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GREATER SAGE-GROUSE IN A GRAZED LANDSCAPE: HABITAT SELECTION, DEMOGRAPHIC RATES, AND POPULATION TRENDS IN CENTRAL MONTANA

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GREATER SAGE-GROUSE IN A GRAZED LANDSCAPE:

HABITAT SELECTION, DEMOGRAPHIC RATES, AND POPULATION TRENDS

IN CENTRAL MONTANA

By

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Greater sage-grouse in a grazed landscape: habitat selection, demographic rates, and population trends in central Montana

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ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus)* abundance has declined across the species' range due to habitat loss, degradation, and fragmentation. To address this decline, information is needed to guide habitat conservation priorities and population management efforts. This includes information about patterns of habitat selection at multiple spatial scales, habitat and land use variables that affect demographic rates, and population trend estimates. We collected ten years of data (2011-2020) on sage-grouse demographic rates and habitat selection, as well as on vegetation and livestock grazing patterns, to address these topics. We were specifically interested in the effects of a rotational grazing system implemented through the United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) Sage Grouse Initiative (SGI). In Chapter 1, we investigated whether sage-grouse hens select seasonal home ranges based on topographic, grazing, and vegetation variables. We found that hens select for shrub cover across all seasons, with seasonal differences in other variables. We also found that sage-grouse located within livestock pastures select for areas with higher used animal unit months ("used AUMs," or a measure of the amount of forage grazed) in addition to shrub cover. In Chapter 2, we evaluated the effects of the SGI rotational grazing system on sage-grouse nest success. We found that neither SGI rotational grazing systems nor other indices of livestock use had measurable effects on nest success, but we saw a very minor positive effect of senesced grass height. The majority of inter- and intra-annual variation in nest success was unexplained by grazing-related variables. Taken together, these results suggest that the patterns of land use and livestock management observed during the study are not affecting sage-grouse in this study area, as there is no evidence for a negative effect of livestock grazing on estimated demographic rates or habitat selection. We note that sagebrush shrublands should remain a key component of sage-grouse conservation strategies, as this land cover type was selected by sage-grouse across seasons and spatial scales. In Chapter 3, we compared two methods of estimating sage-grouse population growth rate, using two different datasets. We found that the population growth rate from annual lek counts was more variable than the growth rate estimated using a matrix model. The population growth rate from the matrix model suggested a 10% decrease over the 10-year study, whereas the lek count estimator suggested a 16% increase over the same period. We suggest that growth rates derived from raw lek counts are interpreted with caution, as they may overestimate population trends relative to other methods due at least in part to observation error.

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DEDICATION

I dedicate this dissertation to the people who made me who I am today. My mother, Dot, shared her love of teaching and learning, while my father, Pete, instilled in me a commitment to conservation. My brother, Ben, inspired me to learn to love coding and data. My partner, Koby, sets a daily example of how courage combined with hard work and creativity can change the world.

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GENERAL INTRODUCTION

Human-induced environmental changes to wildlife habitat have long occurred in the sagebrush steppe ecosystem, one of the most at-risk land cover types in the western United States (Davies et al. 2011). Historically, much of the sagebrush steppe was overgrazed by livestock (Cooper 1960, Fleischner 1994), coincident with the rapid expansion of European settlers in the early- to mid-1800s (Miller and Wigand 1994, Borman 2005). Livestock grazing practices have since improved (Connelly et al. 2004), especially as a result of improved information availability about sustainable grazing practices. An extensive body of work has explored how to minimize the risk of rangeland degradation due to livestock grazing (Krausman et al. 2009) such that grazing is no longer the greatest threat to sagebrush systems (Pyke et al. 2015). Instead, in more recent decades, the sagebrush steppe has faced other major challenges. These include cheatgrass (*Bromus tectorum*) invasion, fire due in part to cheatgrass flammability and historical fire suppression (West 1983, West and Hassan 1985, Wrobleski and Kauffman 2003), conifer encroachment (Aldridge et al. 2008, Davies et al. 2011), cropland conversion (Foley et al. 2011), and fragmentation from energy development (Naugle 2011). Many of these stressors also interact with climate change, posing serious threats into the future. These challenges have decreased the habitat for species that rely on this ecosystem, including greater sage-grouse (*Centrocercus urophasianus).*

The greater sage-grouse is a ground-dwelling, sagebrush-obligate bird that is one of two species of sage-grouse: the greater sage-grouse and the Gunnison sage-grouse (*Centrocercus minimus*), its smaller and rarer relative. Greater sage-grouse (hereafter “sage-grouse”) are cryptic and thus can be difficult to detect; they are gray-brown in color, with tapered tail feathers, white under-wings, and feathered legs and feet (Wallestad 1975). Males and females are sexually dimorphic, and males are approximately two pounds heavier than females. During the breeding season, males and females have distinctive sex-specific plumage (Figure 1, Figure 2), whereas they appear more similar during the rest of the year (Eng 1955, Wallestad 1975). The sage-grouse is the largest North American grouse (family *Tetraonidae*) (Wallestad 1975) and the second-largest North American upland game bird after the wild turkey (Schroeder et al. 1999). This relatively large body size suggests that it resides on the "slow" end of the "slow-fast life history continuum" (Saether and Bakke 2000), with late maturity, few offspring, a long life expectancy, and population dynamics driven largely by adult survival (Stearns 1992, Saether and Bakke 2000). Some evidence supports this hypothesis (Blomberg et al. 2013); for example, sage may not reproduce in the first year or every year, particularly in years with challenging environmental conditions. However, other studies suggest that sage-grouse fall in the middle of the spectrum (Dahlgren et al. 2016, Blomberg et al. 2017), with both reproductive- and survival-based demographic rates driving population trajectories (Taylor et al. 2012, Koons et al. 2014). This would mean that conserving habitat associated with multiple life stages is likely key to protecting this vulnerable species.

Figure 1. A sage-grouse hen pictured during an evening capture session with a brood of chicks (hidden from view under her body). Photo credit: Lorelle Berkeley, spring 2012, near Roundup, MT, USA.

Figure 2. One female sage-grouse (left) pictured with four male sage-grouse on a lek (breeding ground) during the mating season. Note the distinctive, sex-specific plumage during this season. Photo credit: Lorelle Berkeley, spring 2011, near Roundup, MT, USA.

Sage-grouse currently occur across 11 western states (Washington, Oregon, California, Idaho, Nevada, Montana, Wyoming, Utah, Colorado, North Dakota, and South Dakota) and two Canadian provinces (Connelly and Braun 1997). Sage-grouse inhabit sagebrush systems that historically covered nearly 131 million acres (Miller et al. 2010). However, sagebrush now comprises only 55% of its historical extent (Miller et al. 2010). Deteriorating sagebrush habitat led to range-wide sage-grouse population declines that began causing concern in the mid-1950s and 1960s (Connelly and Braun 1997, Connelly et al. 2000, 2004). The sage-grouse was petitioned for listing under the

Endangered Species Act (ESA) eight times between 1999 and 2003 (USFWS 2015), and it was found not warranted for listing in 2005. However, after revisiting the decision in 2008, the United States Fish and Wildlife Service (USFWS) deemed sage-grouse a candidate for listing in 2010 after a listing decision found them "warranted but precluded" due to other priorities (USFWS 2015). The status review five years later found that sage-grouse did not warrant listing due to extensive conservation initiatives during 2010-2015 that involved many state and federal agencies joining together with the public (USFWS 2015). Despite these efforts, continued degradation of sagebrush habitat (Heinrichs et al. 2019, Walker et al. 2020) has raised concerns about additional petitions for listing sage-grouse in the future.

These concerns contribute to sage-grouse inhabiting a complex role in public opinion, politics, and popular culture. Sage-grouse have long been important in Native American culture. As a charismatic species with a dramatic breeding display that attracts birdwatchers and enables people to connect to nature, sage-grouse are well-loved and are even considered an "icon of the west" (Paothong and Love 2017). Sage-grouse are harvested by hunters throughout parts of their range, and sage-grouse hunters state that this opportunity enables them to spend time with family, hold onto traditions, and obtain food (Guttery et al. 2016). The USFWS did not include hunting as a high-priority threat to the species in the non-listing decision (USFWS 2015), but questions remain about whether sage-grouse harvest leads to compensatory or additive mortality (Blomberg 2015, Guttery et al. 2016), as it likely varies according to population status. As such, hunting seasons and bag limits have been reduced or eliminated in some regions to address concern about population trajectories; for example, sage-grouse hunting has not been allowed in South Dakota, USA since 2016 due to declines in annual abundance surveys (South Dakota Game Fish and Parks 2017). Even so, studies of the inhabitants of rural western landscapes suggest that they are supportive of sage-grouse conservation and management efforts due to the collaborative nature of conservation efforts and the shared goal of avoiding a potential future listing under the ESA (Duvall et al. 2017).

