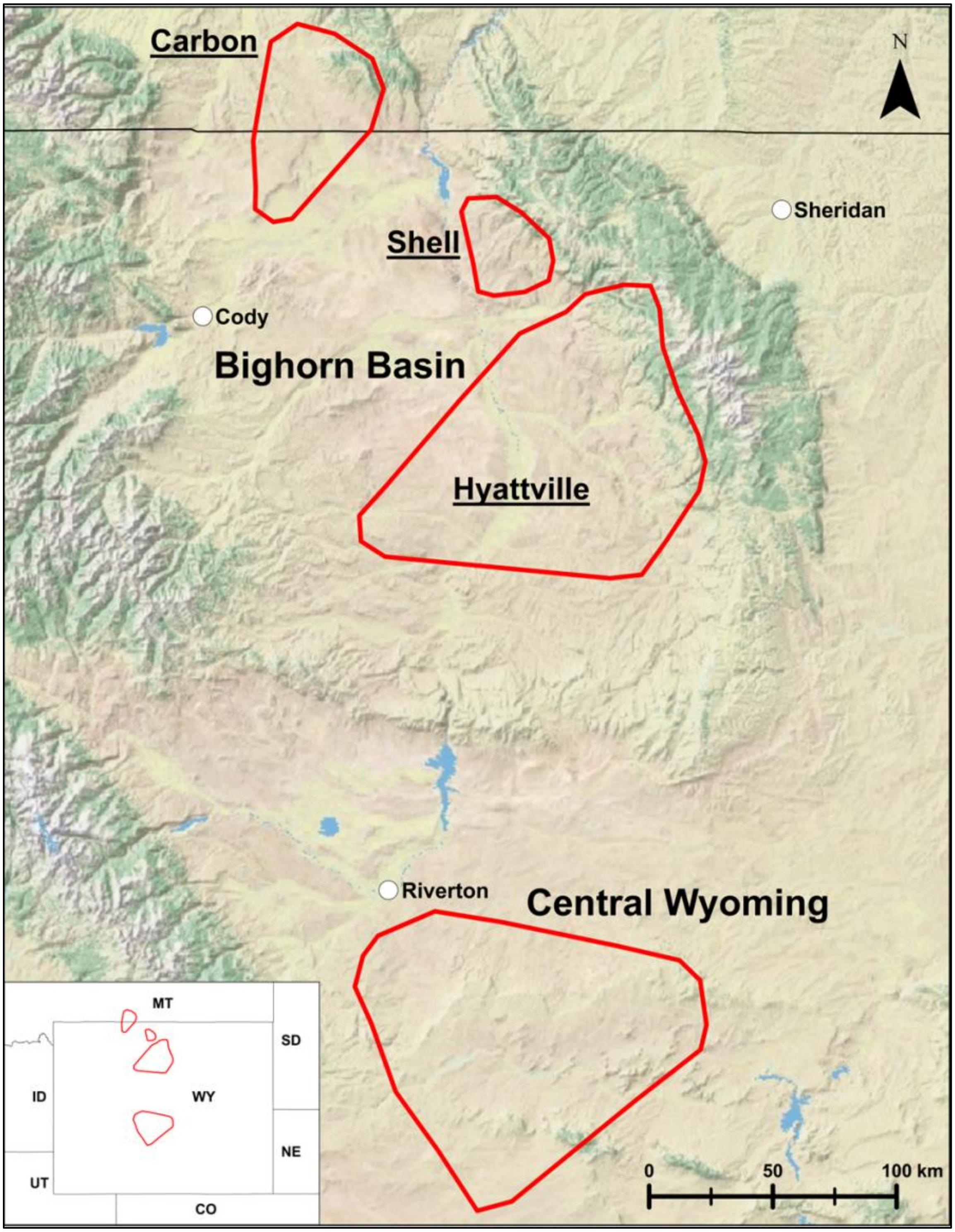


Figure 1.1. Maximum extent of locations of GPS-tagged Greater Sage-Grouse in Bighorn Basin and Central Wyoming, USA, 2011–2015.

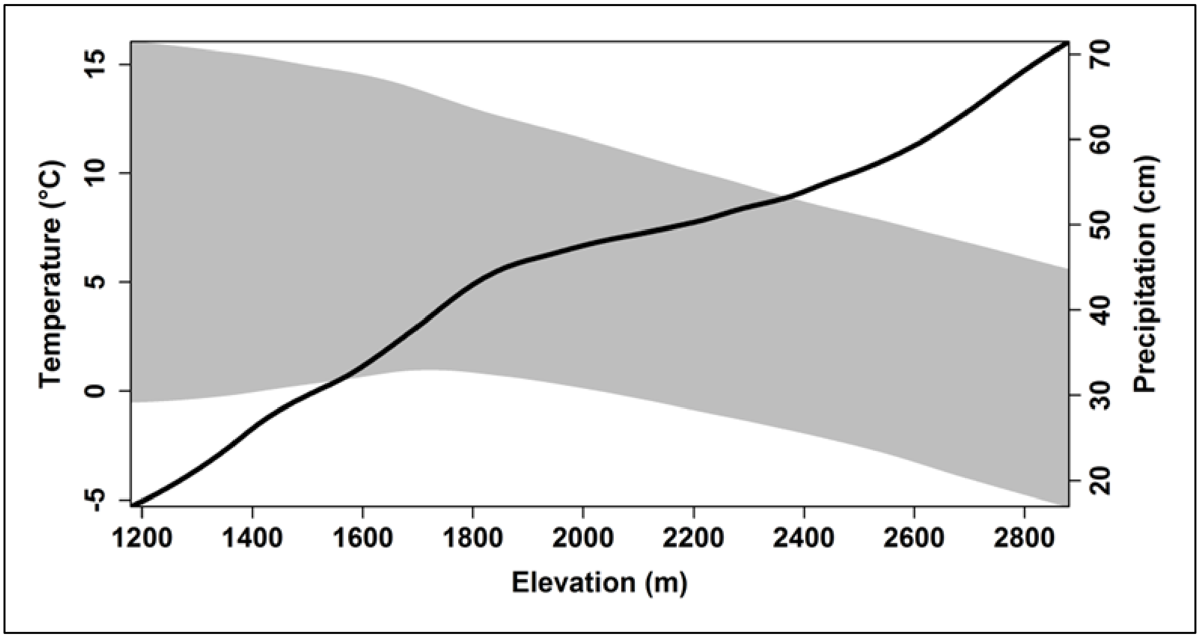


Figure 1.2. Mean 30-year normal (1981–2010; Prism Climate Group 2016) annual maximum and minimum temperatures (shaded region; °C) and precipitation (line; cm) relative to the range of elevations (m) represented by seasonal ranges of GPS-tagged Greater Sage-Grouse in the Bighorn Basin, USA, 2011–2015.

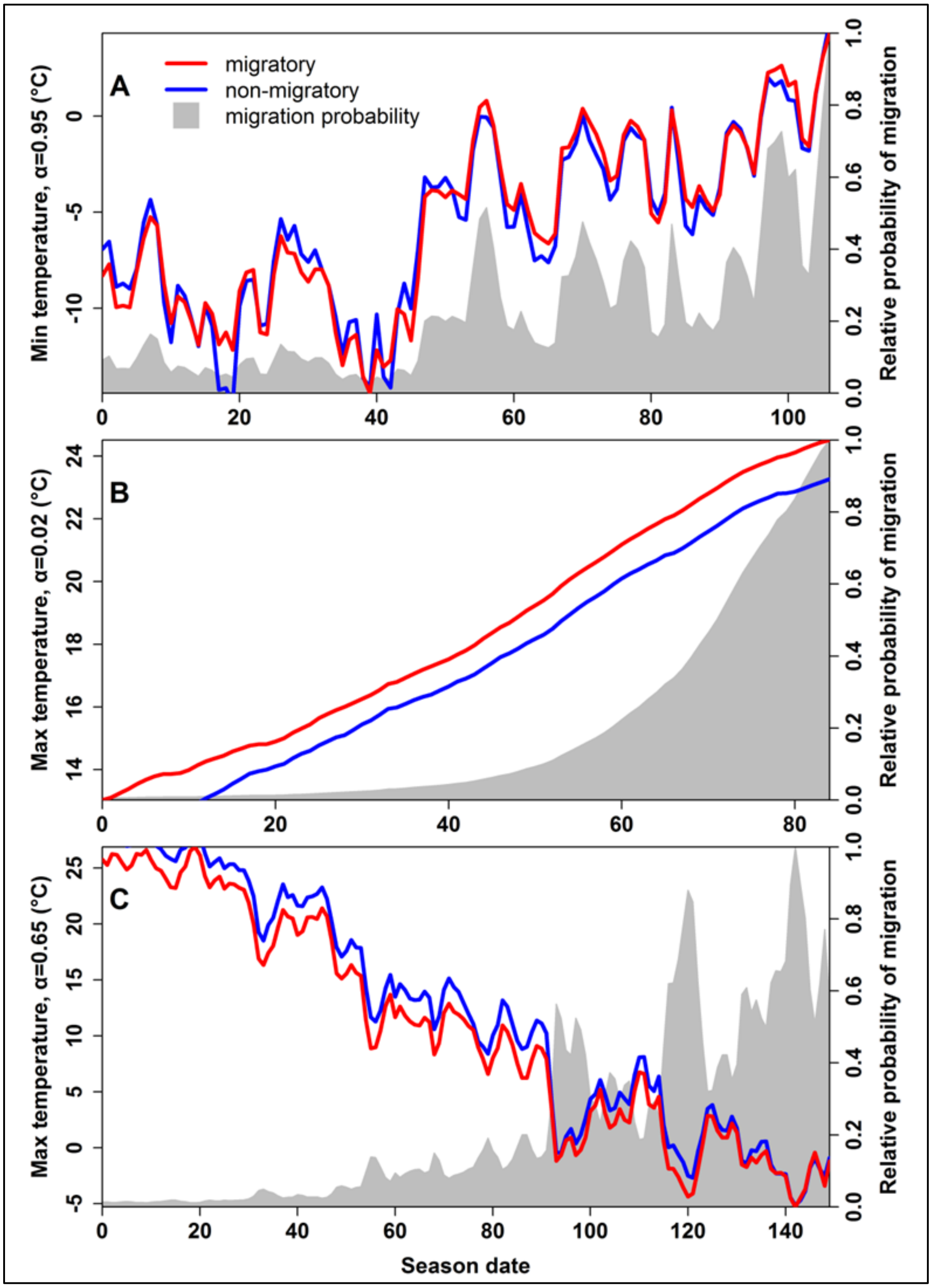


Figure 1.3. Temperature trend between seasonal ranges of migratory and non-migratory Greater Sage-Grouse and effect on migration probability for the spring (**A**), summer (**B**), and fall (**C**) transitional seasons in Bighorn Basin and Central Wyoming, USA, 2011–2015.

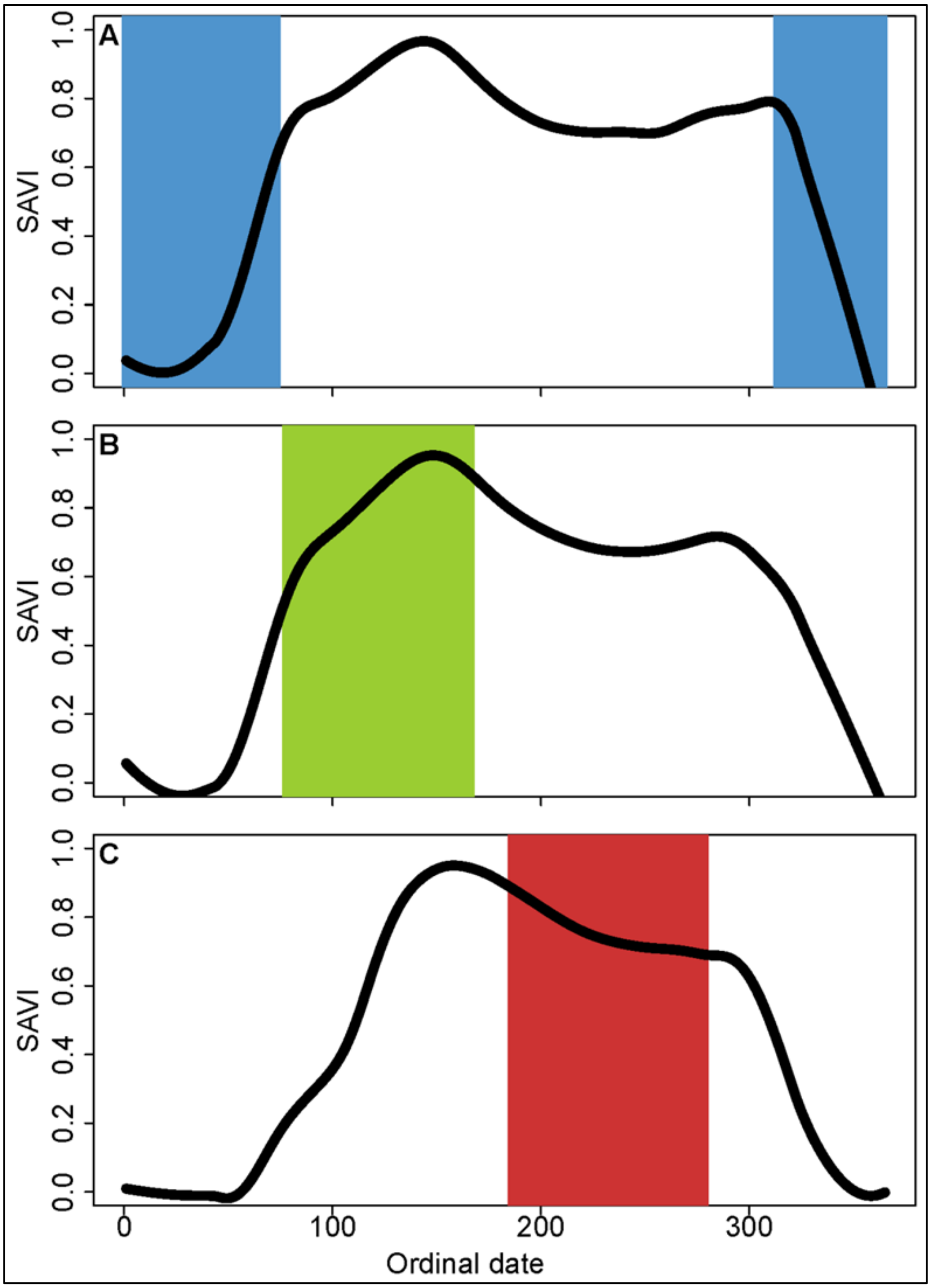


Figure 1.4. Timing of Greater Sage-Grouse presence (shaded regions; based on median departure and arrival dates) on winter (**A**), breeding (**B**), and summer (**C**) seasonal ranges relative to plant phenology as demonstrated by a smoothed soil-adjusted vegetation index (SAVI) curve (bold black line) in Bighorn Basin and Central Wyoming, USA, 2011–2015.

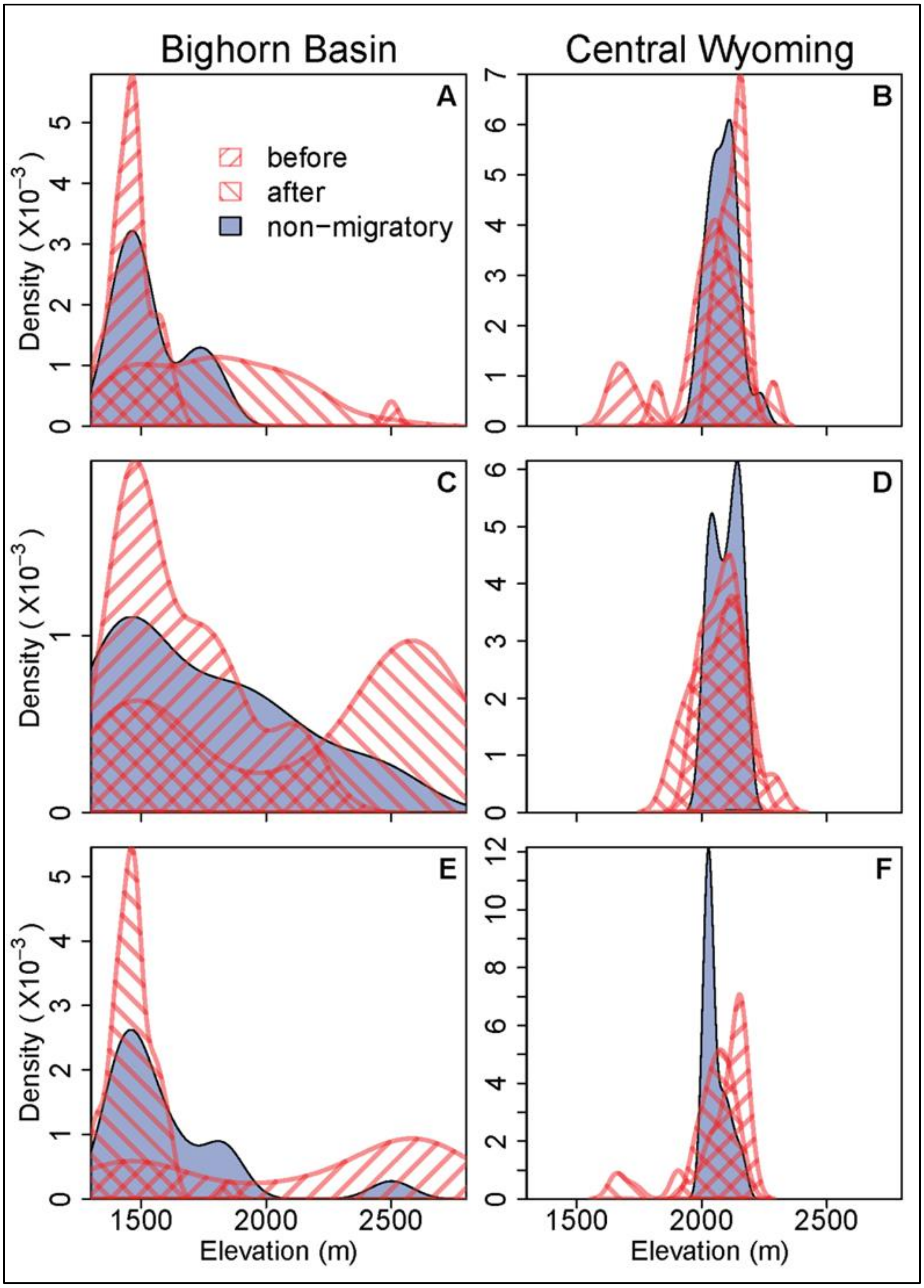
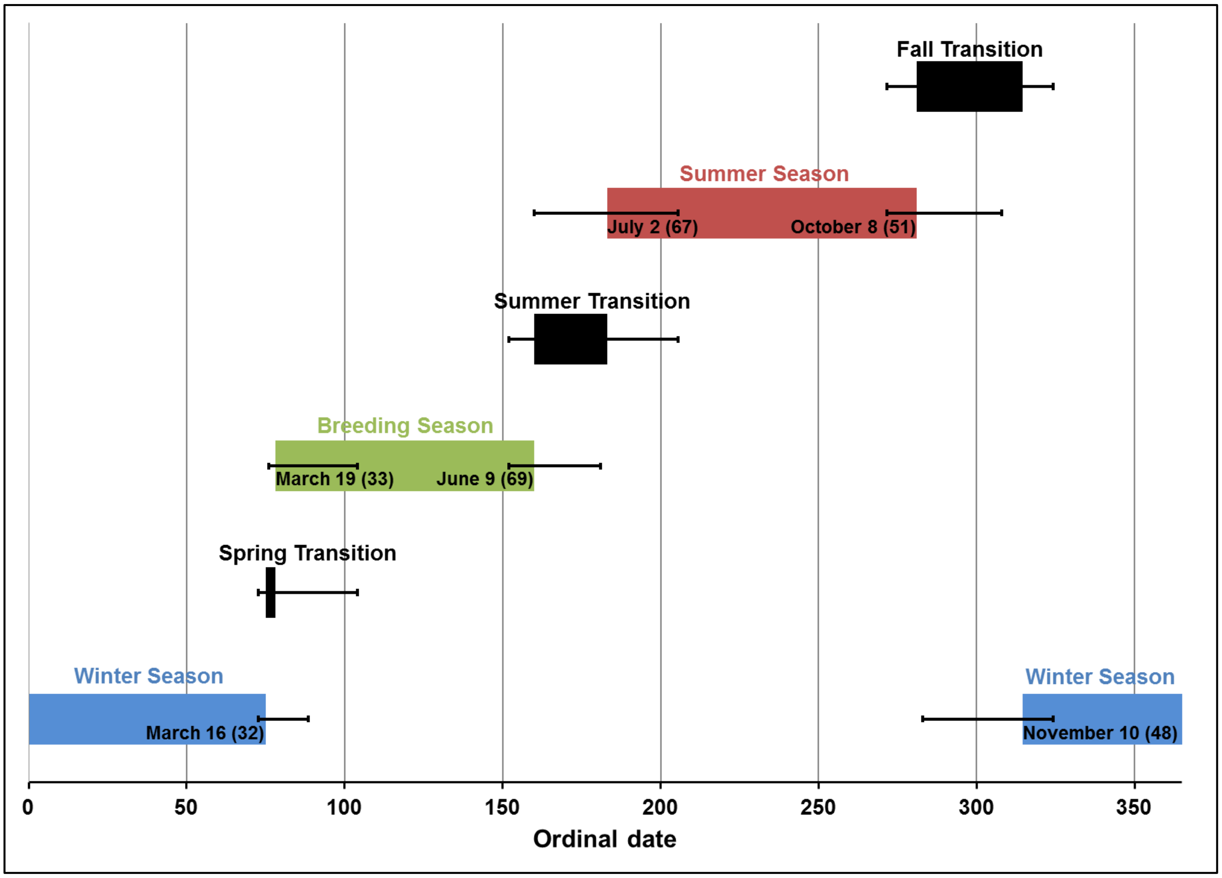
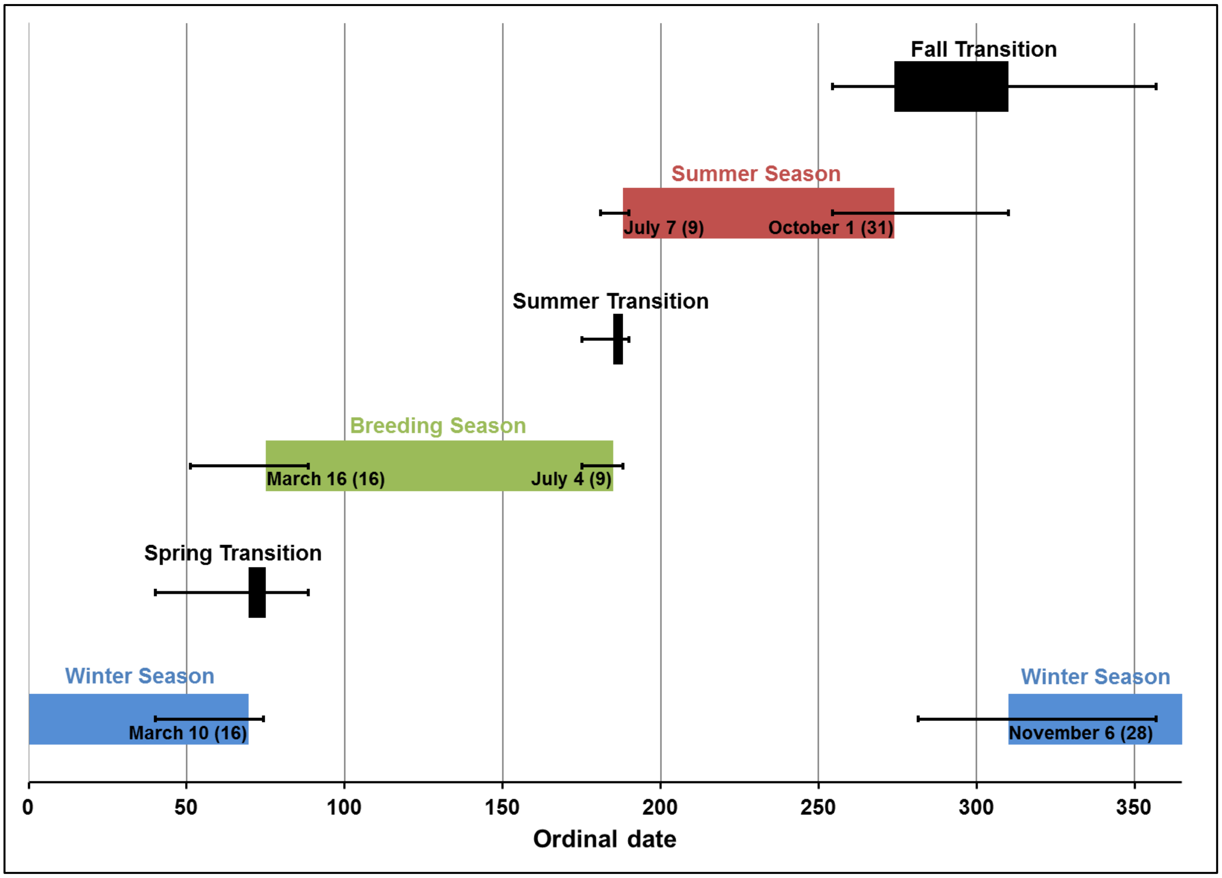