Sage-grouse habitat conservation and management is guided by a number of different policies, legislative acts, and management plans that regulate activities conducted within sage-grouse range, particularly for activities conducted on public lands. Due to the collaborative nature of protecting at-risk species, state wildlife management agencies partner with the Bureau of Land Management (BLM), the United States Forest Service (USFS), Native American nations, nongovernmental organizations, and private land owners to support sage-grouse conservation, with many agencies issuing their own management plans (e.g., BLM: https://www.blm.gov/programs/fish-and-wildlife/sagegrouse/blm-sagegrouse-plans; USFS: https://www.fs.usda.gov/science-technology/fish-wildlife-plants/sage-grouse; Tribal Natural Resources Committee: https://www.bistatesagegrouse.com/general/page/tribal-natural-resources-committee; The Nature Conservancy: https://www.nature.org/en-us/what-we-do/our-priorities/protect-water-and-land/land-and-water-stories/sage-grouse-conservation/; Natural Resources Conservation Service: https://www.nrcs.usda.gov/programs-initiatives/sage-grouse-initiative). This is critical, since, for example, the Bureau of Land Management (BLM) manages the largest proportion of sagebrush-steppe habitat (https://www.blm.gov/programs/fish-and-wildlife/sage-grouse). Many of these collaborations were formalized as part of the Sage Grouse Initiative, part of Working

Lands for Wildlife, which is a program of the United States Department of Agriculture's Natural Resources Conservation Service (NRCS) (Baruch-Mordo et al. 2013). Importantly, these collaborative conservation efforts have been successful at slowing declines (USFWS 2015) despite the fact that galliforms are excluded from other protective legislation such as the Migratory Bird Treaty Act (Blomberg et al. 2022), and they are not listed under the ESA.

In addition to sage-grouse-specific management plans and programs, there are numerous other conservation programs that support sage-grouse and their associated habitat. For example, the USDA's Conservation Reserve Program enhances sagebrush grasslands that are important sage-grouse habitat (Schroeder 2006), and there are state-specific upland bird habitat enhancement programs (e.g. Montana's Upland Game Bird Enhancement Program, https://fwp.mt.gov/conservation/habitat/upland-game-bird-enhancement-program). Further, private land owners can work with the NRCS, state wildlife management agencies, land trusts, and other organizations to implement conservation easements on their land in exchange for financial compensation. In sum, there are numerous tools available to different audiences in different regions of sage-grouse range that are designed to protect land and/or incentivize conservation of sage-grouse habitat.

Wildlife habitat is composed of the biotic and abiotic resources and conditions that affect the survival, reproduction, and presence of an organism (Hall et al. 1997, Mayor et al. 2009). Access to quality habitat is a known driver of population dynamics in wildlife populations (Aldridge and Boyce 2007, Van Allen and Rudolf 2015). The habitat used by a species may vary according to sex (van Toor et al. 2011, Marchand et al. 2015), life stage (Jaxion-Harm et al. 2012), interspecies interactions (MacArthur and Levins 1964), intraspecies interactions (Erikstad 1985), individual preference (Davis and Stamps 2004), and scale (Johnson 1980, Boyce 2006, Mayor et al. 2009). The quality and availability of habitat components directly affects demographic rates such as the probability of survival (Blomberg et al. 2014) and the number of young produced (Specht and Arnold 2018), which can, in turn, affect population abundance and growth rate (Lloyd et al. 2005, Coates et al. 2016). Habitat quality and availability change over time and space, due to both seasonal phenology changes (Peterson 1970, Pennington et al. 2016) and longer-term phenological shifts due to environmental change (Alward et al. 1999). Thus, to prioritize effective conservation strategies for at-risk species, resource managers and policymakers must understand the influences of habitat availability and quality on the distribution, demographic rates, and abundance of species and populations (Fedy et al. 2014, Severson et al. 2017).

Research throughout the sage-grouse range has shown that sage-grouse select for different habitats depending on their life stage (Fedy et al. 2014), which is an important consideration when designating areas of protected habitat. Sage-grouse select taller and broader sagebrush shrubs for nest sites (Holloran et al. 2005, Dinkins et al. 2016), while they prefer mesic areas for brood-rearing (Fischer et al. 1996, Atamian et al. 2010). Additionally, sage-grouse overwintering habitat is associated with areas of high-density sagebrush and less rugged terrain (Eng and Schladweiler 1972, Carpenter et al. 2010). Notably, sage-grouse priority areas for conservation focus on protecting lek (i.e. breeding ground) and nesting habitats (Stiver et al. 2015). As such, current protected areas poorly represent other stage-specific habitats (Fedy et al. 2012). However, more recently, states have recognized the importance of winter habitat protection, and the United States Department of Agriculture Natural Resources Conservation Service (NRCS) has prioritized conserving wet meadows that are important for brood-rearing habitat. This is good news because protecting habitat that supports only a fraction of the annual life cycle is not effective unless the demographic rates associated with that life stage play a disproportionate role in driving population dynamics.

Livestock grazing is an element of sage-grouse habitat that is of particular management interest. Grazing is the "consumption of standing forage [such as] edible grasses and forbs" (Holechek et al. 2011). The sagebrush steppe ecosystem was historically grazed by native species including ungulates, prairie dogs, and grasshoppers. However, domestic livestock grazing (hereafter "grazing") has varied regionally since the early 1800s, altering vegetation structure in some cases (Borman 2005). Grazing is managed in a multitude of ways depending on the context. Many ranchers graze their livestock on a mosaic of public and private land, meaning that public land management agencies (e.g. BLM, USFS) play a role in decision-making around grazing timing and intensity on public land (BLM: https://www.blm.gov/programs/natural-resources/rangelands-and-grazing; USFS: https://www.fs.usda.gov/rangeland-management/grazing/), whereas the NRCS supports ranchers grazing livestock on private land (https://www.nrcs.usda.gov/programs-initiatives/glci-grazing-lands-conservation-initiative).

Due to the potential for grazing to affect wildlife species both directly (e.g., by trampling) and indirectly (e.g., by reducing grass height or changing the composition of functional groups), it is important to understand the relationship between grazing and wildlife population dynamics. This is particularly important because grazing comprises 70% of land uses in the western United States. Indices of grazing intensity, or “the cumulative effects grazing animals have on rangelands during a particular time period (Holechek et al. 1998),” are used to describe the effects of grazing. These indices include counts of dung patties and more qualitative estimates of “low,” “moderate,” and “high” intensities (Holechek and Galt 2000, Bates and Davies 2014, Smith et al. 2018). Aspects of grazing intensity may also be described by the number of livestock in a pasture and the specific dates that they are turned into and turned out of the pasture, especially as related to plant phenology (Holechek and Galt 2000). Timing and duration are key components of grazing intensity due to the cumulative nature of the process and its relationship with vegetation vigor (Natural Resources Conservation Service 2012).

This dissertation explores several of the topics outlined above. In the first chapter, we investigate the vegetation components of habitat that sage-grouse select in the northern Great Plains at different spatial and temporal scales, including whether they select habitat in relation to grazing patterns. In the second chapter, we examine whether demographic rates associated with nesting sage-grouse vary according to grazing system. In the third chapter, we estimate sage-grouse population growth rates using different methods and discuss the status of a population of sage-grouse in the northern Great Plains. Taken together, this dissertation addresses knowledge gaps related to the effects of grazing on habitat selection, the relationship between grazing and demographic rates, and questions about how to monitor sage-grouse populations effectively.

A NOTE ON AUTHORSHIP

Throughout this dissertation, I use the pronoun “we” to acknowledge the collaborative nature of the work and the contributions of my coauthors and project partners.

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CHAPTER 1. Livestock grazing as a habitat component: how a conservation-based grazing program affects greater sage-grouse seasonal habitat selection

ABSTRACT

Patterns of animal habitat selection can inform conservation priorities by identifying areas used disproportionately by species. At broad scales, patterns of home-range selection can drive landscape-scale conservation efforts. At fine scales, habitat selection can inform whether management or conservation initiatives are effective. As part of a decade-long study in central Montana, we investigated whether sage-grouse hens select seasonal home ranges based on topographic and vegetation variables. Our study suggests that hens select for shrub cover across all seasons with other drivers varying seasonally. We also investigated whether sage-grouse located within livestock pastures select habitat characteristics in relation to grazing systems and found that they select for areas with higher used animal unit months ("used AUMs," or a measure of the amount of forage grazed) in addition to shrub cover at this scale. Sagebrush shrublands should remain a key component of sage-grouse conservation strategies, as this vegetation cover type is selected by sage-grouse across both seasons and spatial scales.