Figure 1.5. Elevations of seasonal ranges before and after spring (**A**, **B**), summer (**C**, **D**), and fall (**E**, **F**) migration and for non-migratory Greater Sage-Grouse in Bighorn Basin and Central Wyoming, USA, 2011–2015.



Appendix A Figure 1.6. Timing of presence within seasonal range and transitional movements for 68 GPS-tagged Greater Sage-Grouse in Bighorn Basin, USA, 2011–2015. Median dates (sample size in parentheses; error bars depict the 25th and 75th quartiles) are stated for arrival to and departure from seasonal range. Arrival and departure dates were defined as the threshold between spending more time inside a seasonal range than outside. Solid black rectangles depict when >50% of migratory grouse were in a state of seasonal transition (error bars depict >25%).



Appendix A Figure 1.7. Timing of presence within seasonal range and transitional movements for 25 GPS-tagged Greater Sage-Grouse in Central Wyoming, USA, 2012–2015. Median dates (sample size in parentheses; error bars depict the 25th and 75th quartiles) are stated for arrival to and departure from seasonal range. Arrival and departure dates were defined as the threshold between spending more time inside a seasonal range than outside. Solid black rectangles depict when >50% of migratory grouse were in a state of seasonal transition (error bars depict >25%).

CHAPTER TWO

Prioritizing Seasonal Habitats for Comprehensive Conservation of a Partial Migrant

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Abstract

Conservationists must identify and prioritize seasonal habitats when delineating reserves designed to protect partially-migratory species. Identifying the similarity between and the demographic importance of these seasonal habitats will assist conservationists in prioritizing specific seasonal requirements. Habitat similarity presumably falls along a gradient depending on the degree of migration for a species. How migratory a population is may even vary considerably within a species. A partial migrant of conservation concern is the greater sage-grouse (*Centrocercus urophasianus*), where breeding habitat has been prioritized. A small sage-grouse population may require different approaches to habitat preservation if grouse are using more specialized strategies, such as migration, to meet their requirements. Our goal was to determine if a smaller, peripheral sage-grouse population, that was more migratory, required a different habitat conservation strategy relative to seasonal requirements, than a larger, core population. Firstly, for both populations, prioritization of breeding habitat was justified because breeding habitat was most similar to other seasonal requirements and it had the greatest estimated contribution to population change. Secondly, 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 propose two methods to map comprehensive habitat requirements to help guide reserve delineation: one that weights each season equally and the second that weights each season according to its potential influence on population change. This process can be used to delineate priority areas for other partial migrants of conservation concern.

1. Introduction

Habitat loss and fragmentation from anthropogenic land-use changes is a leading cause of species scarcity. Therefore, habitat conservation has been an utmost concern for conservation biologists as the world's population increases. One factor that can complicate habitat conservation is migration behavior. Species with multiple and unique seasonal habitat requirements cannot be adequately protected if not all annual requirements meeting their life history needs are addressed. The relevancy of conserving all seasonal habitat requirements was made apparent when New-World Nearctic-Neotropical avian migrants continued to decline when only breeding habitat was investigated, while ignoring winter habitat (Robbins et al., 1989; Faaborg et al., 2010). It is now simple to understand that disregard for landscape requirements of migrants for either breeding range, winter range, or even migratory habitat connecting these seasonal ranges may result in population decline (assuming equal threats to each season; Sherry and Holmes, 1995; Faaborg et al., 2010). It is also easily deducible that conservation of landscapes for residents would meet all the annual requirements because habitat use during different seasons overlaps. However, it is less apparent when determining seasonal habitat requirements of partial migrants which fall along a continuum between migrants and residents (Cagnacci et al., 2011). How similar are the landscapes that support the annual requirements for partial migrants and what seasonal habitats should conservation actions prioritize? 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 species, the greater sage-grouse (*Centrocercus urophasianus*; hereafter ‘sage-grouse’), proves an excellent example of a species that falls within the opposing ends of the migration behavior spectrum. Not only are sage-grouse a partially-migrant species, but individual populations exhibit considerable variation in their migratory strategies (Fedy et al., 2012). This complicates what seasonal habitats sage-grouse conservation strategies should prioritize. Habitat conservation is further complicated by the fact that sage-grouse populations generally have three distinct seasonal habitat requirements: breeding, summer, and winter (Connelly et al., 2011), and; therefore, three potential inter-seasonal migratory habitat requirements. 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; WAFWA, 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 (USFWS, 2010). Because of 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. In order for these conservation reserves to fulfill their intended purpose, which was to prevent listing of sage-grouse as an endangered species, they must be effective in protecting all vital habitat requirements. Traditionally, habitat conservation, in general and specifically for sage-grouse, has focused on breeding habitat because of its importance for reproductive activities. The Core Area Strategy was based on sage-grouse breeding densities (State of Wyoming, 2008; Doherty et al., 2011). Even though the Core Area Strategy suggests it incorporates non-breeding season habitat (State of Wyoming, 2015) there are still questions on how well the strategy captures 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 migration habitat which connects seasonal ranges (Fedy et al., 2012; 2014; Walker et al., 2016).

The Core Area Strategy places higher value on areas with higher density. Protecting high-density areas will target the greatest numbers; however, there are benefits of protecting smaller, peripheral populations such as preventing range contractions and maintaining genetic connectivity amongst larger populations. In these ways, the smaller peripheral populations may serve as a protective buffer to core populations. Theoretical models indicate that a partially migratory population will have more individuals than either a fully resident or migratory population (Griswold et al., 2011). Accordingly, the smaller, peripheral populations are likely more specialized in their migratory behavior. As argued earlier, populations with different migratory behavior may require different approaches to habitat conservation. Our overall goal was to determine if a smaller, peripheral sage-grouse population required a different habitat conservation strategy, than a large, core population. To address this overall goal, we developed three specific objectives.

Our first objective was to measure the degree of migratory behavior for the two populations. We predicted that the small, peripheral population would have more specialized migratory behavior, either more migratory or more resident. The first aspect of our second objective was to measure sage-grouse habitat selection to identify important landscape characteristics that distinguish seasonal habitat for both populations. We did this for three main seasons: breeding, summer, and winter. Breeding habitat is sagebrush (*Artemisia* spp.) dominated areas that support pre-nesting, nesting, and early brood-rearing; summer habitat is more mesic sites that support late-brood rearing and provide forage during drier summer conditions, with winter habitat providing sagebrush forage above snow (Connelly et al., 2011). We also identified habitat for three inter-seasonal periods: summer transition (breeding to summer range), fall transition (summer to winter range), and spring transition (winter to breeding range). The second aspect of our second objective was to map and measure the similarity of seasonal habitat for both populations. We predicted that seasonal habitat would be less correlated in the population that was more migratory. Predicted resource selection maps that guide conservation are usually based on habitat use for a single season, so the final component of our second objective was to create a cumulative map depicting the conservation value of an area based on its ability to meet year-long habitat requirements. This comprehensive habitat map weighted each season equally. As an alternative, our third objective identified the potential contribution of each seasonal habitat to population change based from seasonally-specific demographic rates. We then created a second cumulative habitat map depicting conservation value where each season was weighted according to its potential contribution to population change.

2. Methods

2.1. Study areas

Our study was based from observations on 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 (Figure 2.1). The Bighorn Basin study area was a collection of three smaller research sites that represented relatively distinct populations 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. 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 occurs 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 (Figure 2.1). In contrast, our Central Wyoming sample was from a larger contiguous population. The density of known sage-grouse leks was similar between study areas with one lek every 72 km^2 in Bighorn Basin and one every 74 km^2 in Central Wyoming. However, the density of grouse was almost three times higher in Central Wyoming with a displaying male every 2.3 km^2, but only one every 6.6 km^2 in Bighorn Basin. There was little anthropogenic disturbance in both study areas and existing disturbance was localized. However, both study areas have potential for increased disturbance in the future: namely, bentonite mining in the Bighorn Basin, and uranium mining in Central Wyoming. Our analysis was not designed to directly evaluate the Core Area Strategy, but was relevant to the philosophy that the Core Area Strategy was based, which was the prioritization of sage-grouse breeding habitat. To clarify, throughout this paper we defined a core population (e.g., Central Wyoming) as a relatively larger (i.e., more dense) population surrounded by additional occupied habitat which is not equivalent to identified core areas from the Core Area Strategy. Our smaller, peripheral population (i.e., Bighorn Basin) did include areas of protection under the Core Area Strategy.

2.2. Objective 1: Migration and season classification

Female sage-grouse were captured and equipped 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 defined seasonal ranges and migration events (see Pratt et al., 2017) based from a 95% utilization distribution calculated 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). We then classified all grouse locations to the appropriate season (breeding, summer, winter) or inter-seasonal period (summer transition, fall transition, spring transition). We classified locations as migratory if they were outside seasonal range and part of a migration event. We defined seasonal arrival and departure dates for migratory grouse 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. Locations of non-migratory grouse were assigned to season based from the mid-point between the median arrival and departure dates of migratory grouse.

2.3. Objective 2: Seasonal resource selection, habitat correlation, and mapping

We measured sage-grouse population-level resource selection for each season and inter-seasonal period for both study areas with grouse-use locations compared to available locations (Manly et al., 2002). Grouse-use locations were pooled for each study area and habitat availability was defined to the extent of the study area. In the Bighorn Basin we restricted habitat availability to each individual research site. We initially generated 20 times the number of available locations as all combined seasonal grouse-use locations (within minimum convex polygon of use locations), but removed available locations that occurred outside our final study area extents which we delineated by accumulating 95% utilization distributions for every bird-season-year. We removed additional available locations that occurred in non-habitat by censoring land covers that were closed canopy, developed, or non-terrestrial (2011 National Land Cover Database; Homer et al., 2015). This design helped highlight which habitat covariates grouse select for in one season compared to other seasons by eliminating much of the larger regions of non-habitat. We modeled the relative probability of selection for each seasonal analysis with generalized estimating equations (PROC GENMOD, SAS 9.4, SAS Institute Inc., 2012), by assigning available locations equally amongst individuals to form clusters and account for repeated observations of the same individual (Koper and Manseau, 2009; Fieberg et al., 2010). During the model-selection process we selected between independent and compound-symmetric correlation structures (Koper and Manseau, 2009).

Landscape predictor variables were based on climate, grouse features, topography, and vegetation (see Appendix A for details). We wanted to be comprehensive so we included as many biologically-meaningful variables as possible, measured at multiple spatial scales, 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 employed several variable reduction steps as a reasonable compromise between obtaining good habitat predictions and model interpretability. Our final models included a maximum of 10 of the most significant variables. We first compared single-variable models, and their quadratic equivalents, with quasi-likelihood criteria (QIC; Pan, 2001) to evaluate individual variable support. We systematically selected top-performing variables while removing correlated ($|r| \geq 0.6$) variables from further consideration. We then created a global model of all selected variables and implemented a manual backward variable-selection procedure removing the least significant variable with the largest *P*-value. We repeated this step until we reached a maximum of 10 included variables. We continued this process and selected a model with fewer than 10 variables if it had a lower QIC, which occurred in four out of the 12 models. In almost all cases (11 of 12) the final selected models had more than 10 terms because of included quadratic terms. Variables measured at two different scales were allowed in the final model if they were not correlated. We checked for sign switching of parameter coefficients when moderately-correlated variables ($0.3 \leq |r| < 0.6$) were removed from the final model. If this occurred the variable was removed from further consideration and the variable-selection procedure was repeated.

We validated the predictive performance of our final seasonal resource selection models using five-fold cross validation (Johnson et al., 2006). For each of the main seasons, we randomly created five independent folds by estimating parameter coefficients from all locations of 80% of the individuals, withholding a unique 20% for each fold (Koper and

Manseau, 2010). For the inter-seasonal analyses, we retained 80% of the locations of each individual because the small number of locations for many individuals would create highly variable sizes in the folds. We then mapped the predicted resource selection function based from the retained data into five quantiles 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 values (Johnson et al., 2006). Our final seasonal resource selection maps (30-m resolution) were binned into five quantiles (1–5 from lowest to highest relative probability of selection; Sawyer et al., 2006). To ascertain seasonal habitat similarity and potential habitat conservation strategies we calculated correlation coefficients and network plots based from the binned resource selection levels amongst the seasonal resource selection maps (method = Pearson; corrr R package, Jackson, 2016; R version 3.4.1). We then created a comprehensive (i.e., included year-long requirements) habitat map, which weighed each season equally, by summing the binned selection values for all six seasons. This resulted in possible values from six (low probability of selection for all seasons) to 30 (high probability of selection for all seasons). We further binned the final comprehensive map into five quantile bins to represent relative levels of increasing conservation priority (i.e., importance for multiple seasons).

2.4. Objective 3: Seasonal habitat demographic-weight index and mapping

As an alternative to weighting each seasonal habitat equally, we weighted each season by its estimated contribution to population change by measured demographic vital rates (adult survival, nest survival, chick survival, and juvenile survival) that occur in each season. We first used values for the proportion of variation in population change by the three vital rates, female survival (17.5%; adult and juvenile survival), nest survival (34%), and chick survival (22.5%), that accounted for the majority (~74%) of variation, reported from a range-wide analysis (Taylor et al., 2012). We proportionally rescaled these values so they would sum to 100%, as if they explained all the variation in population change. We further split Taylor et al. (2012) contributions from female survival, who lumped adult and juvenile survival, into contributions from adult survival (30%) and juvenile survival (70%) based from amount of variation explained reported from a population in Utah (see table 2 in Dahlgren et al., 2016). Our final demographic weights, representing the contribution to population change from vital rates were: adult survival = 0.07, nest survival = 0.46, chick survival = 0.30, and juvenile survival = 0.17. Next, we divided these demographic weights amongst how much they occurred in each season by recording the proportion of time that our GPS-marked sample spent completing these activities in each seasonal or inter-seasonal period. This can be pictured as an area under the curve as demonstrated for adult survival in Figure 2.2. We assumed that each day for a specific vital rate had equal weight regardless of season. For example, one day of adult survival in the breeding season had the same effect on the variation in population change as one day of survival in the summer season. Finally, we calculated a demographic-weighted index for each season by multiplying the proportion of each vital rate within a season by the demographic weight for that vital rate, and then summing for all the vital rates. This was interpreted as the estimated proportion of population change that was dependent on that seasonal habitat. We then created a second comprehensive (i.e., includes year-long requirements) habitat map that weighted each season according to the demographic-weighted index. We multiplied the binned season-specific resource selection map (described above) by the demographic-weighted index for that season, and summed these values for all six seasons. This map represented the relative conservation value represented in each cell. That is, cells with higher probability of selection for seasons contributing more to population change, and/or high probability of selection for multiple seasons, would have more conservation priority.

3. Results and Discussion

3.1. Objective 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; Table 2.C1). Grouse utilized from one to three seasonal ranges to meet their annual habitat requirements (Figure 2.3; Connelly et al., 2000). For those grouse who were monitored for at least one year, 82% and 63% were classified as migratory for the Bighorn Basin (n = 44) and Central Wyoming (n = 30), respectively. In the Bighorn Basin the most common behavior was to have three seasonal ranges while in Central Wyoming it was most common to have two seasonal ranges (Table 2.1). A greater percentage of grouse in the Bighorn Basin exhibited migratory behavior 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 (Figure 2.4) were 1.7-times farther in the Bighorn Basin for the summer transition (Bighorn Basin: median = 13.0 km, range: 2.5–33.8, n = 59; Central

Wyoming: median = 7.5 km, range: 4.6–12.0, *n* = 14) and 1.8-times farther for the fall transition (Bighorn Basin: median = 19.1 km, range: 4.7–92.3, *n* = 52; Central Wyoming: median = 10.4 km, range: 5.7–46.7, *n* = 28). On average, migration distances were larger in Central Wyoming (Bighorn Basin: median = 11.4 km, *n* = 35; Central Wyoming: median = 15.6 km, *n* = 17), but there were more extreme distances observed in Bighorn Basin (Bighorn Basin: range: 3.0–85.9; Central Wyoming: range: 7.1–40.8) for the spring transition. The Bighorn Basin was a smaller, more isolated population and it was more migratory, having a greater proportion of migratory individuals during all three seasons and greater migration distances during two of the seasons. This was consistent with our prediction that a smaller population should exhibit more specialized behavior. Partially-migratory populations are expected to be larger because of the release of density-dependent effects during non-shared seasons (Griswold et al., 2011). Central Wyoming, our larger study population, had on average about 50% of individuals that exhibited migratory behavior between each seasonal range. However, we do have doubts on how well our more general prediction that larger sage-grouse populations being more behavioral generalists, will apply to other populations because population density can be a function of several factors (e.g., habitat fragmentation level). This seems to be the case for larger sage-grouse populations in western and south-central Wyoming that appear to be quite migratory (Fedy et al., 2012). Both landscapes are more similar to the Bighorn Basin in elevational gradient which is conducive for sage-grouse migration (Pratt et al., 2017). In contrast, the landscape of our Bighorn Basin study area was less expansive and more naturally fragmented which likely contributed to its lower population density. However, theory suggests that these large migratory populations would be even larger if the landscape could support a greater proportion of residents. 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.

3.2. Objective 2: Seasonal resource selection, habitat correlation, and mapping

Seasonal resource selection models included variables from all variable classes and scales of measurement (see Appendix C for details). These models validated well at predicting habitat with 56 of 60 of the cross-validations meeting all standards when predicting withheld data (Table 2.C5; Johnson et al., 2006). The main seasons (breeding, summer, and winter) were less correlated in Bighorn Basin than in Central Wyoming (Table 2.2, Figure 2.5). The mean correlation coefficient of all pairwise combinations for the three main seasons was 0.23 (range: -0.07–0.40) for Bighorn Basin and 0.48 (range: 0.32–0.65) for Central Wyoming. This was consistent with our prediction that more migratory populations would have less similar seasonal habitats. We believe that the Bighorn Basin population was more migratory between less similar seasonal habitat, 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). This was represented by an opposing response to temperature between summer and winter (Appendix C). 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 (Appendix C), but were mostly absent from Central Wyoming. The shorter minimum migration distances (Figure 2.3) in the Bighorn Basin further highlights the contrast between seasonal habitats where Bighorn Basin sage-grouse were sometimes selecting more precise areas. Conversely, migratory habitat was more correlated with the main seasons in Bighorn Basin than in Central Wyoming. The mean correlation coefficient of all pairwise combinations between inter-seasonal periods and the main seasons was 0.42 (range: -0.07–0.74) for Bighorn Basin and 0.29 (range: 0.11–0.50) for Central Wyoming. Migratory habitat in the Bighorn Basin was not very unique and it was most similar to breeding habitat, even for the fall transition which connects summer and winter range (Figure 2.5). This was also a function of the elevational gradient across the landscape: winter range was 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; proximity to leks was even predictive of fall transitional habitat (Appendix C). In contrast, habitat use during the summer and fall transition was unique from other seasonal habitats in Central Wyoming (Figure 2.5).