INTRODUCTION

Understanding the decisions animals make about where to distribute across the landscape is key to understanding their ecology (e.g., Lack 1933, Hilden 1965, Catchpole 1974) and habitat needs (Caughley 1994). Habitat selection, or the disproportionate use of resources or conditions by living things (Manly et al. 2002), involves animals interacting with their environment as they weigh scale-specific trade-offs between rewards and risks (Mayor et al. 2009). For example, an animal decides where and when to forage based on the spatiotemporal distribution of predation risk (Mayor et al. 2009) and seasonal variability of food resources (e.g., Previtali et al. 2009, Donnelly et al. 2019). Therefore, conservation organizations, private land owners, ecologists and wildlife managers need information about scale- and season-specific habitat selection to identify habitat conservation priorities.

We investigated habitat selection across two spatial scales and four seasons for greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse"), which is a species of conservation concern in the United States (Blomberg et al. 2012), an endangered species in Canada (Environment Canada 2013), and a "near-threatened" species on the International Union for the conservation of Nature (IUCN) red list (https://www.iucnredlist.org/). This mixed conservation status in different parts of its range reflects patterns of habitat fragmentation and degradation localized in different areas (Connelly et al. 2004), as well as the proximity of different populations to range edges (Aldridge et al. 2008). Sage-grouse habitat has been fragmented by roads and infrastructure needed for energy development (Naugle 2011) and suburban expansion and housing (Asner et al. 2004, Connelly et al. 2004). This habitat has also been degraded due to historical livestock overgrazing that continues to affect vegetation communities (Cooper 1960, Fleischner 1994), cheatgrass (*Bromus tectorum*) invasion (Bradley et al. 2018), increased incidence and severity of wildfire (West 1983, West and Hassan 1985, Wrobleski and Kauffman 2003), conversion of sagebrush to cropland (Foley et al. 2011), and increased conifer density in areas that were previously dominated by sagebrush grasslands (Aldridge et al. 2008, Davies et al. 2011). As a result of these stressors, sagebrush, and consequently sage-grouse habitat, now comprises only 55% of its historical extent (Miller et al. 2010), meaning that there is less habitat available for sage-grouse, a species that requires large tracts of intact habitat (Knick and Connelly 2011).

The sage-grouse range spans 11 western states and small parts of two Canadian provinces, meaning that there is substantial variability in microclimates, soil types, and vegetation communities in different regions (Chambers et al. 2017). For example, most precipitation in the eastern part of the range (Eastern Montana, Wyoming, and Colorado) falls as summer rain, whereas most precipitation in the western part of the range (Washington, Oregon, and parts of Idaho and Nevada) falls in the winter (Chambers et al. 2017). This difference affects soil water storage (with more water stored in areas dominated by winter precipitation) and thus plant functional types (with woody plants, including sagebrush, dominating these areas) (Chambers et al. 2017). As such, sage-grouse range has been divided into seven management zones that are tightly linked to these climate-driven vegetation communities in each area (Connelly et al. 2004, Stiver et al. 2006). Although each zone has some similarities (e.g. sagebrush makes up some fraction of the vegetation community), there are many differences. For example, the northern part of the range has cool and moist summers (MZ I, frigid/ustic) and is dominated by grass with interspersed silver and Wyoming big sagebrush, while the southwestern part is warm and dry in the winter (MZ III, cryic/aridic) (Chambers et al. 2017).

Each of these management zones has its own set of stressors and management concerns, but one constant throughout sage-grouse range is the need to manage livestock grazing in a way that does not further degrade sage-grouse habitat. Livestock grazing is ubiquitous across the distribution of sage-grouse, but the effects of grazing on vegetation depend on the soil, weather, and vegetation in the particular area (Chambers et al. 2017, Lipsey and Naugle 2017). The relationship between grazing and sage-grouse habitat selection merits further research (Connelly et al. 2004). Varying livestock grazing intensity across space and time may provide sage-grouse with variable heights and growth stages of herbaceous vegetation (Davies et al. 2014), which may be reflected in habitat selection patterns. For example, grazing could reduce the cover of grass at potential nest sites (Gibson et al. 2016, Smith et al. 2018b) since grazing when plants are not actively growing can decrease the height of some vegetation types (Davies et al. 2015). However, higher grazing intensity can also lead to nutrient-rich new growth of fall-season herbaceous plants (depending on the context, e.g., Belsky 1986, 1987), which can serve as supplementary food for hens until snowfall. Given this uncertainty, we investigate whether livestock grazing affects sage-grouse habitat selection.

Sage-grouse habitat selection likely also varies in relation to the spatiotemporal scale of measurement. Two spatial scales of habitat selection (i.e. “selection orders,” Johnson 1980) are particularly important for sage-grouse: the “home range,” or second-order habitat selection (the area traversed by an individual during its regular activities, Burt 1943), and the “habitat component,” or third-order habitat selection (e.g., a breeding or feeding area) within the home range (Johnson 1980). Most sage-grouse habitat selection research focuses on the third order (e.g., Gibson et al. 2017, Smith et al. 2018b), with fewer studies focusing on second-order selection (Drut et al. 1994, Miller and Eddleman 2001, Orning and Young 2016) or multiple scales (Doherty et al. 2010, Fedy et al. 2014). Fine-scale habitat selection has guided habitat management directives to focus on specific vegetation measures such as achieving certain grass heights and shrub cover percentages (Connelly et al. 2000), whereas more recent broader-scale work notes the importance of the broader habitat matrix in driving sage-grouse habitat selection (Fedy et al. 2014).

Range-wide evidence suggests that during the nesting season, females aim to avoid nest predation (Gregg et al. 1994, Dinkins et al. 2014) and seek cover from inclement weather (Gibson et al. 2017), thereby selecting flatter nest sites under shrubs (Smith et al. 2018b). The brood-rearing season is more uncertain; in the Great Basin, chick food preferences for insects and forbs (Drut et al. 1994, Gibson et al. 2016, Pennington et al. 2016) likely lead hens to select mesic areas (Crawford et al. 2004), but more work is needed to elucidate this relationship in wetter areas where moisture is less limiting. In the summer-fall season as broods begin to disperse, sage-grouse are found in habitats ranging from hayfields during summer to uplands in fall, where they forage on sagebrush (Braun et al. 2005). In the winter, hens tend to select taller sagebrush (Connelly et al. 2000, Crawford et al. 2004, Fedy et al. 2014) in drainages and on south and west aspects (Hupp and Braun 1989), likely because sagebrush must be accessible above the snow to serve as a food source. The northern part of the sage-grouse range is cooler and wetter than other regions (Pyke et al. 2015), which has the potential to yield different habitat selection patterns than hotter, drier areas like the Great Basin where thermal cover may be a stronger habitat selection driver for more of the year (Anthony et al. 2021). We investigate whether the seasonal habitat selection patterns in central Montana are similar to those of sage-grouse in other regions.

Across the range, sage-grouse habitat selection varies seasonally, due to shifting vegetation phenology and associated food resource availability in sagebrush habitat across the year (Connelly et al. 2004). For example, during the springtime, sage-grouse chicks select insects that are associated with green vegetation and thus wetter areas (Gibson et al. 2017). During the summer, sage-grouse tend to eat more sagebrush, which continues through the fall and winter when this is their predominant food resource (Eng and Schladweiler 1972, Pennington et al. 2016). Throughout the year, sage-grouse obtain water primarily from the foods they eat, from dew, and from snow in the winter (Klebenow 1969, Roché and Garrett 2020), although they do use standing water in some cases (Naugle et al. 2004). This seasonal variation in sage-grouse habitat selection merits parallel seasonal habitat management strategies to ensure that needs are met across the annual cycle (Connelly et al. 2004).

In addition to investigating the importance of seasonal habitat selection, it can also be useful to study longer-term habitat selection patterns when they relate to specific management actions. Livestock grazing is a common management activity within sage-grouse range, and it occurs over varying time frames within discrete pastures that may also be occupied by sage-grouse. In some cases, livestock grazing data may only be available at longer temporal resolutions such as for the calendar year. By constraining a habitat selection analysis to within livestock grazing pastures, it is possible to investigate the effects of grazing-related variables on sage-grouse habitat selection at a finer spatial resolution, even as a longer temporal resolution (e.g. one year) may be required due to data limitations. This type of analysis is analogous to a third-order habitat selection analysis because it investigates habitat selection patterns in smaller areas that occur within the home range. Taken in tandem, this type of third-order habitat selection analysis can offer additional information to a seasonal analysis that may be relevant to conservation and management decisions.