We mapped the conservation value of our study area landscapes, based on the relative probability of resource use (i.e., raster cells) for multiple seasons (weighting each season equally; Figure 2.D1). Breeding habitat was the most correlated with all other seasonal habitats in both study areas (Table 2.2, Figure 2.5). Therefore, the habitat conservation strategy that would maximize protecting the landscape's conservation value should prioritize breeding habitat. What may differ between study areas are what seasonal habitats to prioritize next because conservation of breeding habitat would not meet these other seasonal needs. In the Bighorn Basin, these would be summer (r = 0.40 between breeding and summer) and winter ($r = 0.36$ between breeding and winter) habitat because they are the most dissimilar to breeding habitat, while in Central Wyoming they would be summer transitional ($r = 0.23$ between breeding and summer transition) and fall transitional ($r = 0.26$ between breeding and fall transition) habitat.

3.3. Objective 3 – Seasonal habitat demographic-weight index and mapping

As an alternative to prioritizing seasonal habitat and predicting comprehensive habitat requirements by weighting each season equally, we calculated the estimated proportion of population change that was dependent on each seasonal habitat by measuring the proportion of demographic rates that occur in each season. For both study areas, winter habitat had the greatest contribution to adult and juvenile survival while chick survival was mostly dependent on breeding habitat (Table 2.3). All vital rates combined, breeding habitat had most of the proportional contribution to population change with about 71% in Bighorn Basin and 73% in Central Wyoming. Summer and winter habitat approximately split about 22% in Bighorn Basin and 24% in Central Wyoming. That left about 7% and 3% of population change dependent on migratory habitat in Bighorn Basin and Central Wyoming, respectively. We mapped the conservation value of our study area landscapes, based on the relative probability of resource use for each season weighted by the season's estimated contribution to population change (Figure 2.D2). The habitat conservation strategy that would maximize protecting the landscape conservation value would prioritize breeding habitat because it would provide the greatest buffer to population change.

Our general conclusion is likely applicable to many sage-grouse populations because we based our calculations from a range-wide demographic analysis (Taylor et al., 2012). If a local population deviated from the average range-wide population, which may be the case for a Utah population where adult and juvenile survival explained more variation in population change (Dahlgren et al., 2016), then the three main seasons would be weighted more equally, though the breeding season would still likely have the largest weight. Our approach to prioritizing seasonal habitats assumed that threats would affect the demographic rates that naturally vary the most (e.g., nest survival; Taylor et al., 2012) which would slightly alter conclusions if this was not the case. For example, if a threat had no impact on nest survival, but decreased adult survival, then the main seasonal habitats would have a more similar demographic-weighted index, resulting in a lowered emphasis on breeding habitat. For sage-grouse, there are documented negative impacts from development associated with both reproductive (e.g., Aldridge and Boyce, 2007; Kirol et al., 2015) and adult survival (e.g., Holloran, 2005) rates so the calculation of the demographic-weighted index may need to be customized to each specific conservation scenario. This analysis also 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 disturbance during the breeding season, but not during the winter season, are not addressed here (State of Wyoming, 2015).

Though our investigation did not intend to directly evaluate the Core Area Strategy some of its conclusions are consistent with another analysis, using similar observations, which did evaluate the Core Area Strategy relative to protecting winter habitat (Smith et al., 2016).

One conclusion in Smith et al. (2016) was that smaller delineated areas of protection through the Core Area Strategy were less likely to capture winter habitat use. We provide further refinement of this conclusion in that migratory populations associated with smaller areas of protection are less likely to have all their seasonal habitat needs fall under the delineated protected area. We feel this conclusion can be expanded to include summer habitat for populations that exhibit migratory behavior between breeding and summer range.

4. Conclusion

The Bighorn Basin population was 30% more migratory and its breeding, summer, and winter seasonal habitats were about 52% less similar than in the larger, core population in Central Wyoming. However, its transitional habitats were less unique because most migrations were through breeding range (Figure 2.5). In contrast, migratory individuals in Central Wyoming during the summer and fall were using unique areas compared to non-migratory birds. In conclusion, comprehensive habitat conservation strategies should take similar initial approaches for both our smaller population and our larger population. Conservation strategies should prioritize breeding habitat first because it was the seasonal habitat that was the most like all other seasons (Table 2.2) and it had the greatest ability to buffer population change accounting for demographic rates that contribute to about 72% of yearly population change. This provides justification for the initial approach taken by the Core Area Strategy. After prioritizing breeding habitat, the optimal conservation strategies do slightly differ 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 dissimilar to breeding habitat. These areas would be easily identified by calculating the differences in probability of selection between summer and winter habitat and the original habitat-prioritization map (Figure 2.D3). In Central Wyoming, some migratory habitat was the most unique seasonal habitat. However, it can be argued that this seasonal habitat deserves less priority because it was used by a smaller proportion of the population or its use by grouse lasted over a short-time period (Figure 2.2); therefore, it accounted for demographic rates that contributed to only about 3% of population change. These conclusions are based on theoretical partial degradations of seasonal habitat from habitat loss and fragmentation. Under no scenario could any seasonal habitat be completely neglected. For example, if migratory habitat in Central Wyoming was completely lost the population would decrease substantially because 63% of the population uses this habitat. Because breeding habitat was the most correlated with other seasonal habitat and it supported demographic rates that contributed the most to population change, both approaches to mapping conservation-priority areas for comprehensive habitat requirements produced very similar predictions (Appendix D).

Strategies to delineate conservation reserves designed to protect vital habitat needs 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 (Fedy et al., 2012; Smith et al., 2016). For a migrant species all seasonal requirements should be prioritized for protection. While for a resident species conserving a landscape for one seasonal requirement will also conserve other seasonal requirements. For partial migrants, our study highlights the need for local information on the extent each seasonal habitat needs to be prioritized because behavior can vary greatly from population to population. Specifically 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). Conservationists delineating habitat conservation reserves that actively address comprehensive, year-long requirements for sage-grouse will be creating the largest umbrella that will protect the greatest number of species. This would also be the case for many similar species of conservation concern worldwide because partial migration is the most widespread form of migration (Chapman et al., 2011).

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Table 2.1. Combinations of seasonal ranges utilized by GPS-marked greater sage-grouse in the Bighorn Basin (*n* = 44) and Central Wyoming (*n* = 30), USA, 2011–2015.

Seasonal Ranges		Bighorn Basin	Central Wyoming
Number	Combinations	%	%
1	Breeding/Summer/Winter	18	37
2	Breeding and Summer/Winter	2	0
2	Summer and Breeding/Winter	14	20
2	Winter and Breeding/Summer	14	23
3	Breeding and Summer and Winter	52	20

Table 2.2. Correlation coefficients (*r*) between greater sage-grouse seasonal habitat binned into five quantiles of relative probability of selection in Bighorn Basin (to top-right of diagonal) and Central Wyoming (to lower-left of diagonal), USA, 2011–2015.

Season	Breeding	Summer transition	Summer	Fall transition	Winter	Spring transition
Breeding		0.61	0.40	0.74	0.36	0.63
Summer transition	0.23		0.56	0.59	-0.07	0.54
Summer	0.65	0.39		0.44	-0.07	0.28
Fall transition	0.26	0.08	0.11		0.30	0.69
Winter	0.46	0.14	0.32	0.34		0.28
Spring transition	0.42	-0.22	0.24	0.27	0.50	

Table 2.3. Descriptive statistics of greater sage-grouse seasonal ranges, relative to timing of presence, proportion of population using inter-seasonal periods, proportion of vital rates (*S* = survival) attributed to each season, and the demographic-weighted index representing the estimated proportion of population change based from each season, in Bighorn Basin and Central Wyoming, USA, 2011–2015.

Season	Median start date[a]	Proportion				Demo. index[bc]
		migratory	adult *S*	chick *S*	juvenile *S*	
Bighorn Basin						
Breeding	19 Mar		0.230	0.758	0.016	0.706
Summer transition	16 Jun	0.79	0.042	0.147	0.046	0.055
Summer	10 Jul		0.295	0.095	0.342	0.107
Fall transition	7 Oct	0.84	0.046	0.000	0.063	0.014
Winter	9 Nov		0.369	0.000	0.508	0.112
Spring transition	16 Mar	0.63	0.018	0.000	0.024	0.005
Central Wyoming						
Breeding	16 Mar		0.309	0.819	0.017	0.730
Summer transition	30 Jun	0.50	0.005	0.010	0.001	0.003
Summer	6 Jul		0.279	0.171	0.380	0.136
Fall transition	1 Oct	0.66	0.061	0.000	0.091	0.020
Winter	6 Nov		0.335	0.000	0.494	0.107
Spring transition	10 Mar	0.44	0.011	0.000	0.017	0.004

[a] based from migratory grouse only

[b] the weights used to calculate the demographic index were 0.07 for adult survival, 0.46 for nest survival, 0.30 for chick survival, and 0.17 for juvenile survival based from Taylor et al. (2012) and Dahlgren et al. (2016)

[c] proportion of nest survival is not shown because, by definition, all weight is associated with breeding habitat

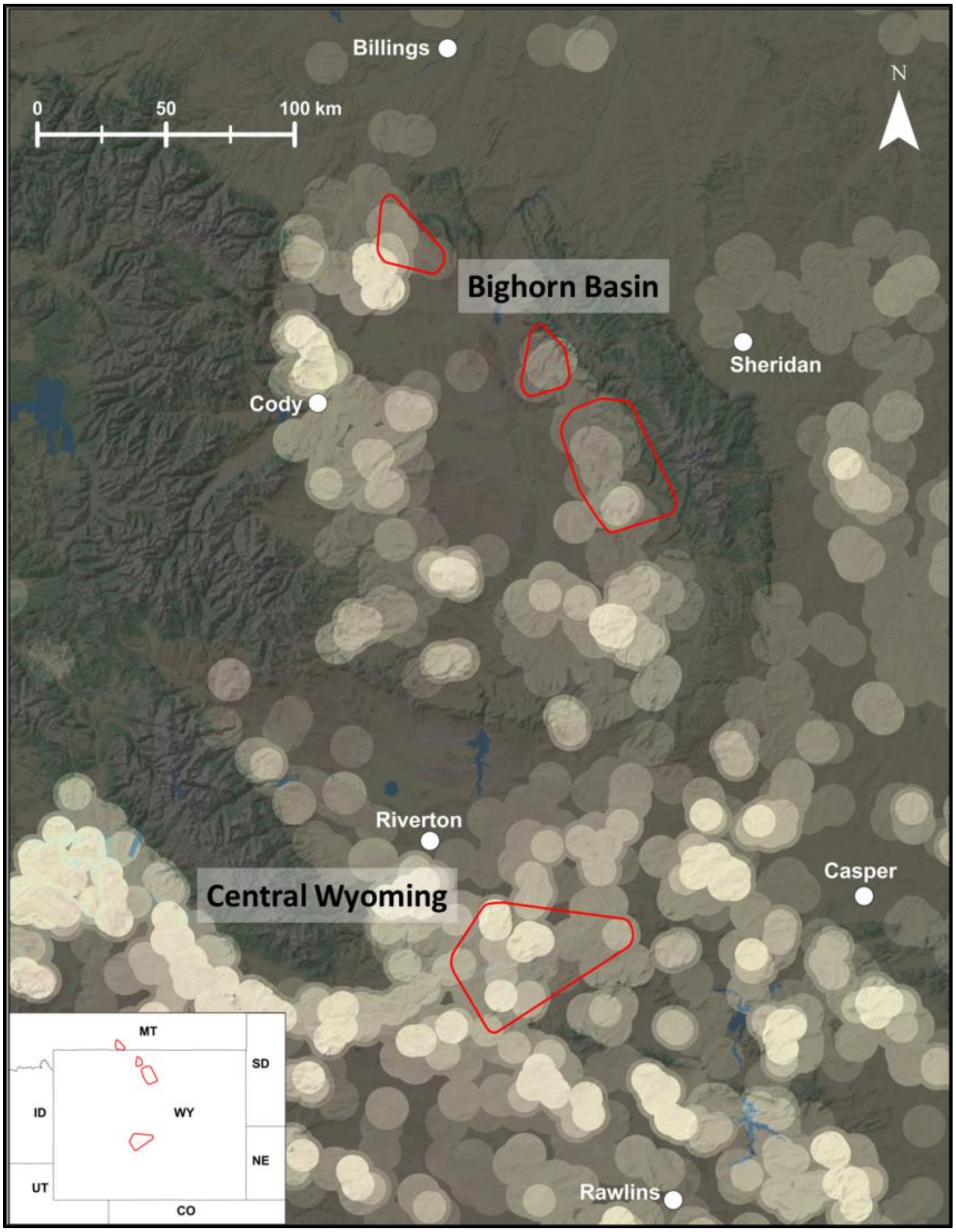

Figure 2.1. Minimum convex polygons (red polygons) of greater sage-grouse capture locations in Bighorn Basin and Central Wyoming, USA, 2011–2014. Regions increasingly highlighted represent increasing breeding kernel density (100%, 75%, 50%, and 25%; from Doherty et al. 2011) of sage-grouse.

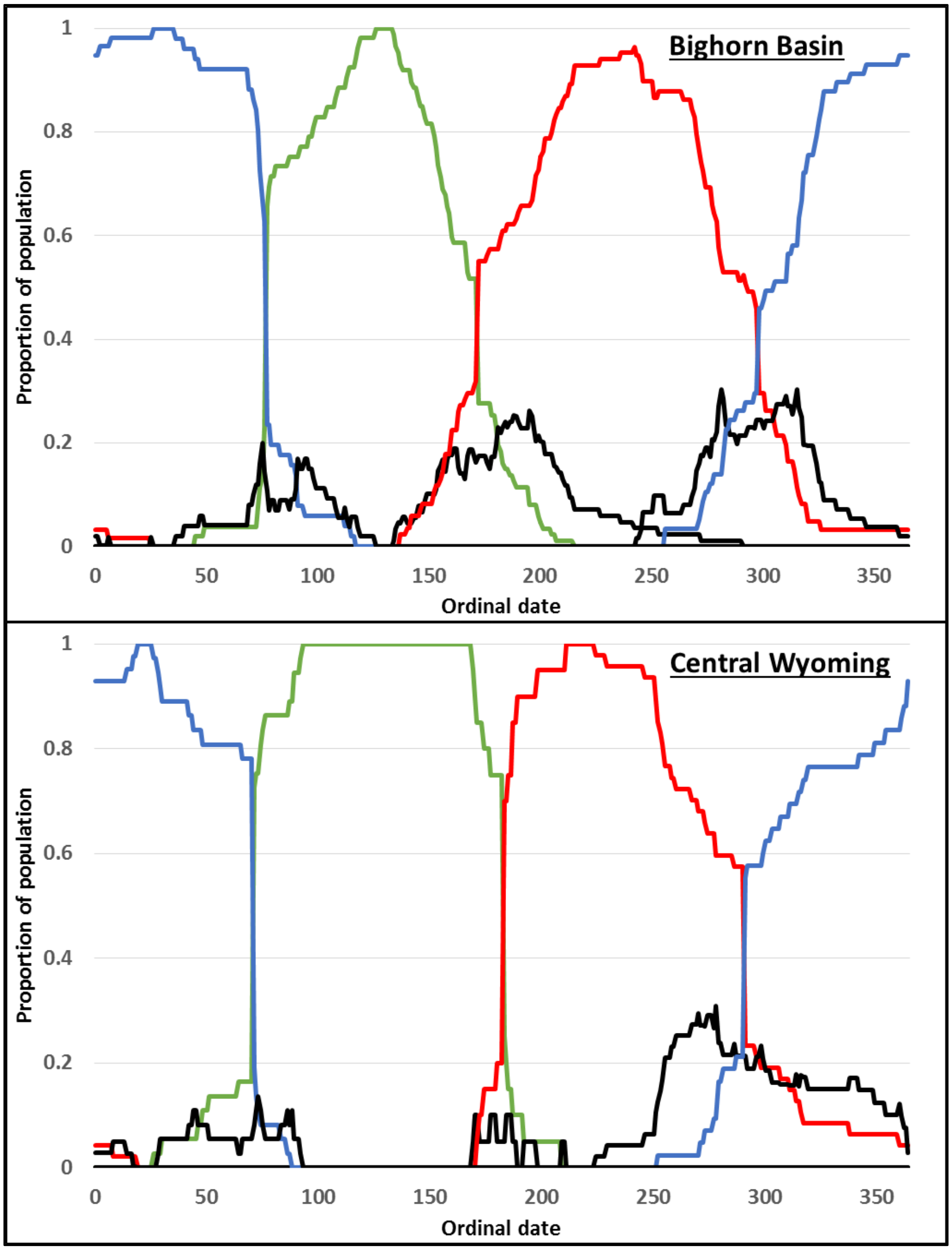

Figure 2.2. Proportion of the GPS-marked greater sage-grouse population during breeding (green), summer (red), winter (blue), and inter-seasonal periods (black) in Bighorn Basin and Central Wyoming, USA, 2011–2015. The proportion of time spent in each season was used to calculate the amount of variation in population change from adult survival that was attributed to each season.

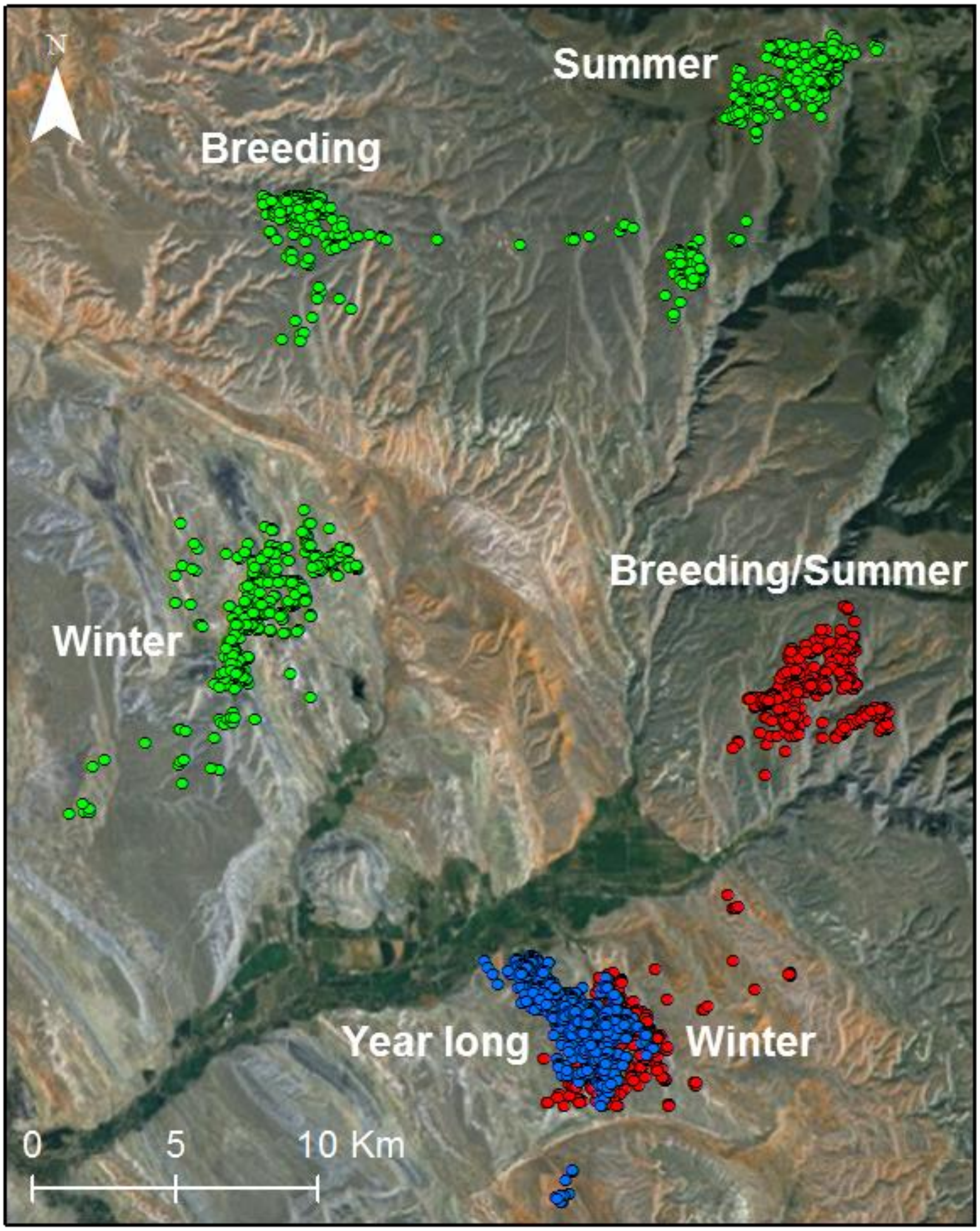

Figure 2.3. Locations over one year for three greater sage-grouse that exemplify different types of migration behavior where grouse utilize one (blue), two (red), or three (green) unique seasonal ranges to meet breeding, summer, and winter habitat requirements.

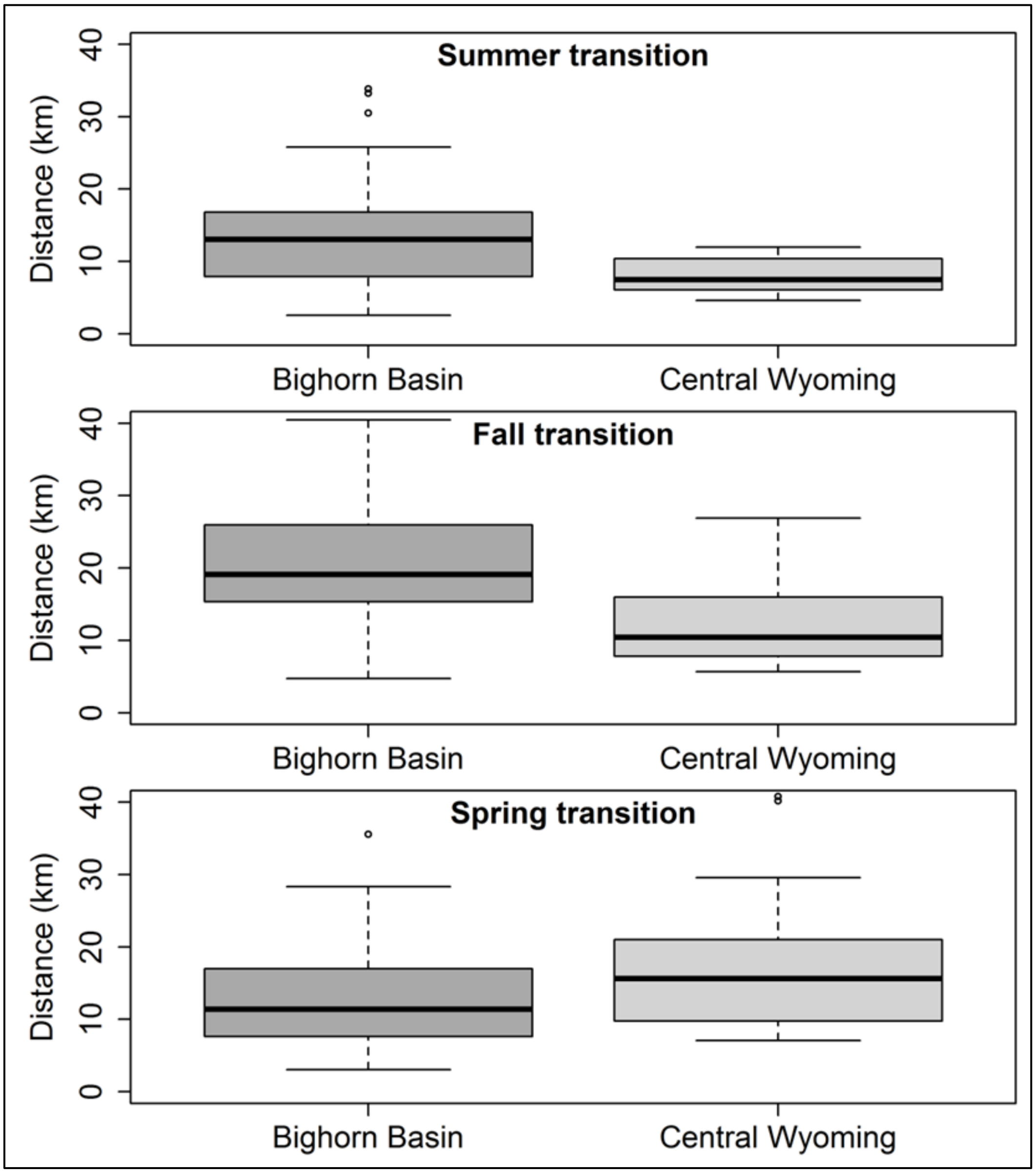

Figure 2.4. Box plots of greater sage-grouse migration distances observed for summer transition (breeding-summer), fall transition (summer-winter), and spring transition (winter-breeding) in Bighorn Basin and Central Wyoming, USA, 2011–2015. Vertical axes are identical for easier comparison among seasons, which resulted in omitting some (fall transition: Bighorn Basin = 5, Central Wyoming = 2; spring transition: Bighorn Basin = 5) outliers from the chart area.

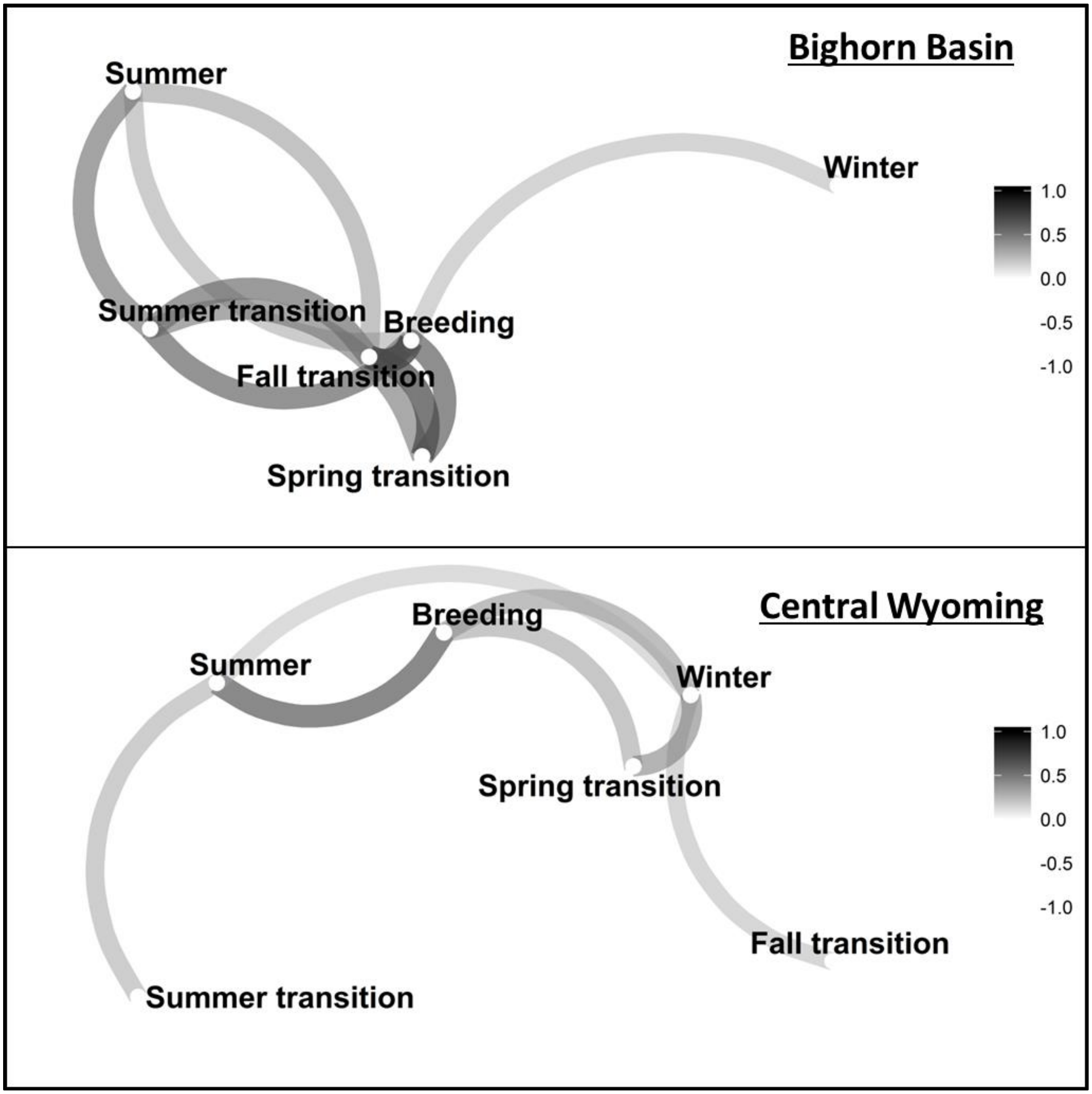

Figure 2.5. Network plot representing the correlations between greater sage-grouse seasonal habitat in Bighorn Basin and Central Wyoming, USA, 2011–2015. Darker shades represent larger correlations. Correlations <0.3 are not displayed for easier readability.

Appendix A. Resource Selection Predictor Variables

Landscape predictor variables for greater sage-grouse (*Centrocercus urophasianus*) resource selection modeling were based on climate, grouse features, topography, and vegetation (Table 2.A1). We wanted to be comprehensive so we included as many biologically-meaningful variables as possible, measured at multiple spatial scales, including variables used in other sage-grouse resource selection studies (e.g., Fedy et al., 2014; Smith et al., 2016; Walker et al., 2016). Climate variables included temperature and snow. Temperature was the mean daily temperature (30-year [1981–2010] normal; 4-km resolution; PRISM Climate Group, 2016) for the days bounded by the study area specific median seasonal arrival and departure dates. Snow was the mean snow depth (for 2011–2015; 750-m resolution; Liston and Elder, 2006) for the days bounded by the study area specific median winter range arrival and departure dates for the winter analysis. For the breeding season analysis, we used the range of estimated study area-specific copulation dates, which we defined as three weeks prior to initiation of nest incubation (Schroeder et al., 1999), to measure mean snow depth. We felt that this period represented the approximate time that females made final commitments to a specific nest site. For the inter-seasonal analyses, we selected the more predictive temperature and snow variable of either the relevant departure or arrival season. We considered Euclidean distance to nearest active lek for all seasonal analyses. For inter-seasonal analyses we also considered cumulative Euclidean distance to the nearest relevant departure and arrival seasonal habitat. For example, for the summer transition, this variable for each location was the sum of the distance to nearest breeding habitat and nearest summer habitat. For this calculation specifically, we defined seasonal habitat as the top 20% quantile relative probability of selection after we completed the resource selection modeling of the main three seasons. Topographic variables included compound topographic index (soil wetness index; Gessler et al., 1995), heat load index (amount of radiation index; McCune and Keon, 2002), slope, and vector ruggedness measure (topographic roughness index; Sappington et al., 2007) calculated from a 10-m digital elevation model (EROS, 2016b) and ArcGIS 10.0 (ESRI, 2011). We calculated compound topographic index and heat load index using the geomorphology and gradient metrics toolbox (Evans et al., 2014) and we calculated vector ruggedness measure using the terrain ruggedness tool (Sappington, 2012).

We also considered several vegetation metrics that included variables of percent cover representing the ground (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*) presence, and probability of juniper presence (*Juniperus* spp.). We predicted these vegetation variables for our study areas by using Random Forest regression or classification (Breiman, 2001) with remotely-sensed spatial data and field measurement plots (30-m resolution; see Appendix B for details). From these continuous vegetation metrics, we created binary (habitat/non-habitat) breeding and winter habitat spatial data. Raster cells were classified as habitat if they met the vegetation requirements (shrub height, sagebrush cover, and herbaceous cover) described for arid sites in Connelly et al. (2000). We also utilized categorical land cover data from National Land Cover Database (NLCD; 30-m resolution;

Homer et al., 2015) to represent agriculture, forest, and wetlands (primarily riparian in our study areas). Our final vegetation variable was the soil-adjusted vegetation index (SAVI; Qi et al., 1994), which represents vegetation ‘greenness.’ We calculated SAVI from a median surface reflectance image (30-m resolution; Landsat 8 Operational Land Imager; EROS, 2016a) from Landsat images associated with the nearest first day of the month (2013–2015) for June (17 May–16 Jun; 17 Apr–16 May images would have been included but they were too cloudy), for breeding-season analysis, and for August/September (17 Jul–16 Sep), for summer season analysis. For the relevant inter-seasonal analyses, we selected the more predictive breeding or summer season vegetation index of either the departure or arrival season.

We considered the topographic and vegetation metrics measured at multiple spatial scales. We created a systematic list of seven radii around each location that started with 0.05 km (that would include at least twice the distance error of GPS locations) and that doubled in size until 3.2 km (approximate size that is still able to distinguish large regions of the study area). Within each of these scales we calculated mean and standard deviation for the topographic and continuous vegetation metrics. For the categorical vegetation metrics, we calculated the proportion of the area for each variable within the radii. In addition, for the NLCD land cover variables we measured Euclidean distance to the nearest appropriate land cover, as well as, distance scaled between 0 (away) and 1 (near) with a decay function ($e^{-d/\alpha}$, d = distance; Aldridge et al., 2012) where α was set to the same values as our radii. The parameter coefficients for distance variables need to be interpreted with caution: a positive coefficient for a Euclidean distance variable demonstrates an avoidance of the variable; while a positive coefficient for a distance decay variable demonstrates a selection for the variable. We considered a quadratic relationship for all variables except the distance decay variables. The distance decay variables and the quadratic variables allowed for non-linear relationships. We did not consider annual grass cover and agriculture for Central Wyoming because these features were mostly absent from the study area.

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Table 2.A1. Variables used for measuring greater sage-grouse seasonal resource selection in Bighorn Basin and Central Wyoming, USA, 2011–2015.

Code	Description
Climate	
Temp	Average (30-year normal) seasonal (breeding, summer, winter) temperature (°C)
Snow	Average seasonal (breeding, winter) snow depth (cm)
Grouse	
Lek	Distance to nearest lek (km)
SeHab	Cumulative distance to seasonal habitat (km)
Topographic	
CTI	Compound topographic index[a]
HLI	Heat load index[a]
Slope	Slope (%)[a]
VRM	Vector ruggedness measure[a]
Vegetation	
Herbaceous/Ground	
AnnG	Annual grass cover (%)[ab]
Bare	Bare ground (%)[a]
Herb	Herbaceous cover (%)[a]
Shrub	
ArC	Big sagebrush cover (%)[a]
BSaP	Black sagebrush (probability of presence)[a]
JunP	Juniper (probability of presence)[a]
NSaC	Non-sagebrush cover (%)[a]
ShC	Shrub cover (%)[a]
ShH	Shrub height (cm)[a]
Land cover	
Ag	Agriculture land cover[bc]
BHab	Breeding vegetation requirements[d]
Fore	Forest land cover[c]
Wetl	Wetland land cover[c]
WHab	Winter vegetation requirements[d]
Vegetation index	
Savi	Soil-adjusted vegetation index[a]

[a] Variable measured on continuous values as mean and standard deviation at multiple spatial scales

[b] Variable not considered for Central Wyoming because it was mostly absent

[c] Variable measured on categorical designations as distance (km) to variable using multiple decay functions and proportion of area of variable at multiple scales

[d] Variable measured on categorical designations as proportion of area at multiple scales

Appendix B. Predicting Landscape Vegetation from Field Measurements

We predicted vegetation data for our Bighorn Basin and Central Wyoming study areas to use as predictor variables when developing seasonal resource selection functions for greater sage-grouse (*Centrocercus urophasianus*). We used Random Forest regression or classification (Breiman, 2001) to predict shrub height (ShH; cm), shrub cover (ShC; %), big sagebrush cover (*Artemisia tridentata*; ArC; %), non-sagebrush cover (not *Artemisia* spp.; NSaC; %), herbaceous cover (Herb; %), bare ground (Bare; %), annual grass cover (AnnG; %; predominately cheatgrass [*Bromus tectorum*]), probability of juniper presence (*Juniperus* spp.; JunP), and probability of black sagebrush presence (*A. nova*; BSaP) at 30-m resolution using a host of spatial predictor data including surface reflectance imagery, climate measures, topographic metrics, vegetation indices, and soil metrics (Table 2.B1) and based on independent field measurements. We employed a Random Forest model selection procedure that removed redundant predictors and that minimized the number of predictors while minimizing classification error or maximizing the variation explained as described in Murphy et al. (2010) and Evans et al. (2011; randomForest [Liaw and Wiener, 2002] and rfUtilities [Evans and Murphy, 2014] R packages, R version 3.2.4 [R Core Team, 2016]). Final prediction rasters were censored to landscapes that were open canopy, natural, and terrestrial (class = 31, 52, and 71) according to the 2011 National Land Cover Database (Homer et al., 2015). We also limited predictions of shrub height to areas with >7.5% predicted shrub cover. We did not predict annual grass cover in Central Wyoming because of its scarcity.

Spatial predictor data

We utilized several publically-available spatial datasets that we deemed as potentially influential on vegetation (Table 2.B1). We used surface reflectance images from Landsat 8 Operational Land Imager (EROS, 2016a) during the 15 March–15 October, 2013–2015 growing season. We removed clouds (>33% confidence of cloud cover) from each image according to the quality assessment band. We then calculated a median image across years and image dates associated with the nearest first day of the month for April, May, June, July, August, September, and October. We were not able to calculate a useful May image because of extensive cloud cover. We also calculated vegetation metrics from these images that represent vegetation ‘greenness’ (Qi et al., 1994), moisture content (Gao, 1996), and leaf area (Homer et al., 2012). We also utilized topographic characteristics based from a digital elevation model (EROS, 2016b) and soil characteristics based from the US General Soil Map (Hanser et al., 2011). We calculated compound topographic index and heat load index using the geomorphology and gradient metrics toolbox (Evans et al., 2014) and ArcGIS 10.0 (ESRI, 2011). We calculated topographic ruggedness using the terrain ruggedness tool (Sappington, 2012). We also utilized 30-year (1981–2010) normal temperature and precipitation data (PRISM Climate Group, 2016).

Independent data from field measurements

We completed 30 x 30 m field measurement plots at sage-grouse use locations (nests, brood-rearing, and roosting sites; *n* = 1161), random locations paired with use locations (random direction and distance between 100–500 m away; *n* = 1051), and non-paired random locations (*n* = 281) during 2011–2015. We delineated plots with 4, 15-m transects (60-m total length) starting at plot center and extending in the 4 cardinal directions. We measured shrub cover (%), by species, with line intercept (proportion of transect intercepted by shrubs [3-cm minimum intercept and gap]; Canfield, 1941; Wambolt et al., 2006) and several categories of ground and herbaceous cover (%) with quadrats (0.1 m^2, *n* = 17/plot; Daubenmire, 1959). We measured the maximum height (cm; excluding inflorescences) of each shrub that intercepted the transect. Herbaceous cover was the sum of annual grass, perennial grass, residual grass, and forb cover (herbaceous cover >100% was possible). Bare ground was the sum of bare soil and rock. We also recorded the presence of juniper and black sagebrush based off the line intercept data. Field measurements occurred during the growing season (mean = 17 June, SD = 18 days). We supplemented our field measurements, to obtain a more complete spatial coverage of our study areas, with measurements (*n* = 417) collected during the same time frame by other agencies with other sampling protocols and objectives. To maintain balanced samples for classification we randomly selected plots absent of juniper or black sagebrush equal to the number of plots where they were present. We also only used plots with shrubs to develop the model to predict shrub height. Final sample sizes were 2387 for shrub height, 2908 for shrub cover, 2910 for big sagebrush cover, 2908 for non-sagebrush cover, 2909 for herbaceous cover, 2721 for bare ground, 1536 for annual grass cover, 196 for probability of juniper presence, and 620 for probability of black sagebrush presence.

Model evaluation

We demonstrated the predictive performance of our models by validating with a random 15% of plots that were withheld from model development. There was a positive relationship between the predicted and measured values for all continuous vegetation predictions with adjusted r^2 values lowest for non-sagebrush cover ($r^2 = 0.30$) and highest for bare ground ($r^2 = 0.51$). There was a tendency to overestimate plots with low values and underestimate plots with high values, which was represented by intercepts greater than zero and slopes less than one for best-fit lines (Figure 2.B1). Homer et al. (2012) created vegetation predictions for Wyoming that have been used by several sage-grouse resource selection modeling studies (e.g., Dzialak et al., 2012; Dzialak et al., 2013; Fedy et al., 2014; Smith et al., 2014; Kirol et al., 2015). They reported prediction validations for bare ground ($r^2 = 0.46$, intercept = 15, slope = 0.65), herbaceous cover ($r^2 = 0.14$, intercept = 12, slope = 0.46), and shrub cover ($r^2 = 0.28$, intercept = 7, slope = 0.40). Our validations for these same vegetation characteristics were better relative to adjusted r^2 values (Bare = 0.51, Herb = 0.42, ShC = 0.34) but poorer relative to best-fit line intercepts (Bare = 19, Herb = 20, ShC = 14) and slopes (Bare = 0.50, Herb = 0.39, ShC = 0.32). The percent correctly classified for 15% withheld data was 87% for juniper presence and 83% for black sagebrush presence.

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Table 2.B1. Spatial data ($n = 101$) considered for prediction of landscape vegetation, Bighorn Basin and Central Wyoming, USA.