Translating sage-grouse habitat selection information into conservation strategies is challenging, particularly when incorporating complex land uses like livestock grazing. For example, sage-grouse breeding ecology suggests that they likely fall in the middle of the “slow-fast life history continuum” (Saether and Bakke 2000, Dahlgren et al. 2016, Blomberg et al. 2017), meaning that multiple demographic rates likely affect population dynamics, which could be a complex management challenge if they need different resources to support different demographic rates (Taylor et al. 2012). Early sage-grouse research and habitat conservation efforts provided a disproportionate amount of information about nesting habitat due to the relative ease of collecting this information (Connelly et al. 2004, Stiver et al. 2006, 2015). However, over the last decade, conservation practitioners have been seeking out more comprehensive information about sage-grouse habitat selection.

We draw on several different types and resolutions of data to address two questions that are relevant to sage-grouse habitat management in Montana and other regions with similar vegetative communities and land uses. First, do sage-grouse hens select seasonal home ranges with certain vegetation cover and topography characteristics (i.e. second-order selection at the seasonal temporal resolution)? We were interested in exploring the effects of broad-scale vegetation cover (e.g. shrub, annual, perennial, litter, bare ground, and tree cover) and topography on seasonal home range selection because these variables are linked to both habitat selection and demographic rates in many other regions (e.g. Baxter et al. 2017, Beers and Frey 2022). Second, we investigate whether characteristics of grazing systems drive third-order habitat selection at the annual temporal scale (i.e. within-pasture habitat selection, constrained to the finer-resolution pastures that hens used within their home range). We were interested in looking at indices of livestock use, grazing system, and the indirect effect of grazing on vegetation at the third order inform habitat management and conservation (Vavra 2005).

METHODS

Study area

The study area was in central Montana in rolling topography that ranged from 975-1,250m in elevation (Smith et al. 2018a) and covered approximately 150,000 hectares in Musselshell and Golden Valley counties. The vegetation was primarily Wyoming big sagebrush (*Artemisia tridentata ssp. wyomingensis*) and silver sagebrush (*A. cana*), with a mix of perennial bunchgrasses, perennial rhizomatous grasses, and forbs. The study area is a mosaic of public (federal, state, and county) and private ownership dominated by rangeland (cattle and sheep) and some dryland farming (Smith et al. 2018a). The average monthly temperature in Roundup (2009-2020) ranged from a low of -3.8º Celsius (25.1º Fahrenheit) in January to a high of 21.8º Celsius (71.2º Fahrenheit) in July (National Centers for Environmental Information 2021). Average monthly precipitation in Roundup (2009-2020) ranged from a low of 9.40 millimeters in January to a high of 73.41 millimeters in June (National Centers for Environmental Information 2021). The climate is cold semiarid (Pyke et al. 2015), with distinct seasons that include cool and wet springs, hot and dry summers, cool and wet autumns, and cold, snowy winters.

Some privately-owned pastures were enrolled in rotational grazing systems implemented through the Sage Grouse Initiative (SGI), a program of the United States Department of Agriculture Natural Resources Conservation Service (NRCS) that is focused on improving livestock production, rangeland health, and sage-grouse habitat (USDA NRCS 2015). The SGI grazing program was implemented on pastures containing potential sage-grouse habitat near known breeding areas, and grazing plans involved: 1) Grazing utilization rates of ≤50% of the current year's key forage species growth, 2) ≥20-day shift annually in the timing of grazing, 3) A plan to address unexpected circumstances like drought or fire, and 4) ≤45-day continuous grazing durations within any one pasture (Natural Resources Conservation Service 2017, Smith et al. 2018a).

Sage-grouse monitoring

Sage-grouse seasons include: nesting (Apr. 1-May 31), brood-rearing (Jun. 1-Jul. 15, Rice et al. 2016), summer-fall (Jul. 16-Nov. 30, Rice et al. 2016, Walker et al. 2016), and winter (Dec. 1-Mar. 31, Walker et al. 2016). To correspond with these seasonal periods, a year in the sage-grouse life cycle begins on April 1 and ends on March 31 of the following calendar year.

In March and April from 2011-2019, we captured hens from a non-migratory population on or near leks using night-time spotlighting (Giesen et al. 1982, Wakkinen et al. 1992). We fit hens with either a 25-g necklace style very high frequency (VHF) transmitter (Model A4060, Advanced Telemetry Systems, Isanti, MN) or a 25 g solar

GPS PTT (2018-2020 only). After capturing an initial sample of 100 hens (2011), we captured hens annually to replace lost or dead hens. When possible, we replaced two-year-old transmitters before failure to increase each hen's monitoring duration. Capturing and handling of sage-grouse hens was approved by the University of Montana's Institutional Animal Care and Use Committee protocols (AUP 009-18VDWB-031418; AUP 011-14DNWB-031914).

Telemetered hens (VHF) were monitored from ground surveys every two days during the nesting and brood-rearing seasons, and aerial surveys 1x/month during summer-fall and winter (Table 1). We monitored GPS-marked hens from an online platform (Woods Hole Group, Inc., Bourne, MA, USA) where satellite-transmitted locations were uploaded on a pre-programmed schedule designed to maximize locations based on seasonal solar charging capacity (8x/day during nesting, 10x/day during brood-rearing, 6x/day during summer-fall, and 4x/day during winter).

Table 1. Summaries of sage-grouse monitoring data available to build seasonal habitat selection models across years, where years are defined as beginning on April 1 (the start of the nesting season) and ending on March 31 of the next calendar year (the end of the winter season). The number of locations per hen and relocation intervals vary across seasons due to different visit rates of ground-based monitoring (May to August) and aerial monitoring (September to March). All data correspond with VHF-monitored hens except for 2019, when some hens were monitored via GPS transmitters.

Year	Season	Median (sd) # locs/hen	Range # locs/hen	Median (sd) reloc. interval (d)	Range of median reloc. Interval	# Hens
2011	Nesting	8 (5.04)	1-19	2 (8.13)	1-53	99
	Brood-rearing	5 (4.65)	1-23	2 (3.50)	1-26	74
	Summer-fall	3 (2.75)	1-19	36 (27.77)	1-98	79
	Winter	1 (0.00)	1-3	56 (12.51)	1-111	90
2012	Nesting	6 (5.01)	1-21	2 (5.22)	1-41	109
	Brood-rearing	2 (5.59)	1-18	2 (4.09)	1-25	84
	Summer-fall	3 (3.63)	1-18	28 (21.04)	1-95	97
	Winter	3 (0.90)	1-4	32 (10.48)	2-61	90

2013	Nesting	8 (4.54)	1-20	2 (4.91)	1-49	75
	Brood-rearing	8 (5.17)	1-20	3 (4.94)	1-41	71
	Summer-fall	4 (2.71)	1-13	7 (20.81)	1-85	74
	Winter	2 (0.85)	1-3	68 (10.82)	33-68	73
2014	Nesting	7 (4.86)	1-18	2 (6.47)	1-51	84
	Brood-rearing	12 (6.08)	1-22	3 (2.06)	1-23	58
	Summer-fall	3 (2.43)	1-10	18 (15.43)	1-59	83
	Winter	4 (1.27)	1-4	39 (12.03)	1-73	86
2015	Nesting	8 (4.80)	1-20	3 (5.19)	1-43	97
	Brood-rearing	10 (4.36)	1-18	3 (3.16)	1-27	89
	Summer-fall	7 (4.28)	1-21	7 (15.42)	1-76	93
	Winter	1 (0.28)	1-3	20 (18.73)	3-40	76
2016	Nesting	9 (7.23)	1-29	2 (5.88)	1-59	99
	Brood-rearing	13 (5.97)	1-24	2 (3.18)	1-34	81
	Summer-fall	11 (5.13)	1-23	4 (10.47)	1-74	88
	Winter	2 (0.49)	1-2	31 (3.35)	5-31	105
2017	Nesting	11 (4.94)	1-22	3 (2.61)	1-26	103
	Brood-rearing	13 (6.05)	1-25	2 (2.95)	1-39	88
	Summer-fall	7 (3.72)	1-19	4 (18.77)	1-117	93
	Winter	2 (0.32)	1-2	55 (0.00)	55-55	52
2018	Nesting	13 (4.09)	1-19	3 (1.89)	1-26	77
	Brood-rearing	13 (5.57)	1-24	2 (3.20)	1-32	69
	Summer-fall	9 (2.81)	1-14	3 (18.39)	1-65	58
	Winter	2 (0.35)	1-2	52 (0.00)	52-52	37
2019 (VHF)	Nesting	15 (11.35)	1-32	2 (4.01)	1-53	48
	Brood-rearing	17 (7.65)	1-21	2 (1.74)	1-28	34
	Summer-fall	8 (6.27)	1-24	3 (15.07)	1-67	44
	Winter	1 (0.51)	1-2	61 (21.56)	1-61	43
2019 (GPS)	Nesting	57 (12.5)	7-60	1 (0.30)	1-5	42
	Brood-rearing	37 (7.46)	9-40	1 (0.99)	1-13	37
	Summer-fall	120 (41.5)	8-131	1 (1.64)	1-59	36
	Winter	102 (42.85)	1-118	1 (2.25	1-61	29

Resource selection functions

First, we conducted second-order habitat selection analyses for four seasons across the sage-grouse annual cycle – nesting, brood-rearing, summer-fall, and winter – using resource selection functions (RSFs) in a used-available framework. This analysis enabled us to investigate important vegetation-related drivers of second-order habitat selection that could be compared across seasons, using remotely-sensed vegetation layers, since point-level vegetation data were not collected in all seasons. Second, we conducted third-order habitat selection analyses within livestock pastures at the annual temporal resolution using RSFs in a used-available framework. These analyses represent third-order habitat selection because they are constrained to smaller livestock grazing pastures located within a home range. This analysis enabled us to investigate grazing-related drivers of habitat selection in discrete areas that were known to be grazed, operating within the constraint that grazing variables were collected at the annual temporal resolution.