Data	Source/reference
Satellite imagery	
April LandSat[a]	EROS, 2016a
May LandSat[b]	EROS, 2016a
June LandSat[ac]	EROS, 2016a
July LandSat[a]	EROS, 2016a
August LandSat[a]	EROS, 2016a
September LandSat[a]	EROS, 2016a
October LandSat[a]	EROS, 2016a
Vegetation metrics	
Soil-adjusted vegetation index[d]	Qi et al., 1994
Normalized-difference water index[cd]	Gao, 1996
Leaf area index[d]	Homer et al., 2012
Topographic	
Elevation	EROS, 2016b
Slope[e]	
Compound topographic index[e]	Gessler et al., 1995
Heat load index[e]	McCune and Keon, 2002
Vector ruggedness measure[e]	Sappington et al., 2007
Soils	
Available water capacity	Hanser et al., 2011
Bulk density	Hanser et al., 2011
Clay content	Hanser et al., 2011
Rock volume	Hanser et al., 2011
Salinity	Hanser et al., 2011
Sand content	Hanser et al., 2011
Silt content	Hanser et al., 2011
Soil depth	Hanser et al., 2011
Soil pH	Hanser et al., 2011
Climate	
Annual and monthly maximum temperature	PRISM Climate Group, 2016
Annual and monthly minimum temperature	PRISM Climate Group, 2016
Annual and monthly precipitation	PRISM Climate Group, 2016
Location	
X coordinate	
Y coordinate	

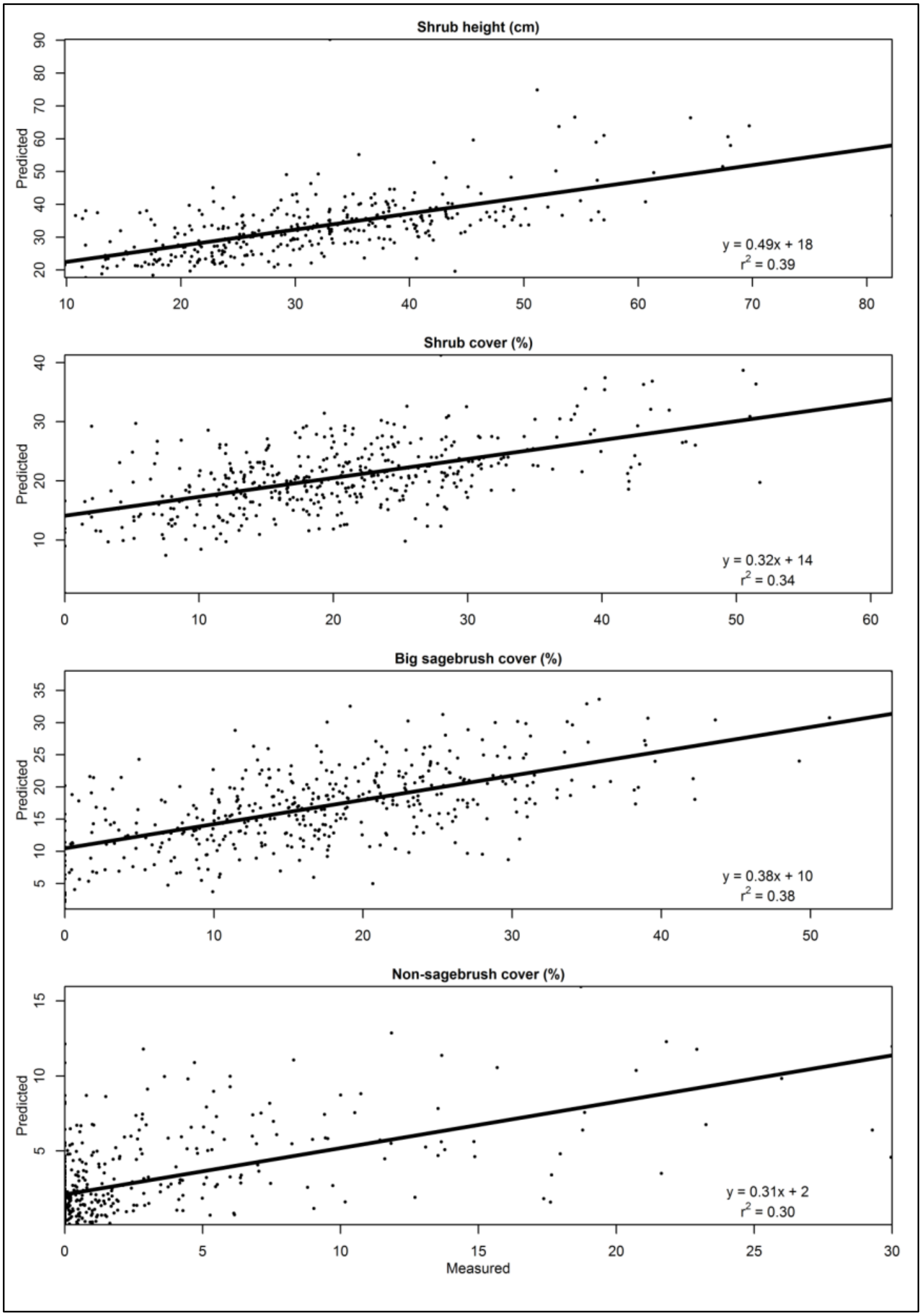
[a] Included blue, green, red, near-infrared, and short wave-infrared bands (bands 2–6)

[b] May Landsat images were too cloudy for use

[c] Spatial coverage of June short wave-infrared band and resultant normalized difference water index was too restricted for use

[d] Calculated from each Landsat image

[e] Calculated from digital elevation model


Shrub height (cm)
Predicted
y = 0.49x + 18
r^2 = 0.39
Shrub cover (%)
Predicted
y = 0.32x + 14
r^2 = 0.34
Big sagebrush cover (%)
Predicted
y = 0.38x + 10
r^2 = 0.38
Non-sagebrush cover (%)
Predicted
y = 0.31x + 2
r^2 = 0.30
Measured

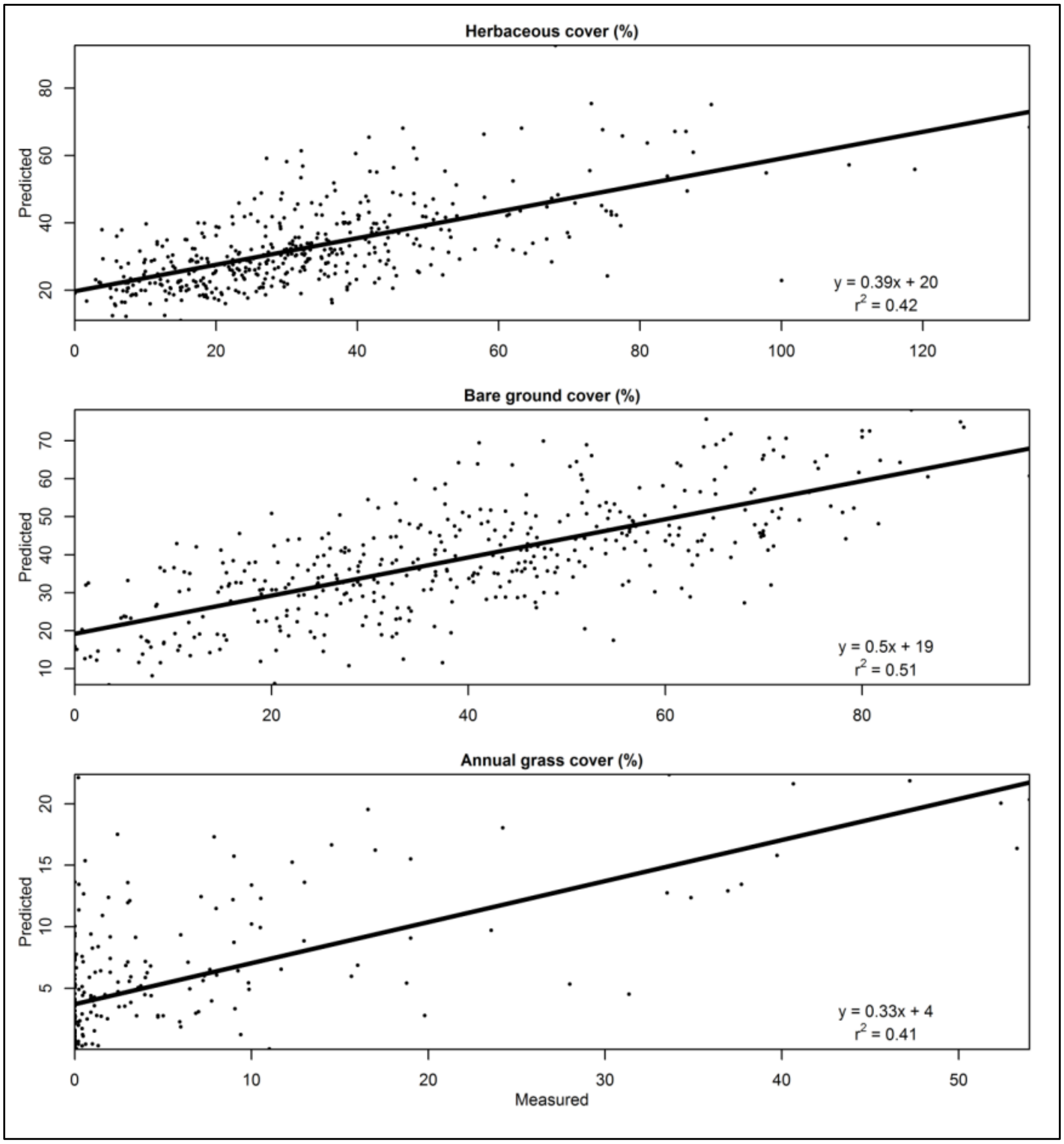


Figure 2.B1. Correlations between vegetation model predictions and field measurements from 15% of plots withheld from model development in Bighorn Basin and Central Wyoming, USA, 2011–2015. Axes span the range of values measured and predicted for withheld data.

Appendix C. Resource Selection Parameter Estimates, Variable Correlations, and Validation

Table 2.C1. Number of GPS-marked greater sage-grouse, grouse-use locations, and the average ratio of available to used locations per grouse that were used to measure seasonal resource selection in Bighorn Basin and Central Wyoming, USA, 2011–2015. Generated available locations were used for each seasonal analysis by equally distributing them amongst individuals to form clusters.

Season	Locations	Grouse	Available:Used
Bighorn Basin			
Breeding	32 885	70	20
Summer transition	6711	42	100
Summer	36 886	69	18
Fall transition	3987	38	169
Winter	26 694	48	25
Spring transition	1360	27	496
Central Wyoming			
Breeding	15 489	38	14
Summer transition	290	10	243
Summer	21 414	46	10
Fall transition	3417	23	64
Winter	14 044	34	16
Spring transition	511	12	428

Table 2.C2. Greater sage-grouse general response to landscape characteristics when selecting seasonal habitat (Br = breeding, SuT = summer transition, Su = summer, FaT = fall transition, Wi = winter, SpT = spring transition) in Bighorn Basin and Central Wyoming, USA, 2011–2015.

Variable	Bighorn Basin						Central Wyoming					
	Br	SuT	Su	FaT	Wi	SpT	Br	SuT	Su	FaT	Wi	SpT
Climate												
Temp			-		+	+			-			
Grouse												
Lek[a]	+			+/-[b]						-/+[c]		
SeHab[a]				+								
Topographic												
CTI-M[d]	+/-									+/-	+/-	+/-
CTI-SD[d]				-	-	-,-[e]				+/-	+,-	
HLI-M	+											
HLI-SD				+								
Slope-M					-							
Slope-SD			-							+/-		
VRM								+/-,-	+/-			+
Vegetation												
Herbaceous/Ground												
AnnG-M	-				+/-							
AnnG-SD				-/+		+						
Bare-M												+/-
Bare-SD		-			+			+			-	
Herb-M		+/-			-					+/-		
Herb-SD	+	+/-	+			+		+/-	+			

Shrub												
ArC-M				+/-			+	-/+	+		+/-	
ArC-SD	+		+/-							+/-		-,+/-
BSaP-M								-/+	-	-/+		
BSaP-SD	+/-						+		+/-			
JunP-M								+			-	
JunP-SD			+	+/-					+			-
NSaC-M	-	-	-/+	-	-	-	-					
NSaC-SD		-				-/+	+		+			
ShC-M					+		+/-			+/-		
ShC-SD		+/-	+/-								+	
ShH-M					-				-/+		-	+/-
ShH-SD			+	-	-	-						
Land cover												
Ag			+/-									
BHab						+/-	-					
Fore	-	-	-/+				-	+		-		
Wetl						-/+	+/-			+	-/+,+/-	
WHab				+/-								
Vegetation index												
Savi-M								+				
Savi-SD	-	+						+				

[a] For Euclidean distance variables, a '+' in this table represents selection for proximity to the variable, which is the opposite of the parameter coefficient

[b] +/- represents quadratic relationship for selection of moderate values

[c] -/+ represents quadratic relationship for avoidance of moderate values

[d] M = mean, SD = standard deviation

[e] Signs separated by a comma show variable was included in final model measured at two scales, smallest scale shown before comma

Table 2.C3. Variable type and scale of measurement, estimated coefficients (β), empirical standard errors (SE), and 95% confidence intervals (CI) for variables in resource selection models for greater sage-grouse seasonal habitat in Bighorn Basin, USA 2011–2015.

Variable	Measure[a]	Scale (km)[b]	β	SE	CI lower	CI upper	*P*
Breeding							
AnnG	mean	0.1	-0.0733	0.0284	-0.1289	-0.0177	0.001
ArC	sd	0.4	0.2962	0.0750	0.1493	0.4431	<0.001
BSaP	sd	3.2	43.195	8.5128	26.510	59.879	<0.001
BSaP-2[c]	sd	3.2	-149.92	32.596	-213.80	-86.030	<0.001
CTI	mean	0.1	3.0858	0.8348	1.4497	4.7219	<0.001
CTI-2	mean	0.1	-0.1760	0.0511	-0.2762	-0.0758	<0.001
Fore	prop.	0.4	-9.1725	3.3637	-15.765	-2.5797	0.006
Herb	sd	0.05	0.1027	0.0272	0.0493	0.1561	<0.001
HLI	mean	3.2	0.0041	0.0016	0.0009	0.0073	0.012
Lek	dist.	Euclidean	-0.2694	0.0909	-0.4476	-0.0912	0.003
NSaC	mean	0.2	-0.3113	0.0642	-0.4371	-0.1856	<0.001
Savi	sd	0.4	-37.164	10.176	-57.108	-17.220	<0.001
Summer transition							
Bare	sd	1.6	-0.2595	0.1084	-0.4720	-0.0470	0.017
Fore	dist.	0.05	-4.2630	2.1742	-8.5243	-0.0016	0.050
Herb	mean	3.2	0.4431	0.1744	0.1012	0.7849	0.011
Herb-2	mean	3.2	-0.0041	0.0018	-0.0070	-0.0006	0.022
Herb	sd	3.2	1.3806	0.7362	-0.0622	2.8235	0.061
Herb-2	sd	3.2	-0.0917	0.0461	-0.1820	-0.0013	0.047
NSaC	mean	0.2	-0.1221	0.0502	-0.2205	-0.0237	0.015
NSaC	sd	0.2	-0.9164	0.1370	-1.1848	-0.6479	<0.001
Savi	sd	0.05	14.846	3.1777	8.6172	21.0737	<0.001
ShC	sd	0.8	2.1912	0.7357	0.7492	3.6332	0.003
ShC-2	sd	0.8	-0.2304	0.0882	-0.4033	-0.0575	0.009

Summer							
Ag	prop.	0.4	5.6547	1.2393	3.2257	8.0837	<0.001
Ag-2	prop.	0.4	-5.9743	1.6202	-9.1499	-2.7987	<0.001
ArC	sd	0.4	0.5130	0.2031	0.1150	0.9111	0.012
ArC-2	sd	0.4	-0.0733	0.0315	-0.1350	-0.0116	0.020
Fore	prop.	0.1	-19.907	4.2834	-28.302	-11.512	<0.001
Fore-2	prop.	0.1	23.647	5.4070	13.049	34.245	<0.001
Herb	sd	0.8	0.0899	0.0264	0.0381	0.1417	<0.001
JunP	sd	0.8	6.7929	2.8179	1.2699	12.316	0.016
NSaC	mean	0.2	-0.2118	0.0877	-0.3837	-0.0398	0.016
NSaC-2	mean	0.2	0.0085	0.0047	-0.0007	0.0176	0.070
ShC	sd	3.2	4.2582	1.2624	1.7839	6.7325	<0.001
ShC-2	sd	3.2	-0.4545	0.1483	-0.7451	-0.1639	0.002
ShH	sd	0.1	0.0536	0.0157	0.0227	0.0844	<0.001
Slope	sd	0.4	-0.1905	0.0292	-0.2478	-0.1333	<0.001
Temp	-	-	-0.4608	0.0705	-0.5990	-0.3225	<0.001
Fall transition							
AnnG	sd	0.4	-0.4904	0.1438	-0.7724	-0.2085	<0.001
AnnG-2	sd	0.4	0.0523	0.0132	0.0264	0.0781	<0.001
ArC	mean	0.2	0.5606	0.1244	0.3167	0.8044	<0.001
ArC-2	mean	0.2	-0.0134	0.0033	-0.0199	-0.0070	<0.001
SeHab	dist.	Euclidean	-0.0978	0.0177	-0.1325	-0.0631	<0.001
CTI	sd	0.4	-2.6984	0.4309	-3.5429	-1.8539	<0.001
HLI	sd	3.2	0.0045	0.0010	0.0025	0.0065	<0.001
JunP	sd	3.2	60.476	16.682	27.781	93.172	<0.001
JunP-2	sd	3.2	-151.64	47.659	-245.05	-58.232	0.002
Lek	dist.	Euclidean	-0.5454	0.0930	-0.7276	-0.3631	<0.001
Lek-2	dist.	Euclidean	0.0322	0.0065	0.0195	0.0449	<0.001
NSaC	mean	0.2	-0.2241	0.0670	-0.3554	-0.0927	<0.001
ShH	sd	3.2	-0.4032	0.0897	-0.5791	-0.2274	<0.001
WHab	prop.	3.2	10.203	2.3000	5.6955	14.711	<0.001
WHab-2	prop.	3.2	-9.8331	2.2223	-14.189	-5.4775	<0.001
Winter							
AnnG	mean	3.2	0.8542	0.1960	0.4699	1.2384	<0.001
AnnG-2	mean	3.2	-0.0496	0.0135	-0.0760	-0.0232	<0.001
Bare	sd	3.2	0.2234	0.0672	0.0917	0.3551	<0.001
CTI	sd	0.2	-0.6243	0.1849	-0.9868	-0.2619	<0.001
Herb	mean	3.2	-0.1525	0.0375	-0.2261	-0.0790	<0.001
NSaC	mean	0.1	-0.3267	0.0501	-0.425	-0.2285	<0.001
ShC	mean	0.05	0.1620	0.0530	0.0582	0.2658	0.002
ShH	mean	0.1	-0.0999	0.0249	-0.1487	-0.0511	<0.001
ShH	sd	3.2	-0.3348	0.0967	-0.5243	-0.1454	<0.001
Slope	mean	0.2	-0.1597	0.0181	-0.1952	-0.1242	<0.001
Temp	-	-	1.3863	0.2389	0.9181	1.8546	<0.001

Spring transition							
AnnG	sd	3.2	0.2186	0.0958	0.0309	0.4063	0.022
BHab	prop.	3.2	12.224	4.1879	4.0160	20.432	0.004
BHab-2	prop.	3.2	-16.698	5.4320	-27.345	-6.0516	0.002
CTI	sd	0.1	-0.5533	0.1511	-0.8495	-0.2571	<0.001
CTI	sd	0.4	-2.7566	0.5288	-3.7931	-1.7202	<0.001
Herb	sd	0.2	0.1136	0.0313	0.0522	0.1750	<0.001
NSaC	mean	0.05	-0.1779	0.0671	-0.3095	-0.0464	0.008
NSaC	sd	0.05	-0.2924	0.1630	-0.6119	0.0271	0.073
NSaC-2	sd	0.05	0.0773	0.0197	0.0388	0.1158	<0.001
ShH	sd	0.2	-0.3344	0.0940	-0.5186	-0.1502	<0.001
Temp	-	-	1.1967	0.2692	0.6692	1.7243	<0.001
Wetl	prop.	3.2	-80.327	27.189	-133.62	-27.039	0.003
Wetl-2	prop.	3.2	703.32	263.96	185.98	1220.7	0.008

[a] sd = standard deviation, prop. = proportion, dist. = distance

[b] scale for distance statistics is α in the distance decay function

[c] 2 represents a quadratic variable

Table 2.C4. Variable type and scale of measurement, estimated coefficients (β), empirical standard errors (SE), and 95% confidence intervals (CI) for variables in resource selection models for greater sage-grouse seasonal habitat in Central Wyoming, USA, 2012–2015.

Variable	Measure[a]	Scale (km)[b]	β	SE	CI lower	CI upper	*P*
Breeding							
ArC	mean	0.05	0.1206	0.0276	0.0665	0.1746	<0.001
BHab	prop.	0.2	-2.7916	1.0627	-4.8743	-0.7088	0.009
BSaP	sd	3.2	8.4442	4.4814	-0.3392	17.228	0.060
Fore	prop.	0.4	-17.623	8.8260	-34.922	-0.3241	0.046
NSaC	sd	0.2	0.3095	0.1392	0.0367	0.5824	0.026
NSaC	mean	0.8	-0.2036	0.0904	-0.3808	-0.0264	0.024
ShC	mean	3.2	4.2777	1.6792	0.9865	7.5689	0.011
ShC-2[c]	mean	3.2	-0.0991	0.0389	-0.1753	-0.0228	0.011
ShC	sd	0.05	0.2498	0.0683	0.1159	0.3838	<0.001
Wetl	prop.	0.05	5.6760	1.8225	2.1039	9.2481	0.002
Wetl-2	prop.	0.05	-6.4173	1.9165	-10.174	-2.6609	<0.001
Summer transition							
ArC	mean	0.2	-0.5452	0.2589	-1.0526	-0.0378	0.035
ArC-2	mean	0.2	0.0198	0.0065	0.0070	0.0325	0.002
Bare	sd	0.05	0.1360	0.0401	0.0575	0.2146	<0.001
BSaP	mean	1.6	-22.657	3.9655	-30.429	-14.885	<0.001
BSaP-2	mean	1.6	24.597	3.2285	18.270	30.925	<0.001
Fore	prop.	1.6	50.929	8.0222	35.206	66.652	<0.001
Herb	sd	0.2	0.1488	0.0631	0.0251	0.2725	0.018
Herb-2	sd	0.2	-0.0097	0.0019	-0.0134	-0.0059	<0.001
JunP	mean	0.1	2.0364	0.6353	0.7912	3.2816	0.001
Savi	sd	0.8	25.231	3.6467	18.084	32.378	<0.001
Savi	mean	0.05	6.7825	1.1527	4.5232	9.0417	<0.001
VRM	mean	0.1	22.270	4.5715	13.310	31.229	<0.001
VRM-2	mean	0.1	-212.38	43.269	-297.19	-127.57	<0.001
VRM	mean	1.6	-75.274	21.073	-116.58	-33.973	<0.001