The used-available RSF framework estimates the relative amount of time an individual spends using a resource as a function of the proportional availability of that resource (McLoughlin et al. 2006), such that resource selection is proportional to the probability of use (Johnson et al. 2006). We used a combination of a VHF telemetry dataset (hereafter "VHF dataset") spanning 2011-2019 and a smaller GPS monitoring dataset (hereafter "GPS dataset") collected in 2018-2019. We combined the VHF and GPS datasets, and then divided them into the four seasonal subsets and used conditional logistic regression. To account for individual variation in habitat availability, we randomly sampled available points in proportion to the number of used points each year to control for variation across years (Picardi et al. 2020) from each individual's home range as represented by a 99% minimum convex polygon.

For the second-order RSFs, we ran nine univariate models containing the candidate variables for each of the four seasons, and selected the top five univariate models using AIC. Then, we constructed additive models from the top five variables, added these models to the model set containing the original five top models, and selected the top overall model for the season using AIC. For the third-order RSFs, we followed the same process, but started with five univariate models containing the candidate variables. We conducted all analyses in Program R (R Core Team 2020).

Covariates

Seasonal second-order selection

We explored various vegetative and topography metrics on second-order habitat selection at the seasonal temporal resolution. We extracted annual estimates of percent vegetation cover (shrub, annual forbs and grass, perennial forbs and grass, bare ground, trees, and litter) at points from the Rangeland Analysis Platform (30m grain size, https://rangelands.app/products/, Allred et al. 2021) using Google Earth Engine (Gorelick et al. 2017). Topographic variables (elevation, slope, and aspect) were derived from the National Elevation Dataset (1/3 arc-second grain size, The National Map, United States Geological Survey, https://apps.nationalmap.gov/downloader/). We extracted elevation directly at points, whereas we derived slope and aspect from each point's eight nearest neighbors using package "raster" (Hijmans 2022) in Program R (R Core Team 2020). We originally included terrain ruggedness index (TRI), but ultimately excluded it due to a strong correlation with slope (Pearson's product-moment correlation = 0.966). We explored differences in covariate values across used and available points (Figure 3, Figure 4, Figure 5, Figure 6). Prior to inclusion in models, we centered and scaled variables by subtracting the mean value of the variable and dividing by the variable's standard deviation, using the "scale" function in package "raster" (Hijmans 2022) in Program R (R Core Team 2020).

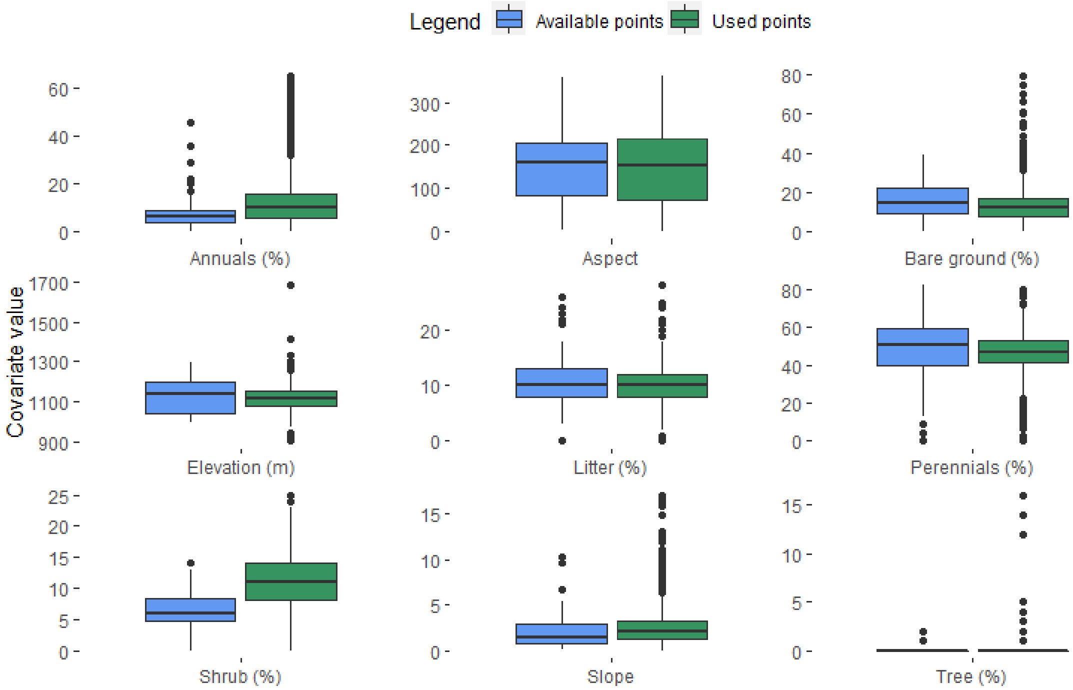


Figure 3. Boxplots showing differences in the covariate values across used and available points during the nesting season.

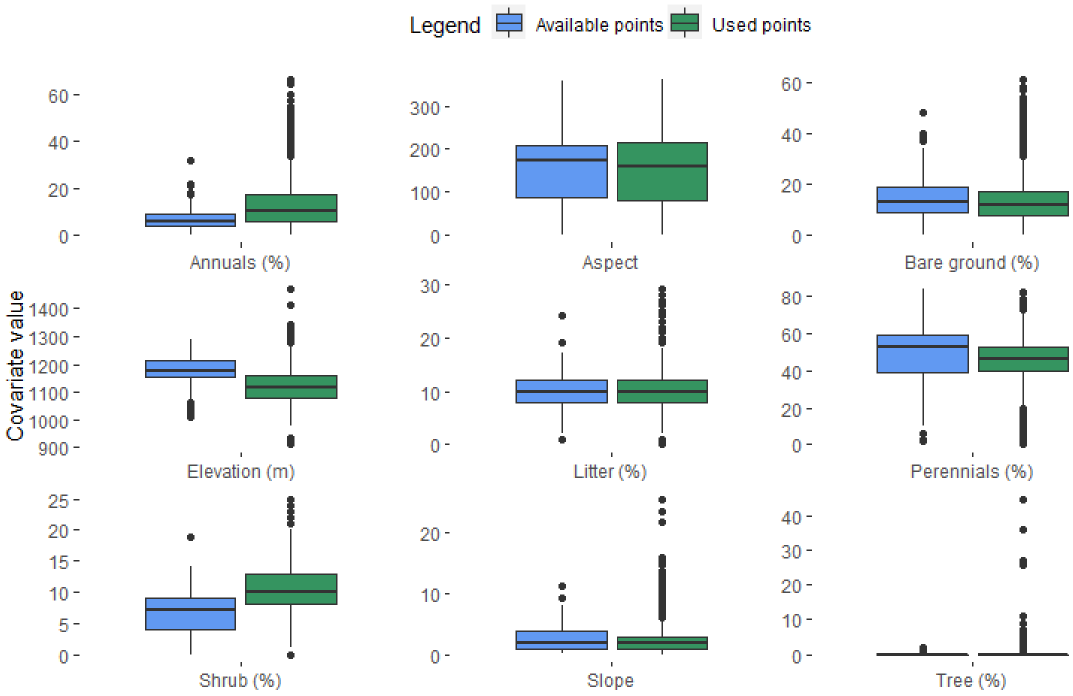


Figure 4. Boxplots showing differences in the covariate values across used and available points during the brood-rearing season.

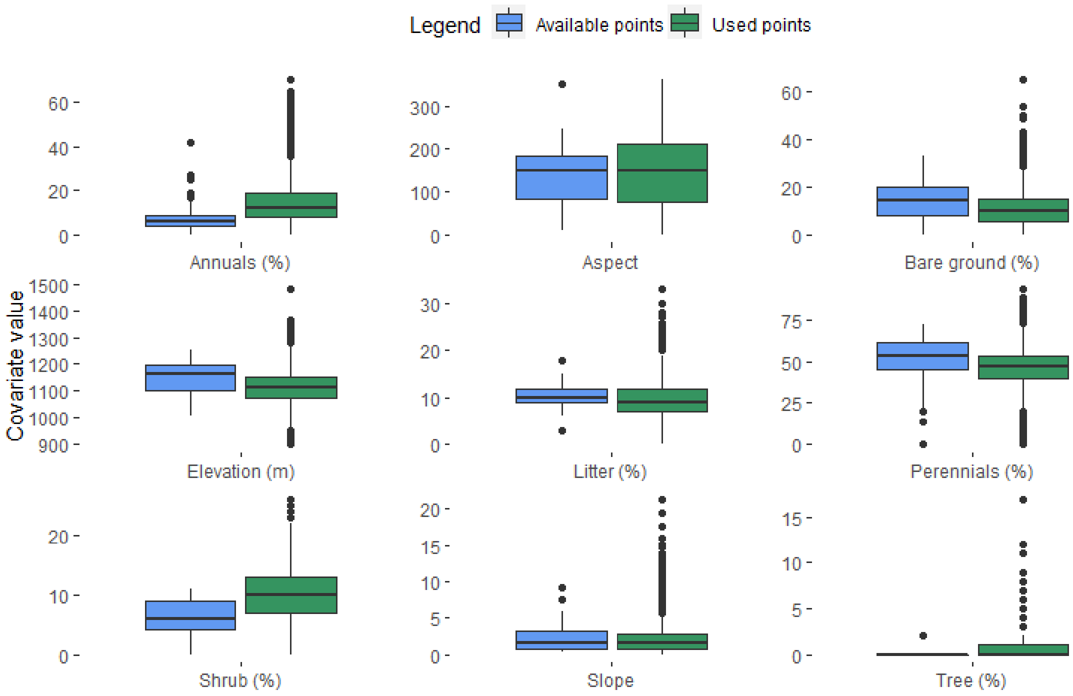


Figure 5. Boxplots showing differences in the covariate values across used and available points during the summer-fall season.

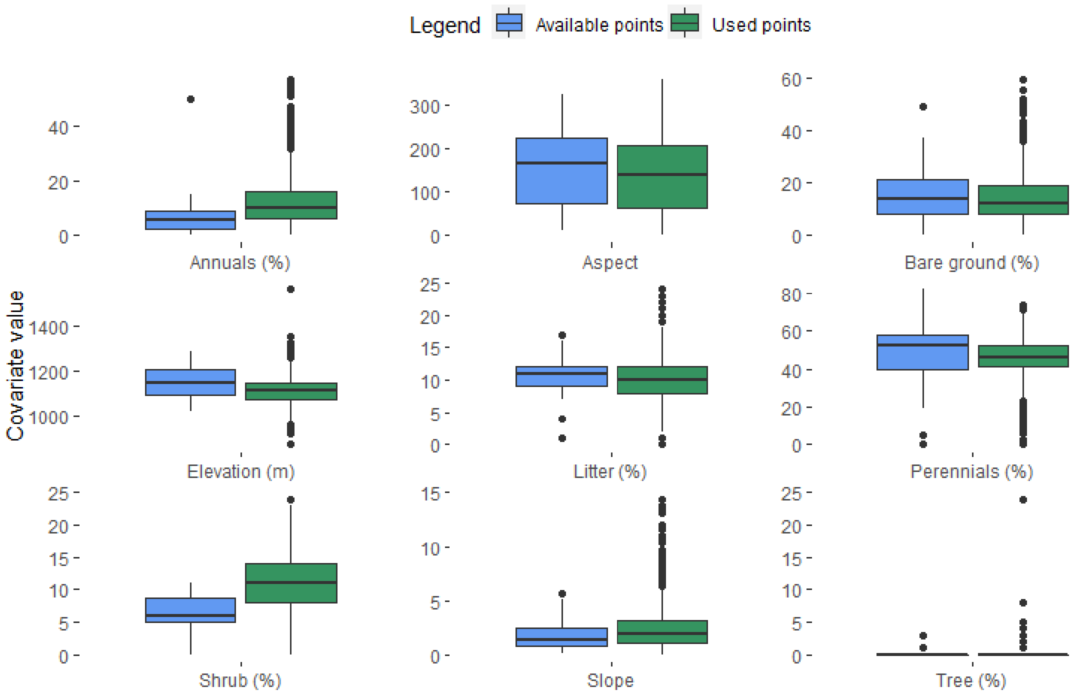


Figure 6. Boxplots showing differences in the covariate values across used and available points during the winter season.

Annual third-order selection

In the third-order habitat selection models, we investigated the effects of the two vegetation cover variables that appeared in the most top seasonal models: shrub cover (which appeared in 4 of 4 seasonal models) and annual forb and grass cover (which appeared in 3 of 4 seasonal models). We also investigated the effects of three grazing variables: SGI status, used Animal Unit Months (U-AUMs), and number of days grazed. We extracted two of the three grazing variables, SGI status and U-AUMs, at points located in livestock grazing pastures. We categorized a point as “Yes” for SGI status if the pasture in which it was located was either concurrently or previously enrolled in an SGI grazing regime. We defined U-AUMs as the amount of forage used during a year per cattle-head or a head-equivalent (e.g., 1 heifer = 0.8 head-equivalent (1000 lb cow) and 1 sheep = 0.17 head-equivalent) and assigned U-AUMs to points if the point was used during the same year that the U-AUMs were reported. We calculated the number of days grazed by summing the total number of days the pasture was grazed across the year. These variables were calculated at used and available points (Figure 7).

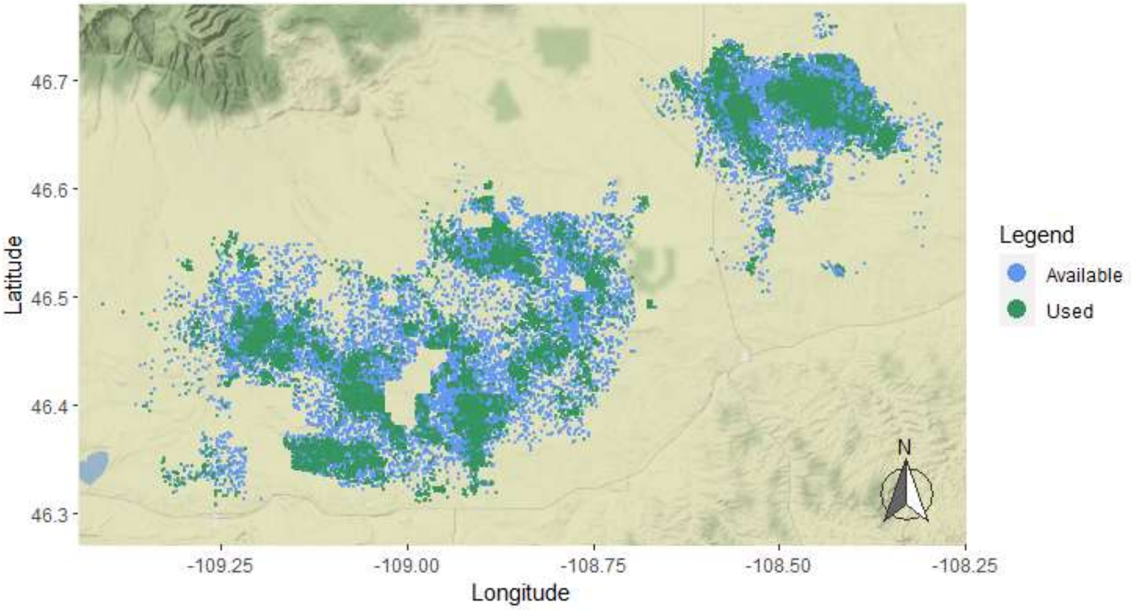


Figure 7. A map of used and available points within known livestock pasture boundaries.