Summer							
ArC	mean	0.05	0.1049	0.0311	0.0439	0.1659	<0.001
BSaP	mean	0.1	-4.3929	0.8564	-6.0714	-2.7144	<0.001
BSaP	sd	3.2	68.242	28.365	12.647	123.84	0.016
BSaP-2	sd	3.2	-229.77	87.391	-401.05	-58.482	0.009
Herb	sd	1.6	0.3060	0.0615	0.1856	0.4265	<0.001
JunP	sd	3.2	9.6260	3.8306	2.1182	17.134	0.012
NSaC	sd	0.05	0.4009	0.1095	0.1862	0.6155	<0.001
ShH	mean	3.2	-1.9934	0.5457	-3.0629	-0.9240	<0.001
ShH-2	mean	3.2	0.0313	0.0098	0.0121	0.0504	0.001
Temp	-	-	-1.2438	0.4696	-2.1641	-0.3235	0.008
VRM	mean	1.6	114.47	61.183	-5.4520	234.38	0.061
VRM-2	mean	1.6	-991.01	560.63	-2089.8	107.80	0.077
Fall transition							
ArC	sd	1.6	2.7447	1.1683	0.4549	5.0345	0.019
ArC-2	sd	1.6	-0.4446	0.1779	-0.7934	-0.0959	0.013
BSaP	mean	3.2	-21.748	7.4917	-36.431	-7.0642	0.004
BSaP-2	mean	3.2	21.166	8.6185	4.2736	38.057	0.014
CTI	mean	0.1	1.7506	0.7949	0.1925	3.3087	0.028
CTI-2	mean	0.1	-0.0884	0.0434	-0.1736	-0.0033	0.042
CTI	sd	1.6	75.683	26.385	23.969	127.40	0.004
CTI-2	sd	1.6	-23.929	7.9081	-39.428	-8.4292	0.003
Fore	dist.	0.8	-3.3433	1.8051	-6.8813	0.1947	0.064
Herb	mean	0.05	0.4023	0.1958	0.0186	0.7859	0.040
Herb-2	mean	0.05	-0.0063	0.0032	-0.0125	-0.0001	0.047
Lek	dist.	Euclidean	1.5690	0.4628	0.6620	2.4760	<0.001
Lek-2	dist.	Euclidean	-0.2272	0.0657	-0.3560	-0.0983	<0.001
ShC	mean	0.8	3.3252	1.0626	1.2425	5.4078	0.002
ShC-2	mean	0.8	-0.0750	0.0250	-0.1240	-0.0259	0.003
Slope	sd	0.8	0.6565	0.4166	-0.1600	1.4730	0.115
Slope-2	sd	0.8	-0.0835	0.0428	-0.1674	0.0003	0.051
Wetl	dist.	3.2	2.0845	0.8174	0.4824	3.6867	0.011

Winter							
ArC	mean	0.05	0.4570	0.1495	0.1639	0.7500	0.002
ArC-2	mean	0.05	-0.0111	0.0039	-0.0187	-0.0035	0.004
Bare	sd	0.4	-0.1279	0.0508	-0.2274	-0.0284	0.012
CTI	mean	0.1	1.7569	0.5566	0.6659	2.8479	0.002
CTI-2	mean	0.1	-0.0820	0.0273	-0.1355	-0.0284	0.003
CTI	sd	0.2	-0.3949	0.1273	-0.6444	-0.1454	0.002
CTI	sd	0.05	0.2292	0.0544	0.1225	0.3359	<0.001
JunP	mean	0.2	-3.1094	1.5363	-6.1205	-0.0982	0.043
ShC	sd	0.2	0.2144	0.0894	0.0393	0.3895	0.016
ShH	mean	3.2	-0.1386	0.0609	-0.2580	-0.0193	0.023
Wetl	prop.	1.6	32.737	9.8557	13.421	52.054	<0.001
Wetl-2	prop.	1.6	-227.09	75.555	-375.18	-79.007	0.003
Wetl	prop.	0.2	-10.616	3.6598	-17.790	-3.4433	0.004
Wetl-2	prop.	0.2	11.077	3.9913	3.2539	18.899	0.006
Spring transition							
ArC	sd	3.2	5.0858	2.6617	-0.1310	10.303	0.056
ArC-2	sd	3.2	-0.7312	0.3676	-1.4518	-0.0107	0.047
ArC	sd	0.4	-0.6028	0.2632	-1.1186	-0.0871	0.022
Bare	mean	0.1	0.4984	0.2613	-0.0138	1.0105	0.057
Bare-2	mean	0.1	-0.0058	0.0031	-0.0118	0.0002	0.060
CTI	mean	3.2	19.039	10.869	-2.2634	40.341	0.080
CTI-2	mean	3.2	-1.1572	0.6142	-2.3610	0.0466	0.060
JunP	sd	0.1	-10.376	3.5817	-17.396	-3.3561	0.004
ShH	mean	1.6	3.0226	1.2935	0.4873	5.5578	0.020
ShH-2	mean	1.6	-0.0586	0.0253	-0.1082	-0.0091	0.020
VRM	mean	0.05	6.3240	1.8161	2.7829	9.9019	<0.001

[a] sd = standard deviation, prop. = proportion, dist. = distance

[b] scale for distance statistics is α in the distance decay function

[c] 2 represents a quadratic variable

Table 2.C5. Mean (SE) coefficient of determination (r^2) and regression statistics (β_0 = intercept, β_1 = slope; CI = 95% confidence interval) from 5-fold cross-validation, and the number of each of the five individual folds where all regression criteria was met, for seasonal resource selection models for greater sage-grouse in Bighorn Basin and Central Wyoming, USA, 2011–2015.

Season	r^2	β_0 CI lower	β_0 CI upper	β_1 CI lower	β_1 CI upper	Criteria met (no.)
Bighorn Basin						
Breeding	0.99 (0.00)	-311 (66)	255 (100)	0.89 (0.06)	1.15 (0.04)	4
Summer transition	0.99 (0.00)	-103 (3)	61 (3)	0.92 (0.01)	1.24 (0.01)	5
Summer	0.99 (0.01)	-619 (227)	272 (83)	0.95 (0.03)	1.31 (0.14)	3
Fall transition	0.98 (0.00)	-89 (6)	54 (3)	0.85 (0.01)	1.37 (0.03)	5
Winter	0.98 (0.01)	-462 (138)	388 (150)	0.81 (0.10)	1.24 (0.07)	5
Spring transition	0.99 (0.00)	-20 (1)	15 (1)	0.87 (0.01)	1.23 (0.02)	5
Central Wyoming						
Breeding	0.95 (0.03)	-317 (45)	280 (97)	0.67 (0.16)	1.36 (0.08)	5
Summer transition	0.95 (0.01)	-14 (1)	7 (1)	0.76 (0.04)	1.87 (0.06)	5
Summer	0.99 (0.01)	-327 (76)	227 (109)	0.88 (0.08)	1.30 (0.09)	5
Fall transition	0.98 (0.00)	-82 (5)	51 (3)	0.82 (0.01)	1.41 (0.02)	5
Winter	0.94 (0.02)	-258 (53)	331 (127)	0.57 (0.15)	1.35 (0.10)	4
Spring transition	0.96 (0.01)	-14 (1)	12 (1)	0.65 (0.04)	1.46 (0.05)	5

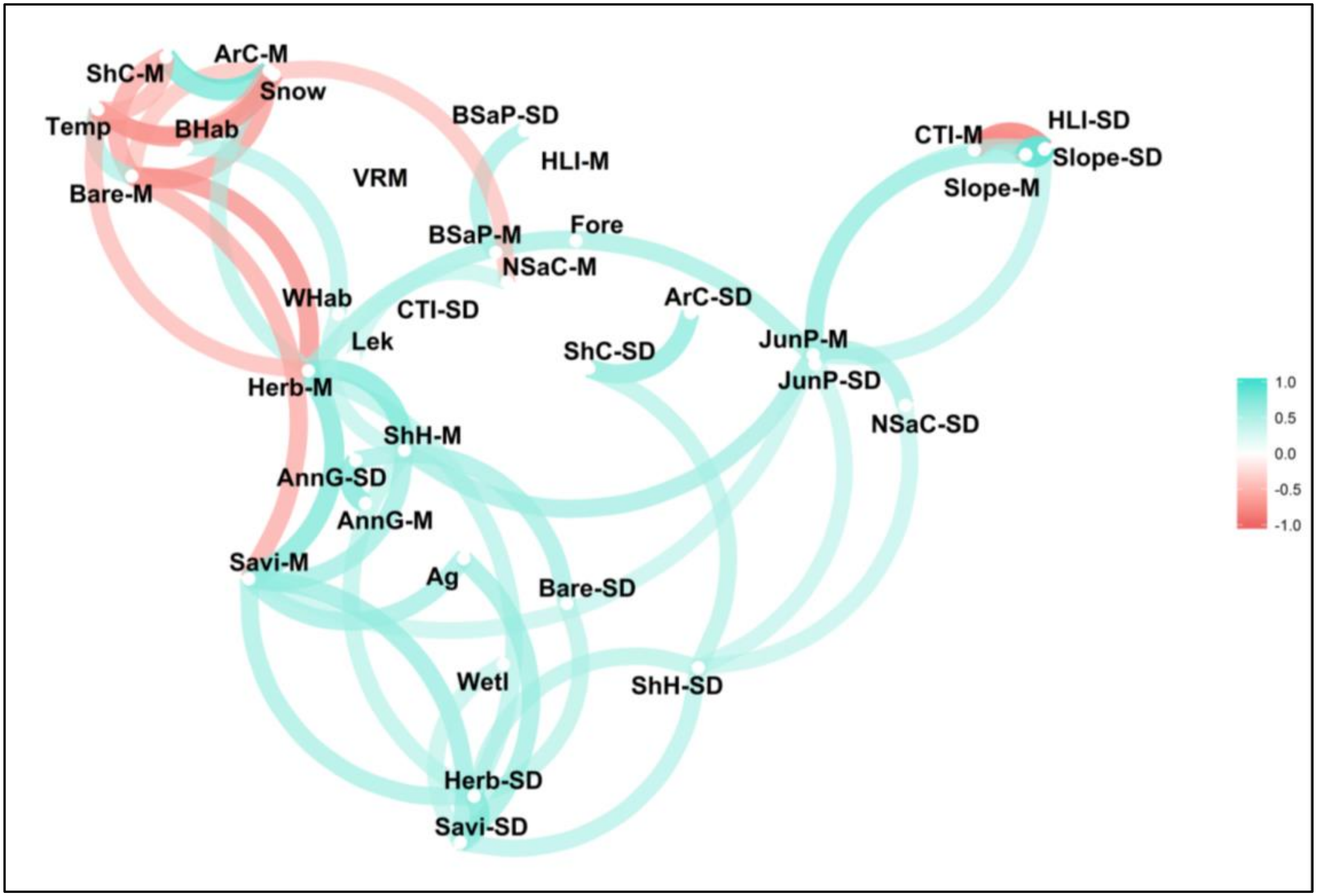

ArC-M
ShC-M
Snow
Temp
BHab
BSaP-SD
HLI-M
VRM
Bare-M
BSaP-M
Fore
NSaC-M
WHab
CTI-SD
ArC-SD
Lek
ShC-SD
JunP-M
JunP-SD
Herb-M
NSaC-SD
ShH-M
AnnG-SD
AnnG-M
Savi-M
Ag
Bare-SD
Wetl
ShH-SD
Herb-SD
Savi-SD
CTI-M
HLI-SD
Slope-SD
Slope-M
1.0
0.5
0.0
-0.5
-1.0

Figure 2.C1. Network plot representing the correlations (turquoise = positive, red = negative) between variables (all measured at the 0.4-km scale) used for measuring greater sage-grouse resource selection in Bighorn Basin and Central Wyoming, USA, 2011–2015. Darker shades represent larger correlations. Correlations <0.5 are not displayed for easier readability.

Appendix D. Comprehensive Habitat Conservation Value Prediction Maps

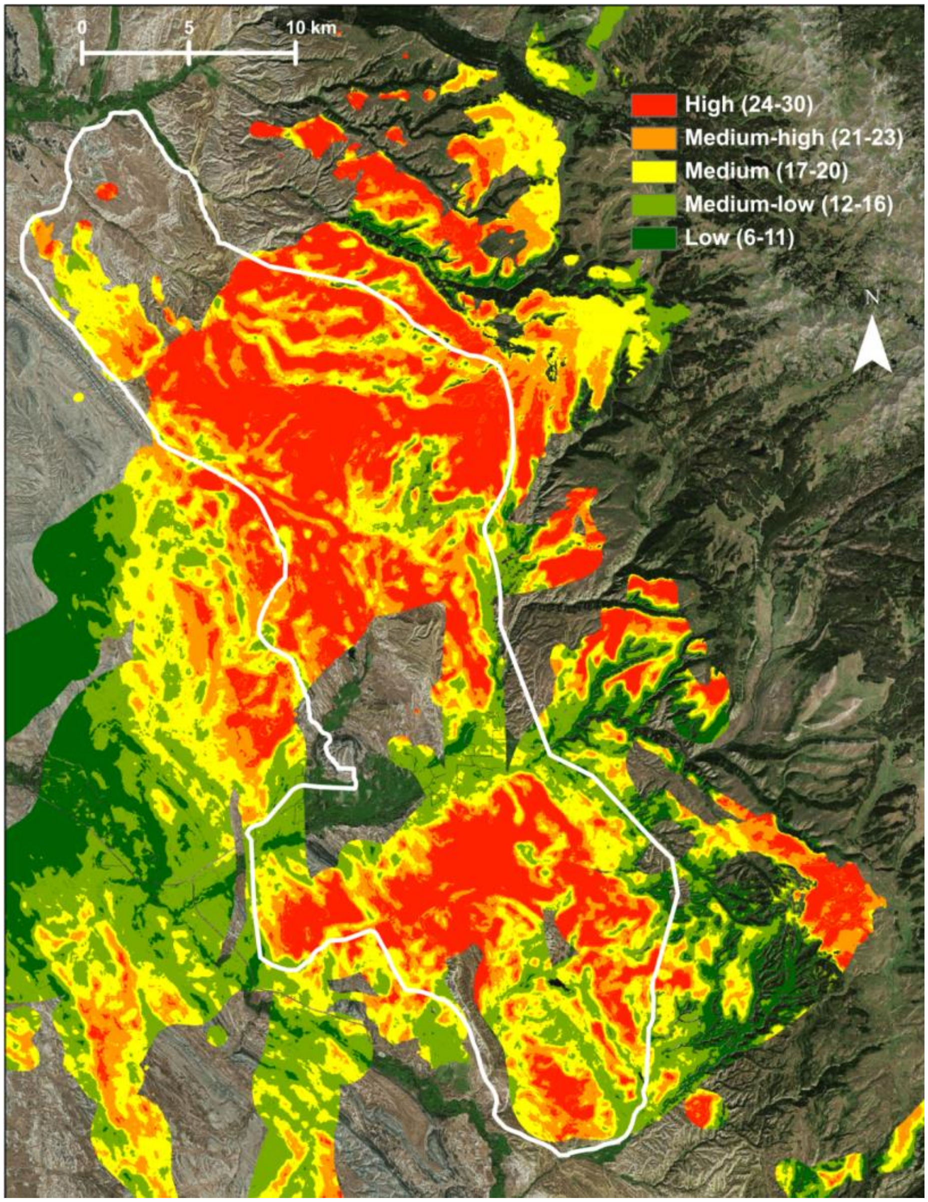


Figure D1. Example map of relative conservation priority for comprehensive greater sage-grouse habitat requirements, when each season had equal weight, for part of the Bighorn Basin study area, USA. White outline delineates area under current protection through the Core Area Strategy which was based on breeding habitat.

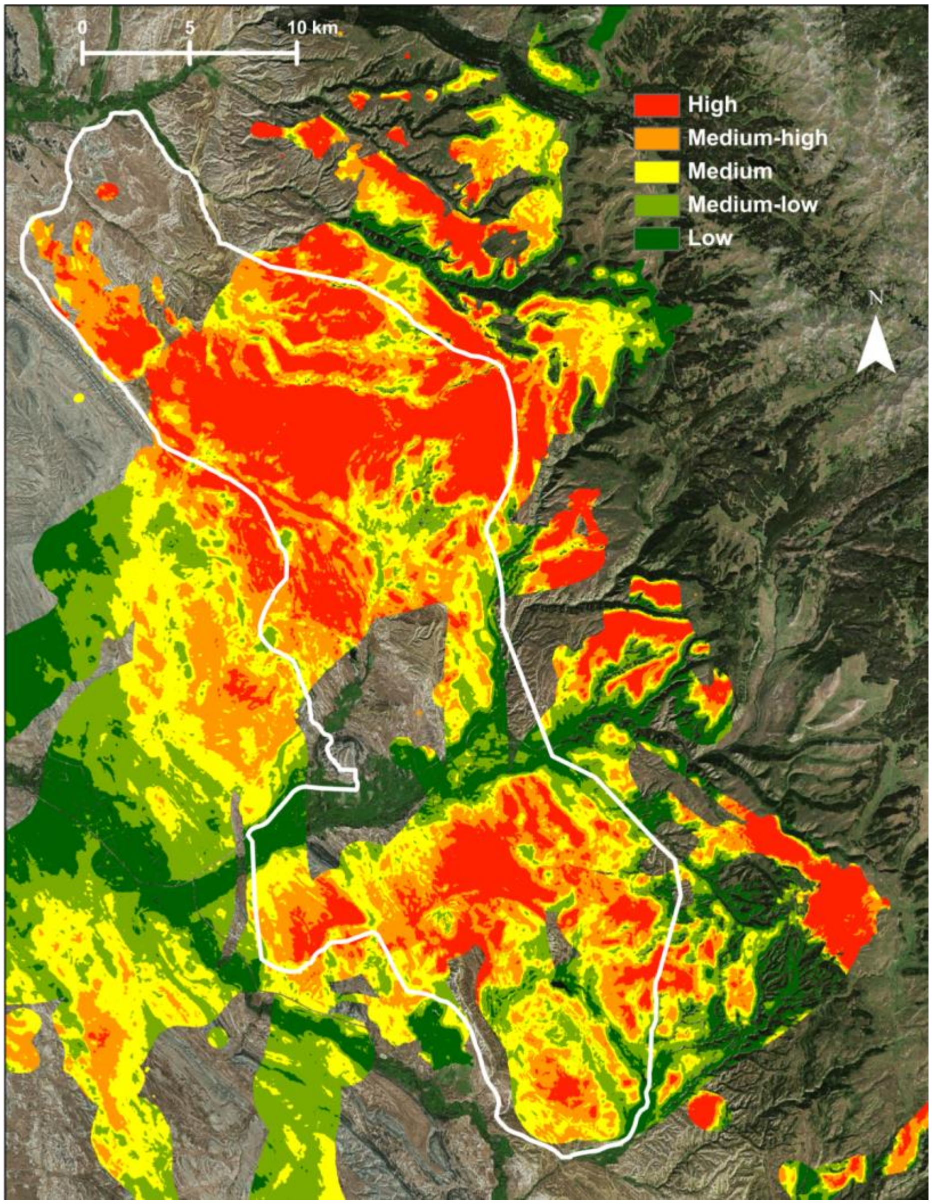


Figure 2.D2. Example map of relative conservation priority for comprehensive greater sage-grouse habitat requirements, when each season was weighted according to its estimated contribution to population change, for part of the Bighorn Basin study area, USA. White outline delineates area under current protection through the Core Area Strategy which was based on breeding habitat.

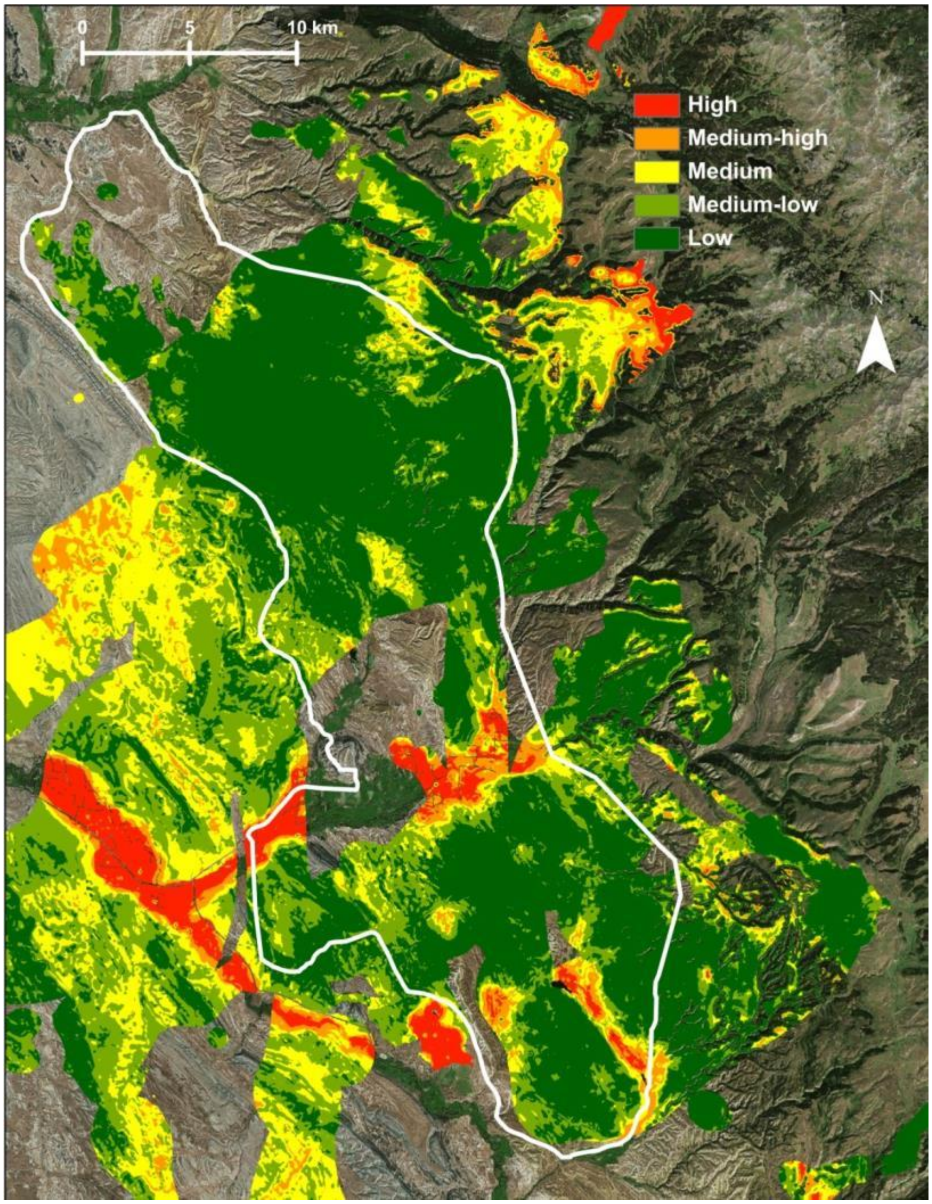


Figure 2.D3. Example map of relative conservation priority of greater sage-grouse summer and winter habitat that was not prioritized by mapping comprehensive requirements, when each season was weighted according to its estimated contribution to population change, for part of the Bighorn Basin study area, USA. White outline delineates area under current protection through the Core Area Strategy which was based on breeding habitat.