Table 2. Additional grazing metrics summarized across SGI status to assist with interpretation of similarities and differences among pastures in different SGI categories. The "number of pastures" and the "pasture area" refer to the number of distinct pastures and the pasture area in the specified SGI grazing category for a given year. The "mean used AUMs" refers to the mean animal unit months (a measure of grazing pressure) used by livestock in the pastures in the specified SGI grazing category for a given year. The "mean days grazed" refers to the total number of days a pasture was grazed during a given year. The "mean first turn-in date" is the mean of the first dates when livestock were put out to pasture in a given year (measured April 1 – March 31). Sample sizes ("n") of the number of pastures used to calculate mean values are included for "mean

days grazed" and "mean first turn-in date" due to these data types only being available for a subset of the pastures within each year.

SGI status	Year	Number of pastures	Pasture area (km^2)	Mean used AUMs	Mean days grazed	Mean first turn-in date
Yes	2011	52	138.15	139.74 (sd=106)	27.73 (sd=16d, n=30)	July 24 (sd=90d, n=30)
No	2011	458	1378.16	138.04 (sd=193)	59.21 (sd=67d, n=80)	June 15 (sd=102d, n=81)
Yes	2012	128	361.39	122.07 (sd=97)	27.26 (sd=17d, n=86)	August 2 (sd=77d, n=87)
No	2012	388	1159.77	136.52 (sd=221)	83.48 (sd=76d, n=50)	May 24 (sd=116d, n=51)
Yes	2013	152	394.68	123.85 (sd=109)	32.72 (sd=23d, n=76)	July 3 (sd=84d, n=80)
No	2013	369	1121.70	185.78 (sd=515)	68.86 (sd=68d, n=69)	May 12 (sd=104d, n=69)
Yes	2014	181	514.18	131.67 (sd=131)	32.54 (sd=21d, n=100)	July 2 (sd=101d, n=101)
No	2014	342	1002.19	122.85 (sd=240)	76.78 (sd=73d, n=58)	May 2 (sd=95d, n=58)
Yes	2015	189	536.27	184.34 (sd=160)	35.18 (sd=27d, n=78)	July 2 (sd=101d, n=80)
No	2015	334	978.79	170.48 (sd=252)	77.40 (sd=66d, n=93)	May 2 (sd=93d, n=93)
Yes	2016	233	582.72	162.78 (sd=175)	37.50 (sd=26d, n=109)	July 11 (sd=70d, n=110)
No	2016	292	934.66	187.65 (sd=244)	80.27 (sd=67d, n=116)	May 27 (sd=99d, n=121)
Yes	2017	231	575.03	159.05 (sd=151)	37.56 (sd=30d, n=104)	July 8 (sd=78d, n=108)
No	2017	298	941.33	203.46 (sd=296)	80.39 (sd=75d, n=104)	May 21 (sd=90d, n=111)
Yes	2018	231	575.02	153.44 (sd=181)	49.84 (sd=42d, n=100)	July 6 (sd=85d, n=100)
No	2018	298	941.36	212.25 (sd=327)	77.26 (sd=72d, n=136)	May 19 (sd=82d, n=138)
Yes	2019	229	574.97	NA	40.97 (sd=27d, n=66)	July 10 (sd=72d, n=66)
No	2019	300	941.66	216.07 (sd=287)	77.33 (sd=65d, n=123)	December 31 (sd=111d, n=123)

RESULTS

Data summaries

The quantity of data available for analyses varied across seasons and years. The number of birds in the sample was relatively similar across years and seasons until a decline throughout the year in 2018 (Table 1).

The highest number of points per season occurred in 2019 due to the use of GPS transmitters during this year (Table 1); for the rest of these summaries, we report on VHF data only. In general, the most bird locations were recorded during the nesting and brood-rearing seasons, which corresponds with the highest sampling effort (when technicians were locating birds on the ground every few days). For example, the median number of locations during the nesting season ranged from 6 (2012) to 15 (2019). During the brood-rearing season, the median number of locations ranged from 2 (2012) to 17 (2019). During the summer-fall season, the median number of locations ranged from only 3 (2011, 2012, and 2014) to 11 (2016). The winter season had far fewer locations in general, ranging from a median of 1 location (2011, 2015, and 2019) to 4 (2014). (Table 1)

Similarly, the median relocation interval was substantially shorter during the nesting and brood-rearing seasons, due to the frequent visits by technicians, and it typically ranged between 2 and 3 days. The median relocation interval was variable during the summer and fall season; sometimes it was longer than a month due to accessibility challenges from weather or road conditions, while other times it was closer to a week. In the winter, this interval was regularly longer than a month, corresponding with the monthly aerial telemetry flights that technicians used to track birds during this season. (Table 1)

In general, ranges of covariate values were very similar across used and available points and across seasons (Figure 3, Figure 4, Figure 5, Figure 6). In particular, aspect and litter were most similar across seasons and point types. Variables including shrub cover, annual forb and grass cover, and elevation showed more variation across both seasons and point types, with the direction of the difference occasionally varying depending on the season (Figure 3, Figure 4, Figure 5, Figure 6).

Seasonal second-order selection

Sage-grouse hen home range sizes were highly variable, with a right-skewed distribution (median = 2.75 km^2, mean = 6.09 km^2, sd = 11.08 km^2). Drivers of sage-grouse habitat selection varied depending on the season (Figure 8, Figure 9, Figure 10, Figure 11, Table 3, Table 4). Across all four seasons, sage-grouse most strongly selected for the percent of shrub cover. During the nesting season, hens also selected higher proportions of annual forbs and grasses and higher slopes, whereas they selected areas with lower proportions of bare ground. Similarly, during the brood-rearing season, hens selected higher proportions of shrub and annual grasses, but they selected lower elevations. During the summer-fall season, hens selected for higher proportions of shrub and annual forbs and grasses, while they selected lower elevations, lower bare ground cover, and lower perennial forb and grass cover. During the winter, hens selected higher shrub cover and lower elevations (Figure 8, Figure 9, Figure 10, Figure 11, Table 3).

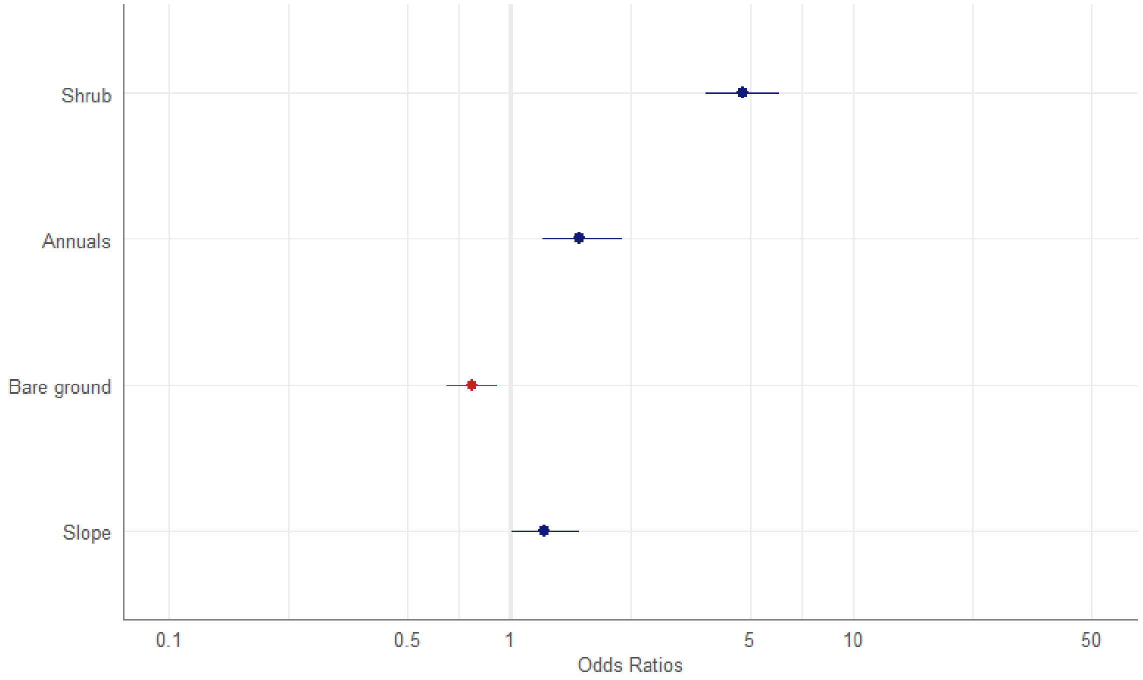


Figure 8. Plots showing the odds ratios and 95% confidence intervals of the coefficients in the top model for the seasonal home range selection model for the nesting season. Coefficient effects in blue are positive, and effects in red are negative.