CHAPTER THREE

Do Greater Sage-Grouse Match Habitat Selection with Apparent Survival and Reproductive Costs Relative to Bentonite Mining and Other Anthropogenic Disturbance?

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Abstract

Maladaptive habitat selection, where animals are selecting habitat where their fitness is lower or avoiding habitat where they would perform better, exacerbates the threat of extinction for species already vulnerable from habitat loss and fragmentation. The greater sage-grouse (*Centrocercus urophasianus*) is a species of conservation concern for which recent research has identified possible scenarios where populations may be under the influence of maladaptive habitat selection. Our research objective was to perform an initial evaluation of whether sage-grouse selected habitat relative to apparent habitat quality (i.e., ability to provide for higher survival or reproductive success), and, secondarily, to identify any habitat characteristics where they were not matching selection with apparent costs and

benefits, during the nesting, brood-rearing, adult breeding, adult summer, and adult winter survival seasons. We only measured a positive relationship between habitat selection and survival in winter. For brood-rearing and adult breeding survival there was no relationship, and there was a negative relationship for nest and adult summer survival. We documented a specific habitat characteristic that was selected contrary to apparent costs or benefits for all five demographic rates. We identified 26 specific habitat characteristics that influenced sage-grouse reproductive success or survival and 13 (50%) had a positive relationship, whereas ten (38%) had a negative relationship. Most (80%) of the habitat characteristics we observed that were selected contrary to apparent costs or benefits were associated with environmental variables. The majority (86%) of negative effects from anthropogenic disturbance were avoided by sage-grouse. This was the case for bentonite mining, an important source of habitat disturbance in our study, where we found evidence that mining had negative effects on brood and adult breeding survival, but grouse were also avoiding mining during these same seasons. The exception was adult sage-grouse selecting for proximity to minor roads during the breeding season where they were more likely to die. Grouse also were not selecting for non-irrigated agricultural disturbance, which provided a survival benefit during the breeding and winter seasons. Our research has identified areas that warrant further investigation relative to whether the observed apparent negative relationships are cases of maladaptive selection or possible sources of secondary benefits from riskier habitats.

Introduction

The classic model of animal distribution assumes variability in habitat quality will lead individual animals to choose the best unoccupied site (Pulliam and Danielson 1991). The assumption that individuals will select habitat that maximizes their fitness is reasonable if habitat selection is adaptive, and they are capable of investigating and choosing from a large number of sites when deciding where to live. Stated another way, high-quality habitat, or habitat that supports greater fitness, should have a higher probability of use than lower-quality habitat, or habitat that supports lower fitness. If individuals are to select the highest-quality habitat available then they must identify cues for necessary resources to support successful reproduction and reduce risk of mortality (Williams and Nichols 1984, Kristan 2003). Situations where animals are not able to properly identify these features can result in an ecological trap (first identified by Dwernychuk and Boag 1972). An ecological trap occurs where an individual preferentially selects habitat that reduces its fitness (Robertson and Hutto 2006). In this case, the individual perceives the landscape as being ‘good’ when it is in fact ‘bad.’ More recently, the concept of a perceived trap has been described (Patten and Kelly 2010). Perceived traps are scenarios where an individual preferentially avoids habitat that would increase its fitness. In this case, an individual perceives the landscape as being ‘bad’ when it is in fact ‘good.’ A central concept to these ideas is the misperception by the animal of the habitat features that influence fitness (Schlaepfer et al. 2002, Robertson and Hutto 2006). This maladaptive selection of habitat features distinguishes these concepts from source-sink habitats. Populations under source-sink dynamics demonstrate adaptive habitat selection when individuals select high-quality habitat or avoid low-quality habitat (Patten and Kelly 2010).

Impacts of anthropogenic disturbance on habitat selection and fitness are well documented for many wildlife species (Johnson et al. 2004, Johnson et al. 2005, Sawyer et al. 2006, Kight and Swaddle 2007, Gilbert and Chalfoun 2011, Buchanan et al. 2014). Therefore, it is not surprising that ecological and perceived traps are mainly a result of reactions to anthropogenic activity (Remes 2000, Battin 2004, Bock and Jones 2004, Robertson and Hutto 2006, Patten and Kelly 2010). A population in a source-sink dynamic should remain stable unless the amount of source habitat is very limited (Pulliam and Danielson 1991). In contrast, a population under the influence of ecological and perceptual traps will tend toward extinction unless the population can adapt fast enough (Donovan and Thompson 2001, Kokko and Sutherland 2001). Therefore, there are potentially profound consequences for population persistence if the dynamic under which a population operates is not identified. Resource selection maps are used by land managers and policy makers to guide conservation and regulatory actions, but these may have limited success if habitat selection is maladaptive. If habitat selection is maladaptive proper conservation actions will be dependent on identifying the areas of maladaptive habitat use and the reasons why.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter ‘sage-grouse’) is a species of conservation concern that has received several petitions to be listed under the U.S. Endangered Species Act of 1973 (Stiver 2011). These petitions have cited habitat loss and fragmentation as a primary threat and the 2010 finding considered the listing of sage-grouse as warranted (USFWS 2010). If existing populations are influenced by ecological and perceptual traps, then there is an increased risk of extinction. Significant threats of habitat loss and fragmentation to sage-grouse are from land surface disturbances such as agricultural development (e.g., Smith et al. 2016), energy development (e.g., Kirol et al. 2015), residential development (Connelly et al. 2004), livestock grazing (e.g., Beck and Mitchell 2000), and fire (e.g., Lockyer et al. 2015). Sage-grouse is a species with strong habitat selection tendencies relative to environmental and anthropogenic landscape features, which also influences its survival. There have been recent studies that have combined resource selection models with fitness metrics to define habitat quality for sage-grouse during various life stages (Aldridge and Boyce 2007, Atamian et al. 2010, Dzialak et al. 2011, Smith et al. 2014, Kirol et al. 2015, Gibson et al. 2016). Firstly, in these studies, it was demonstrated that there are possible scenarios where sage-grouse do better or worse in terms of habitat selection and fitness choices, and therefore create potential for ecological and perceptual traps (selected sink habitat and unselected source habitat, respectively; Aldridge and Boyce 2007, Kirol et al. 2015). In each study, anthropogenic disturbance influenced selection and contributed to reduced survival or reproductive success. Secondly, through our research, we wanted to contribute a more thorough investigation of the overall response of selection relative to habitat quality through the annual cycle and identify the specific habitat characteristics that may be contributing to sage-grouse not matching selection with fitness benefits.

Our research objective was to evaluate whether sage-grouse selected habitat relative to habitat quality for combinations of the most critical demographic rates and seasonal habitat requirements (i.e., nest, brood, adult breeding, adult summer, and adult winter survival; Connelly et al. 2011, Taylor et al. 2012), and to identify any habitat characteristics that were being selected contrary to the apparent costs or benefits associated with those characteristics. We completed three steps to address this objective. First, we identified which habitat characteristics most influenced survival and reproductive success and predicted habitat quality based on estimated relative performance (i.e., mortality risk) of grouse using these habitats. We then measured selection relative to predicted habitat quality. We expected sage-grouse to demonstrate a general positive relationship of selecting habitat relative to quality, but that this selection may not necessarily be a strong relationship because of potential negative selection relationships relative to specific habitat characteristics. Thirdly, we measured selection relative to the habitat characteristics that most influenced grouse performance. We expected negative selection relationships to be associated with anthropogenic disturbance because these disturbances are recent and rapid changes to the landscape that could create mismatches between the cues grouse use to evaluate habitat quality and the realized costs or benefits of using disturbed habitat.

An economically important source of surface disturbance in our study area was derived from bentonite mining. Wyoming contains 70% of the world's bentonite clay deposits, and mines in the region where our study was located produce >50% of Wyoming's annual supply (Wyoming Mining Association 2016). Bentonite clay extraction is carried out by shallow open-pit mining that leads to loss of sagebrush (*Artemisia* spp.) habitat. To date, most bentonite mining has occurred in areas dominated by salt desert shrub communities, but plans call for mining operations to increase in sagebrush communities, which are occupied by sage-grouse. Since anthropogenic disturbance is expected to be the main cause of maladaptive habitat selection and bentonite mining is a growing source of surface disturbance, we specifically evaluated whether mining was a cause of sage-grouse not matching selection with apparent costs or benefits from mining activity.

Methods

Study area

Our study included sage-grouse location and demographic data from sagebrush habitats in the Bighorn Basin of north-central Wyoming and extreme south-central Montana, USA. This area had a 30-year (1981–2010) normal average annual precipitation and temperature of 31 cm and 7.0 °C, respectively (PRISM Climate Group 2016). The landscape forming our study was approximately associated with the Carbon Sage-Grouse Core Conservation Area in Montana (State of Montana 2015), and the Shell, Hyattville, and Washakie Sage-Grouse Core Areas in Wyoming (State of Wyoming 2015). Elevations ranged from ~1,180 m to ~2,880 m. Plant communities were dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*) at lower elevations and mountain big sagebrush (*A. t. vaseyana*) at higher elevations. Black sagebrush (*A. nova*) was common in localized areas at moderate elevations. Juniper (*Juniperus* spp.) occurred in localized areas at moderate-to-high elevations. Coniferous forest dominated elevations above sagebrush and Gardner's saltbush (*Atriplex gardneri*) dominated elevations below sagebrush. Sage-grouse winter habitat was mostly located in sagebrush at lower elevations, whereas summer habitat was mostly located in either mountain big sagebrush communities at higher elevations or in irrigated hayfields or pastures at lower elevations (Chapter 2). Breeding habitat occurred at a wide range of elevations. Anthropogenic disturbance was not widespread across the study area but was abundant in localized areas (Table 3.1). Agricultural fields (row crops, hayfields, and pastures) were the most common disturbance and were located along the major floodplains of the Bighorn Basin. An economically important source of surface disturbance in the Bighorn Basin was derived from bentonite mining. Bentonite mining was present in localized areas at lower elevations where sagebrush transitioned to saltbush. Land ownership included U.S. Bureau of Land Management (61%), State of Wyoming or Montana (6%), U. S. Forest Service (10%), and private (23%).

Data collection

During 2011–2015, female sage-grouse were captured by spotlighting and hoop netting (Giesen et al. 1982, Wakkinen et al. 1992) in the vicinity of leks during the spring. Additional females were located and captured during the summer or winter at night-roosting locations of previously marked grouse. We aged grouse as yearlings or adults (Eng 1955). Females were either marked with very-high frequency (VHF) radio transmitters (22-g necklace-mounted VHF transmitter Model A4060, Advanced Telemetry Systems, Isanti, MN, USA), or with Global Positioning System (GPS) equipped Platform Transmitter Terminals (22-g Solar Argos/GPS PTT-100 [Microwave Telemetry, Columbia, MD, USA] or Model 22 GPS PTT [North Star Science and Technology, King George, VA, USA]). Global Positioning System transmitters were programmed to acquire from four to six locations (~ 20-m error) per day depending on season (Pratt et al. 2017). Grouse equipped with VHF transmitters were located by triangulating on the ground from ~50-m away during April through August and were located by airplane (<200-m error, Dinkins et al. 2017) from September through March. Locations for GPS-marked grouse were assigned to season based from behavior (see Pratt et al. 2017), whereas locations for VHF-marked grouse were assigned based from the population-average seasonal bounding dates (Chapter Two). Locations from GPS-marked grouse were rarified to the actual sampling intensity of VHF-marked grouse. Locations from nesting females were only used once for the adult breeding season analysis. Average location sampling for VHF-marked grouse was one location every seven days, 16 days, 22 days, and 26 days of exposure for broods, adults during the breeding season, adults during summer, and adults during winter, respectively. Very-high frequency transmitters were equipped with 8-hour mortality switches and any mortality signal detected was located on the ground. Mortalities also were confirmed for GPS-marked birds after the transmitter was consistently not moving. Nesting females, equipped with VHF transmitters, were visually confirmed after they were relocated in the same location on two occasions. After observing a female grouse on a nest, we monitored it every four days by triangulating from the nearest 2-track road until the conclusion of the nesting effort. We searched for nests from GPS-equipped females at the estimated nest location after the female left the area. Any GPS female that appeared to be incubating for at least one day was checked for a nest on the ground (a nest was discovered in all cases except one). We determined nest success (i.e., nests with at least one egg hatching) by examining egg shells after the female left the area (Sowls 1948). We defined brood success as at least one chick surviving to 5-weeks post hatch. Any female that had hatched a nest that was suspected to have lost her brood was confirmed twice by checking her at night. In addition, we confirmed the presence of chicks from night roosting females at 35-days post hatch.

Spatial predictor variables

We considered several predictor variables for habitat-specific survival and resource selection modeling that were based on topography, vegetation, and anthropogenic land surface disturbance (Table 3.2). Topographic variables included compound topographic index (soil wetness index; Gessler et al. 1995), heat load index (amount of radiation index; McCune and Keon 2002), slope, and vector ruggedness measure (topographic roughness index; Sappington et al. 2007) calculated from a 10-m digital elevation model (EROS 2016b) and ArcGIS 10.0 (ESRI 2011). We calculated compound topographic index and heat load index using the geomorphology and gradient metrics toolbox (Evans et al. 2014) and we calculated vector ruggedness measure using the terrain ruggedness tool (Sappington 2012). The vegetation metrics included variables of percent cover representing the ground (bare ground), herbaceous (annual grass and herbaceous cover), and shrub layers (big sagebrush, non-sagebrush [not *Artemisia* spp.], and total shrub cover). We also utilized shrub height, probability of black sagebrush presence, and probability of juniper presence. We predicted these vegetation variables for our study area by using Random Forest regression or classification (Breiman 2001) with remotely-sensed spatial data and field measurement plots (30-m resolution; Chapter 2). We also utilized categorical land cover data from National Land Cover Database (NLCD; 30-m resolution; Homer et al. 2015) to represent forest and wetlands (primarily riparian in our study area). Our final vegetation variable was the soil-adjusted vegetation index (SAVI; Qi et al. 1994), which represents vegetation ‘greenness.’ We calculated SAVI from a median surface reflectance image (30-m resolution; Landsat 8 Operational Land Imager; EROS 2016a) from Landsat images associated with the nearest first day of the month

(2013–2015) for June (17 May–16 Jun; 17 Apr–16 May images would have been included but they were too cloudy), for breeding-season analysis, and for August/September (17 Jul–16 Sep), for summer season analysis. We digitized anthropogenic disturbance using the World Imagery basemap (0.3-m resolution) within ArcGIS 10.0 (ESRI 2011). We classified disturbance into two categories based on whether it was an active higher-intensity (e.g., gravel/paved road, active mining, residence) or a lower-intensity (e.g., 2-track trail, reclaimed mine, field) disturbance. We also classified bentonite-mining specific variables into active mining disturbance and reclaimed mining disturbance. Roads were classified as major (bladed dirt/gravel and paved) and minor (2-track trail). We classified disturbance from agricultural practices as irrigated hayfields/pastures and all other forms of disturbance. These classifications were based on our observations that irrigated fields were frequently used as summer habitat by grouse in our study areas (Chapter 2), but there was no apparent benefit from other forms of disturbance from agriculture.

Variables were measured at multiple, circular spatial regions around locations with radii that started at about twice location error (i.e., 50 m for nest locations, 100 m for brood and breeding locations, and 400 m for summer and winter locations) and systematically increased by doubling in size until the radius of circular analysis regions was 3,200 m. Within these regions we calculated the mean and standard deviation for each continuous topographic and vegetation variable. For the categorical land cover variables and for the categorical disturbance variables we calculated the proportion of the landscape within each circular region. In addition, for the categorical variables we measured Euclidean distance to the nearest feature, as well as, distance scaled between zero (away) and one (near) with a decay function ($e^{-d/\alpha}$, d = distance; Aldridge et al., 2012) where α was set to the same values as our analysis region radii. The distance decay variables allowed for non-linear relationships. We standardized all variables so observations had a mean equal to zero and standard deviation equal to one so model coefficients were directly comparable.

Survival analysis

We evaluated the effect of spatial predictor variables on mortality risk for nests, broods, and seasonal adult survival using mixed-effects Cox proportional hazards regression, which uses the variation in exposure time to a mortality event relative to covariates (Cox 1972; coxme R package, Therneau 2015; R version 3.4.1, R Core Team 2016). The values for the spatial covariates were the average for each experimental unit (i.e., each nest, brood, or adult-season combination). For the nest survival analysis, covariates were measured within concentric analysis regions surrounding each nest location. For the brood survival analysis, covariates were measured in circular analysis regions surrounding brood locations and averaged for each individual brood. For the adult seasonal survival analyses, covariates were measured within the circular analysis regions surrounding the relevant seasonal locations and averaged over the lifetime of each individual female. Therefore, covariates were time independent and represented the average habitat use for each experimental unit. We implemented several steps to screen variables for model selection. We first determined which random effects should be included by comparing null models with all possible combinations of random effects from individual, bird age, transmitter type, research site, and year using Akaike's information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002; AICcmodavg R package, Mazerolle 2017). We then compared single-variable models with AIC_c to select the most predictive scale of measurement for each variable and to eliminate any variables that performed poorer than the null model. To avoid multicollinearity, we carried forward top-performing variables while removing those that were correlated ($|r| \geq 0.6$) from further consideration. We then created a global model of all remaining variables and employed a backward variable-selection procedure by systematically removing the least significant variable (i.e., largest *P*-value) until all remaining variables had a *P*-value ≤ 0.1 and there was a minimum of ten events per fixed-effect variable (Harrell et al. 1984). We removed any variables from further consideration if they demonstrated coefficient instability or sign switching when moderately-correlated variables ($0.3 \leq |r| < 0.6$) were removed from the final model. We checked that the proportional hazards assumption was met which is represented by a slope not different from zero for Schoenfeld residuals (Schoenfeld 1982).

Resource selection

To first evaluate overall population resource selection relative to habitat quality we mapped relative mortality risk across our study area based from the final survival models. We mapped mortality risk at 30-m resolution and binned into five quantiles (1-5 from lowest to highest relative mortality risk). We then used this as an explanatory variable in our resource selection model comparing grouse-use locations to available locations (Manly et al. 2002). We generated 20 times the number of available locations as use locations that were restricted to each research site. The extents of the research sites were delineated from minimum convex polygons of use locations with areas of non-habitat masked out (i.e., closed canopy, developed, and non-terrestrial land covers, 2011 National Land Cover Database, Homer et al.

2015). We modeled relative probability of selection with generalized estimating equations (PROC GENMOD, SAS 9.4, SAS Institute Inc. 2012). We accounted for repeated observations from the same individual by assigning use and available locations into clusters and by selecting between independent and compound-symmetric correlation structures to estimate robust standard errors (Koper and Manseau 2009, Fieberg et al. 2010). After measuring selection of overall habitat quality, we then measured selection relative to the individual landscape characteristics that were most influential to survival. We followed the same process as the overall habitat quality model, but instead of only one explanatory variable we incorporated all the variables in each relevant final survival model. Finally, we graphed standardized coefficients to compare their influence on mortality risk and resource selection and interpreted this response relative to a theoretical perfect matching of habitat selection to survival costs or benefits (Figure 3.1A). In these graphs, positive values along the X-axes represented greater mortality risk and positive values along the Y-axes represented greater resource selection. Variables that fell within the upper-left or lower-right quadrants represented a positive relationship between selection and survival and we considered it strong evidence for this relationship if 95% confidence intervals overlapped the 1 X : -1 Y line (Figure 3.1A). Variables that fell within the upper-right or lower-left quadrants represented a negative relationship between selection and survival and we considered it strong evidence if 95% confidence intervals did not overlap any axes.

Results

When modeling habitat-specific survival and resource selection we utilized data collected from 321 female sage-grouse captured in the Bighorn Basin during 2011–2015 (Table 3.3). Significant random effects for survival modeling included transmitter type and research site for nesting analysis; bird age and research site for brood-rearing analysis; year for adult breeding analysis; year and research site for adult summer analysis; and year and research site for adult winter analysis. Our final nest survival model indicated strong evidence for increased nest failure risk for birds that nested in areas with more black sagebrush, less non-sagebrush shrub cover, more topographic ruggedness, and more high-intensity disturbance (Table 3.4). There was moderate evidence for increased risk with more variability in soil moisture, less variability in shrub cover, and more wetland. There was evidence that sage-grouse were choosing riskier areas when selecting nest sites (Table 3.5). This was a result of avoiding non-sagebrush cover, and by not avoiding black sagebrush and topographic ruggedness (Figure 3.1B). Our final brood survival model indicated strong evidence for increased brood failure risk with less variability in heat load, less plant 'greenness,' more variability in shrub cover, and more active bentonite mining disturbance (Table 3.4). There was no evidence that sage-grouse were selecting for brood-rearing areas relative to predicted brood success (Table 3.5). Brood-rearing females were not selecting for landscape characteristics that promoted brood success, and they were selecting for higher variability in shrub cover (Figure 3.1C).

Our final adult breeding season survival model indicated strong evidence for increased adult mortality risk in areas with less disturbance from agricultural practices (i.e., not irrigated fields), but with more high-intensity disturbance and in closer proximity to minor roads (Table 3.4). There was moderate evidence for increased risk with more variability in soil moisture, more active bentonite disturbance, and more irrigated fields. There was no evidence that sage-grouse were selecting habitat during breeding season relative to predicted adult survival (Table 3.5). Female sage-grouse were not selecting for more disturbance from agricultural practices that were apparently providing a survival benefit, and they were selecting for proximity to minor roads (Figure 3.1D). Our final adult summer season survival model indicated strong evidence for increased adult mortality risk with less variability in juniper presence, less non-sagebrush shrub cover, and more variability in plant ‘greenness’ (Table 3.4). There was moderate evidence for increased risk with less variability in soil moisture, less wetland, and more minor roads. There was evidence that sage-grouse were selecting for riskier areas when selecting summer habitat (Table 3.5). This was a result of avoiding non-sagebrush cover and variability in soil moisture, and by selecting for more variability in plant ‘greenness’ (Figure 3.1E). Our final adult winter season survival model indicated strong evidence for increased adult mortality risk in areas with more topographic ruggedness and with less disturbance from agricultural practices (i.e., not irrigated fields; Table 3.4). There was moderate evidence for increased risk with less variability in soil moisture. There was evidence that sage-grouse were selecting for less riskier areas relative to survival when selecting winter habitat (Table 3.5). Even so they were not selecting for more disturbance from agricultural practices that were apparently providing a survival benefit (Figure 3.1F).

Of the 26 specific habitat characteristics that influenced sage-grouse performance, 13 (50%) had at least weak evidence for a positive relationship, ten (38%) had at least weak evidence for a negative relationship, and three (12%) were inconclusive or not strongly selected for. Of the ten habitat characteristics where we documented at least a weak negative relationship, three (30%) were relative to topography, five (50%) were relative to vegetation, and two (20%) were relative to anthropogenic disturbance. There was at least one negative influence on survival from anthropogenic disturbance for four of the five demographic rates we investigated. However, of the seven total negative effects, six (86%) showed at least a weak positive relationship. The one case of a strong negative selection relationship relative to disturbance was breeding adults selecting for proximity to minor roads where they were more likely to die.

Discussion

It is easy to assume that animals, including sage-grouse, select habitat that maximizes their selection relative to apparent survival and reproductive costs and benefits. However, of the five demographic rates we investigated, only during winter was there a positive relationship between habitat selection and performance. For breeding season survival and for brood survival there was no relationship between habitat selection and performance, and there was a negative relationship for nest and adult summer survival. We documented a specific habitat characteristic that was associated with a negative selection relationship for all five demographic rates, but the most cases coincided with the two rates (i.e., nest and adult summer survival) that had the poorest overall positive habitat selection relationship. Only half of the specific habitat characteristics that influenced sage-grouse performance had a positive selection relationship.

Ecological traps, when animals select for habitat where they perform poorly, have been proposed as an expression of maladaptive habitat selection. Examples of ecological traps include Bell's sparrows (*Artemisiospiza belli*) that selected undisturbed habitats having lower nest success (Misenhelter and Rotenberry 2000) and indigo buntings (*Passerine cyanea*) attracted to artificial forest edges having lower reproductive success (Weldon and Haddad 2005). We documented five potential habitat characteristics that may pose as ecological traps for sage-grouse: black sagebrush and topographic ruggedness for nesting; variability in shrub cover for brood rearing; minor roads for breeding season survival; and variability in plant 'greenness' for summer survival. Perceptual traps, where animals avoid areas where they would perform well, have also been proposed as an expression of maladaptive habitat selection. Examples of perceptual traps include shorebirds (suborder Charadrii) avoiding nesting near man-made structures even though there was no effect on nest success (Wallander et al. 2006) and lesser prairie-chickens (*Tympanuchus pallidicinctus*) avoiding powerlines and highways where there was no effect on nest success (Pruett et al. 2009). We documented five potential habitat characteristics that may pose as perceptual traps for sage-grouse: non-sagebrush shrub cover for nesting; variability in heat load for brood rearing; variability in soil moisture and non-sagebrush shrub cover for summer season survival; and non-irrigated agriculture disturbance for winter survival. Similarly, Aldridge and Boyce (2008) documented decreased sage-grouse brood selection for high grass cover even though more grass cover decreased chick mortality.

It is argued that maladaptive habitat selection should be associated with anthropogenic disturbance because it is a rapid landscape change and populations may not have had the necessary time to adapt (Battin 2004). Even though there are many examples of negative impacts from anthropogenic disturbance causing traps there also are cases where environmental features appear to cause traps. Two examples include black-throated sparrows (*Amphispiza bilineata*) nesting more frequently in shrub communities where nest success was lower (Pidgeon et al. 2003) and lesser prairie-chickens avoiding areas of low shrub density where nest success was no different than areas with high shrub density (Patten and Kelly 2010). Only 20% of the habitat characteristics where we documented a negative selection relationship were relative to anthropogenic disturbance. We did document negative influences on survival from anthropogenic disturbance; however, for most of these negative effects grouse were responding adaptively by also avoiding these disturbances.

Sage-grouse were avoiding more intensive forms of disturbance which negatively influenced performance. This was true for bentonite mining, where we found evidence that active mining decreased brood and adult survival during the breeding season. Nest survival was also lower relative to cumulative high-intensity disturbance (which included active mining). This is the first detailed assessment of mining impacts relative to sage-grouse, but there have been multiple studies on impacts from oil and gas development. Similar to our results, brood survival was lower in proximity to more oil and gas development (Aldridge and Boyce 2007, Kirol et al. 2015). Holloran (2005) documented lower annual adult survival for grouse impacted by oil and gas development. In contrast, Kirol et al. (2015) documented higher survival for adult female grouse closer to anthropogenic edge (high-intensity disturbance). Along with the negative survival impacts we also found evidence that grouse were avoiding active mining and other high-intensity disturbances during these same seasons. There is more evidence relative to grouse avoiding oil and gas development and related high-intensity disturbance during nesting and brood-rearing (Holloran 2005, Aldridge and Boyce 2007, Kirol et al. 2015), and during winter (Doherty et al. 2008, Carpenter et al. 2010, Smith et al. 2014). It appears that most evidence suggests that sage-grouse react adaptively relative to high-intensity disturbances such as active bentonite mining and oil and gas development, and that these activities will not likely result in ecological traps because of grouse avoidance of these features. The one case of a strong negative selection relationship relative to disturbance was breeding adults selecting for proximity to minor roads where they were more likely to die. In contrast, Dinkins et al. (2014) observed higher survival with greater road density. Kirol et al. (2015) documented selection for minor roads for brood-rearing females, whereas Carpenter et al. (2010) documented avoidance of minor roads during winter. We also documented increased mortality of adults near minor roads during summer, but unlike the breeding season, during the summer season minor roads were avoided.

In contrast to the negative effects from disturbance, non-irrigated agricultural disturbance provided survival benefits for both the breeding and winter season. In general, sage-grouse were not taking advantage of this survival benefit during the breeding season and were avoiding it during winter. There is no clear understanding of how agricultural disturbances could provide survival benefits, and in conjunction with the large coefficient values (and with high uncertainty around the estimates), we were suspicious of a spurious result. However, this relationship occurred in two separate seasonal analyses. The agriculture variables in this analysis do not represent massive conversion of sagebrush to agriculture, which clearly has a negative effect on sage-grouse populations (Swenson et al. 1987, Smith et al. 2016). In general, anthropogenic disturbances can create scenarios of perceptual traps because animals can perceive anthropogenic activity as a predation risk and avoid habitat that only has the appearance of greater risk of mortality (Frid and Dill 2002).

Animals cannot directly observe the fitness consequences of their selection decisions but can only observe the physical characteristics of their environment. The potential for mismatch between the environmental cue and the fitness outcome increases the more indirect the cue is (e.g., deciding where to forage based on current food abundance vs. vegetation structure around a nest at hatching based on vegetation structure at nest initiation; Schlaepfer et al. 2002, Kristan 2003). This could partially explain why we observed a negative relationship between selection and performance for nesting. Our research has documented an apparent disconnect between habitat selection and performance, but this does not directly represent a disconnect with fitness because these areas could be providing alternative benefits. This is a likely explanation for the negative association between selection and performance we observed during the summer season. During summer adults were selecting for more variability in plant ‘greenness,’ which represents a selection for irrigated fields or other sharp transitions between mesic sites and dry upland sites, but these areas were associated with higher mortality. These areas provide better forage during the hot, dry summer and could help sage-grouse recover from the physically-demanding breeding season (Fischer et al. 1996, Connelly et al. 2011). Therefore, these higher-quality forage areas could provide fitness benefits that are worth the increased mortality risk. This was similarly suggested by Aldridge and Boyce (2008) in that brood-rearing females could be selecting riskier areas with less grass cover to maximize foraging opportunities. This was also suggested by Gibson et al. (2016) in that nest-site selection by a female may be a function of her selecting brood-rearing habitat and not necessarily for nest survival.

Robertson and Hutto (2006) argue that you cannot prove existence of an ecological trap without proving actual preference for the habitat, which is not possible through a nonrandom habitat use study such as ours because animal density is not necessarily a good indicator of habitat preference. Though this technically may be true, density is usually not a good indicator of preference only when the majority of individuals are replaced by the minority of dominant individuals, which is the case for territorial species (Van Horne 1983). There is no reason to expect this with sage-grouse and any sage-grouse biologist would assume higher-quality habitat if they observed several sage-grouse in an area. Regardless if we documented actual ecological and perceptual traps, in the practical sense, as it relates to conservation, it appears that there are several disconnects between selection and performance. In addition, we argue that ecological and perceptual traps are practically the same thing. Theoretically, there are likely two different phenomena, but it is probably impossible to distinguish between the two without knowing the actual thought process made by the animal. Whether an animal selects, or avoids, a habitat characteristic is ‘two sides of the same coin’ (or variable). For example, do sage-grouse select for the presence of sagebrush or do they avoid the absence of sagebrush? However, when it comes to conservation, a biologist will have to speculate because addressing ecological traps requires removing the attractant while a perceptual trap requires removing the deterrent.

We acknowledge that this analysis has identified associations between sage-grouse and landscape characteristics and results do not necessarily represent cause and effect relationships. We want to emphasize that we do not believe that our analysis proves that sage-grouse are driven by maladaptive habitat selection of the identified habitat characteristics because of the viable alternative explanation that grouse are gaining secondary fitness benefits from riskier areas. We believe that the greatest benefit from our study is that we have identified areas that warrant further investigation. Further investigations should address the possible mechanisms explaining apparent maladaptive selection, or what are potential secondary fitness benefits that grouse are gaining from selecting risky areas.

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Table 3.1. Amounts (%) of anthropogenic surface disturbance within the five seasonal greater sage-grouse study areas in Bighorn Basin, USA, 2011–2015.

	nest	brood	breeding	summer	winter
Size (km^2)	2,348	2,347	2,954	3,421	5,381
Disturbance (%)					
All[a]	6.5	6.2	6.3	7.4	9.2
High	0.5	0.6	0.6	0.6	0.9
Low	5.9	5.5	5.6	6.7	8.3
BeAll	1.2	1.2	1.1	0.7	0.8
BeAct	0.2	0.2	0.2	0.2	0.2
BeRec	0.9	1.0	0.9	0.6	0.6
RdMaj	0.2	0.2	0.2	0.2	0.2
RdMin	0.3	0.3	0.3	0.3	0.3
AgAll	4.6	4.2	4.3	5.7	7.2
Field	3.2	3.1	2.9	4.0	5.6
AgOth	1.5	1.2	1.3	1.7	1.7

[a] See Table 3.2 for description of disturbance types

Table 3.2. Variables used for measuring greater sage-grouse habitat-specific nest, brood, and seasonal adult survival in Bighorn Basin, USA, 2011–2015.

Code	Description
Topographic	
CTI	Compound topographic index[a]
HLI	Heat load index[a]
Slope	Slope (%)[a]
VRM	Vector ruggedness measure[a]
Vegetation	
Herbaceous/Ground	
AnnG	Annual grass cover (%)[a]
Bare	Bare ground (%)[a]
Herb	Herbaceous cover (%)[a]
Shrub	
ArC	Big sagebrush cover (%)[a]
BSaP	Black sagebrush (probability of presence)[a]
JunP	Juniper (probability of presence)[a]
NSaC	Non-sagebrush cover (%)[a]
ShC	Shrub cover (%)[a]
ShH	Shrub height (cm)[a]
Land cover	
Fore	Forest land cover[b]
Wetl	Wetland land cover[b]
Vegetation index	
Savi	Soil-adjusted vegetation index[a]
Disturbance	
All	All anthropogenic surface disturbance[b]
High	All high-intensity disturbance (e.g. high-intensity road, active mining, residence)[b]
Low	All low-intensity disturbance (e.g. 2-track trail, reclaimed mine, field)[b]
BeAll	All bentonite mining disturbance (i.e. active and reclaimed)[b]
BeAct	Active bentonite mining disturbance[b]
BeRec	Reclaimed bentonite mining disturbance[b]
RdMaj	High-intensity major roads (e.g. bladed dirt/gravel and paved)[b]
RdMin	Low-intensity minor roads (e.g. 2-track trail)[b]
AgAll	All agriculture disturbance (e.g. access road, building, reservoir, field)[b]
Field	Irrigated field[b]
AgOth	Any non-irrigated agriculture disturbance[b]

[a] Variable measured on continuous values as mean and standard deviation at multiple spatial scales

[b] Variable measured on categorical designation as distance (m) to variable using multiple decay functions and proportion of area of variable at multiple scales

Table 3.3. Sample sizes utilized for modeling habitat-specific survival and resource selection for greater sage-grouse in Bighorn Basin, USA, 2011–2015.

Analysis	events	locations	nests/broods	grouse
Nest	207	378	378	246
Brood	48	754	157	128
Adult Breeding	62	1,978		285
Adult Summer	77	1,696		289
Adult Winter	31	1,365		220

Table 3.4. Variable type, scale of measurement, and statistics (estimated standardized coefficients [β] and standard errors [SE]) for variables in habitat-specific survival and resource selection models for greater sage-grouse in Bighorn Basin, USA, 2011–2015.

Variable	Measure[a]	Scale (m)[b]	Mortality Risk			Resource Selection		
			β	SE	*P*	β	SE	*P*
Nest								
BSaP	mean	50	0.146	0.057	0.010	0.073	0.064	0.249
CTI	sd	3200	0.193	0.106	0.069	-0.084	0.067	0.211
High	prop.	100	0.711	0.330	0.031	-0.339	0.221	0.125
NSaC	mean	400	-0.369	0.143	0.010	-1.556	0.155	<0.001
ShC	sd	200	-0.138	0.085	0.100	0.128	0.081	0.114
VRM	mean	800	0.283	0.108	0.009	0.063	0.068	0.352
Wetl	prop.	3200	0.225	0.132	0.089	-0.188	0.081	0.021
Brood								
BeAct	prop.	1600	0.430	0.167	0.010	-0.110	0.093	0.237
HLI	sd	1600	-0.690	0.240	0.004	-0.148	0.083	0.075
Savi	mean	400	-0.916	0.261	<0.001	0.042	0.075	0.575
ShC	sd	100	0.815	0.218	<0.001	0.166	0.061	0.006
Adult Breeding								
AgOth	prop.	400	-10.922	5.427	0.044	0.070	0.044	0.111
BeAct	prop.	800	0.291	0.178	0.100	-0.203	0.076	0.007
CTI	sd	3200	0.359	0.195	0.065	-0.289	0.054	<0.001
Field	prop.	800	0.372	0.194	0.056	-0.164	0.083	0.050
High	prop.	100	2.274	0.721	0.002	-0.224	0.070	0.001
RdMin	dist.	800	0.305	0.154	0.047	0.109	0.055	0.047
Adult Summer								
CTI	sd	1600	-0.331	0.189	0.080	-0.650	0.087	<0.001
JunP	sd	1600	-0.506	0.224	0.024	0.149	0.053	0.005
NSaC	mean	1600	-0.545	0.237	0.022	-0.906	0.096	<0.001
RdMin	prop.	1600	0.302	0.168	0.072	-0.119	0.056	0.035
Savi	sd	400	0.557	0.132	<0.001	0.810	0.046	<0.001
Wetl	prop.	400	-0.246	0.148	0.096	0.038	0.036	0.297
Adult Winter								
AgOth	prop.	800	-58.405	21.791	0.007	-1.111	0.291	<0.001
CTI	sd	1600	-0.697	0.395	0.078	-0.094	0.053	0.077
VRM	mean	400	0.813	0.359	0.024	-0.473	0.050	<0.001

[a] sd = standard deviation, prop. = proportion, dist. = distance

[b] scale for distance statistic is α in the distance decay function

Table 3.5. Statistics (estimated coefficients [β], empirical standard errors [SE], and 95% confidence intervals [CI]) for greater sage-grouse nest, brood, and adult seasonal habitat selection relative to habitat quality (i.e., predicted mortality risk) in Bighorn Basin, USA 2011–2015. Positive coefficient depicts selection for riskier areas.

Analysis	β	SE	CI lower	CI upper	*P*
Nest	0.073	0.034	0.007	0.139	0.031
Brood	-0.008	0.047	-0.099	0.084	0.869
Adult Breeding	-0.036	0.032	-0.099	0.027	0.259
Adult Summer	0.394	0.039	0.319	0.470	<0.001
Adult Winter	-0.048	0.024	-0.095	-0.001	0.048

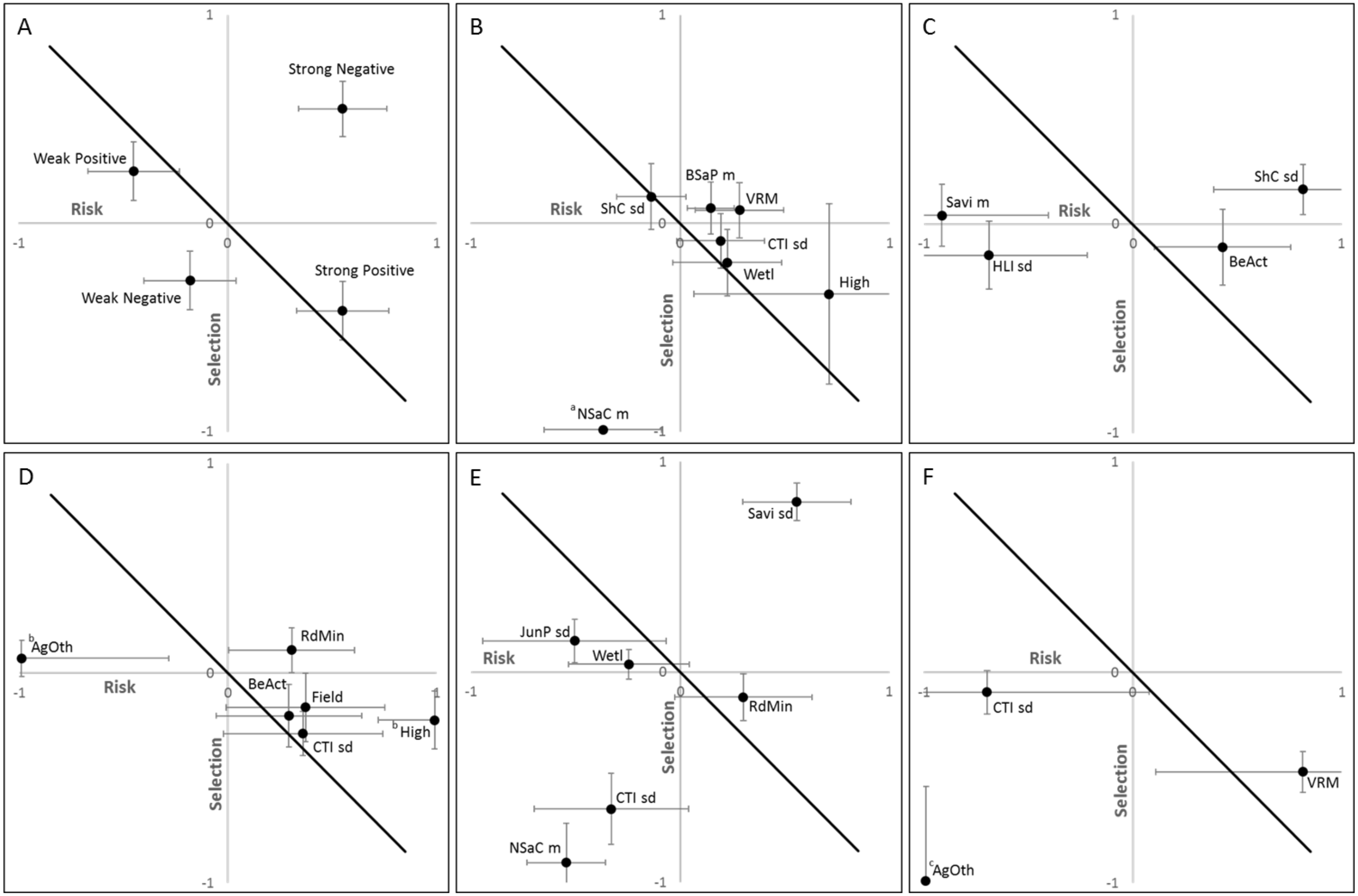
A
Strong Negative
Weak Positive
Risk
Weak Negative
Strong Positive
Selection
1
0
-1
B
BSaP m
VRM
ShC sd
CTI sd
Wetl
High
aNSaC m
Risk
Selection
C
ShC sd
Savi m
Risk
HLI sd
BeAct
Selection
D
bAgOth
RdMin
Risk
BeAct
Field
CTI sd
bHigh
Selection
E
Savi sd
JunP sd
Wetl
Risk
RdMin
Selection
CTI sd
NSaC m
F
Risk
CTI sd
VRM
Selection
cAgOth

Figure 3.1. (A) Interpretations of habitat selection for hypothetical landscape variables relative to greater sage-grouse mortality risk and resource selection. X and Y coordinates are standardized coefficients from habitat-specific survival and resource selection models, respectively. Diagonal line represents a perfect positive relationship between habitat selection and apparent survival costs or benefits. Strong and weak evidence is based from overlap of confidence intervals with axes and the positive relationship line. Standardized coefficients for landscape variables relative to nest (B), brood (C), adult female breeding (D), adult female summer (E), and adult female winter (F) mortality risk and resource selection for greater sage-grouse in Bighorn Basin, USA, 2011–2015. [a] Y-value for 'NSaC m' is off the chart area. Vertical error bars are not shown for 'NSaC m' because their extent is also off the chart area. [b] X-values for 'AgOth' and 'High' are off the chart area. Horizontal error bars depict the actual limits. [c] X and Y-values for 'AgOth' are off the chart area. Horizontal error bars are not shown for 'AgOth' because their extent is also off the chart area. Vertical error bar for 'AgOth' depicts the actual upper limit.