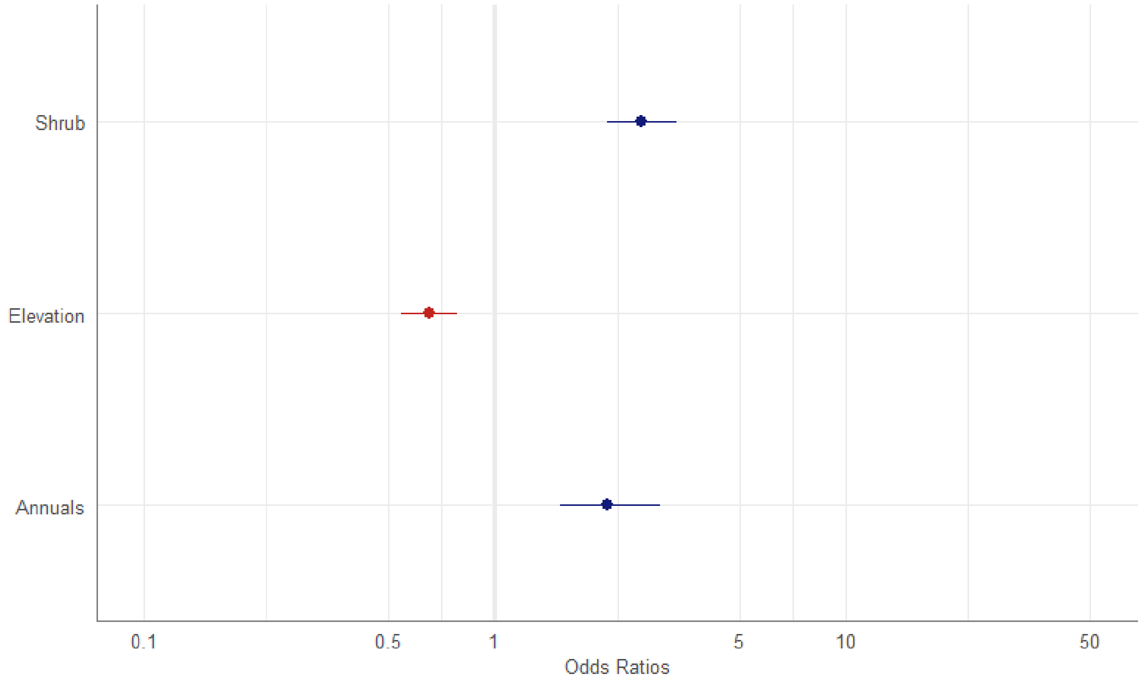


Figure 9. Plots showing the odds ratios and 95% confidence intervals of the coefficients in the top model for the seasonal home range selection model for the brood-rearing season. Coefficient effects in blue are positive, and effects in red are negative.

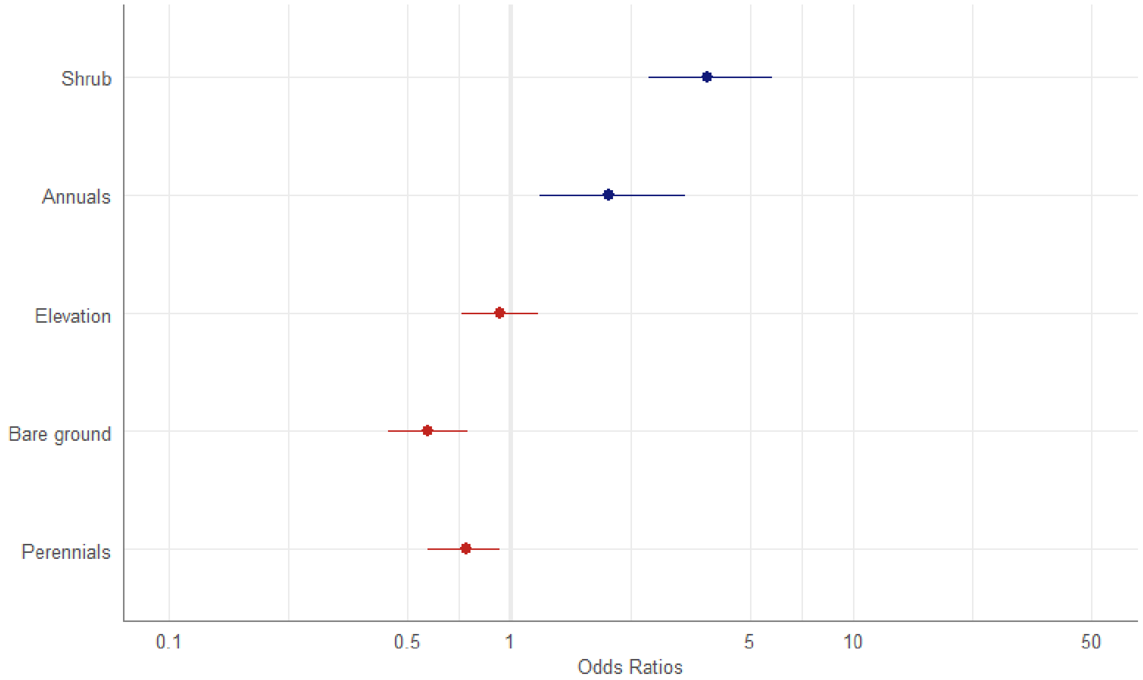


Figure 10. Plots showing the odds ratios and 95% confidence intervals of the coefficients in the top model for the seasonal home range selection model for the summer-fall season. Coefficient effects in blue are positive, and effects in red are negative.

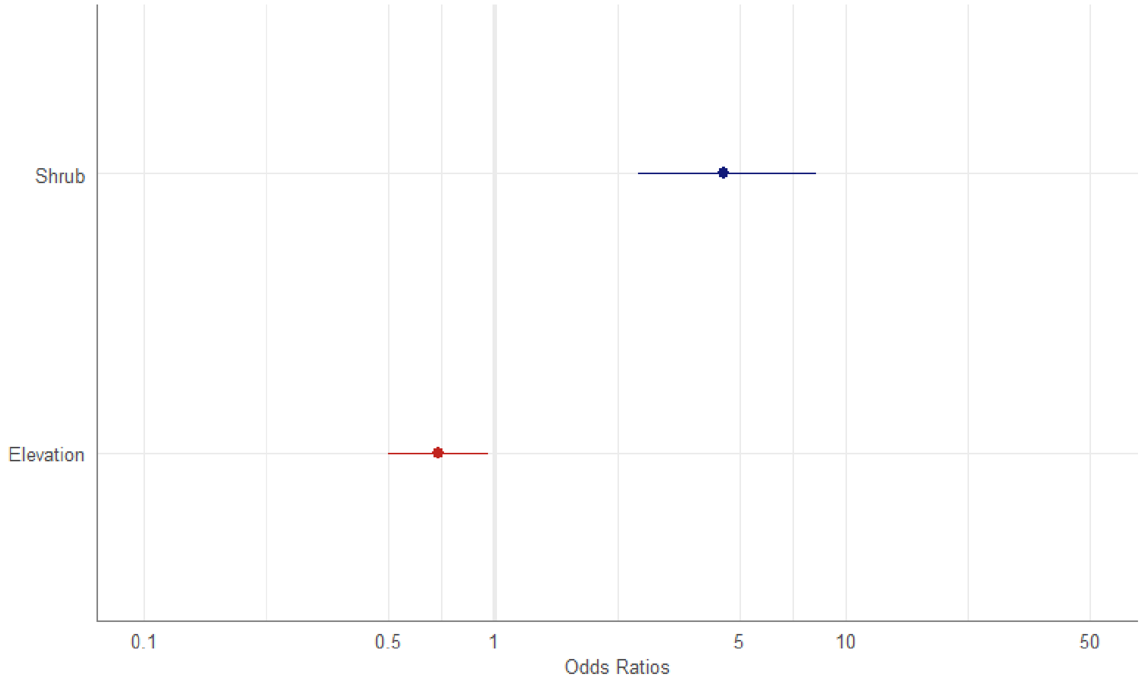


Figure 11. Plots showing the odds ratios and 95% confidence intervals of the coefficients in the top model for the seasonal home range selection model for the winter season. Coefficient effects in blue are positive, and effects in red are negative.

Table 3. Coefficient estimates from the top model of female sage-grouse home range selection. All vegetation variable (shrub, annual forbs and grasses, or “annuals”, bare ground, tree, perennial forbs and grasses, or “perennials”, and litter) are measures of percent cover at the 30m^2 resolution.

Season	Covariate	Estimate	Standard error	Pr(>|z|)
Nesting	Intercept	5.587	0.186	0.000
	Shrub (scaled)	1.558	0.127	0.000
	Annual forbs & grass (scaled)	0.459	0.136	0.000
	Bare ground (scaled)	-0.265	0.086	0.002
	Slope (scaled)	0.221	0.118	0.061
Brood-rearing	Intercept	5.246	0.173	0.000
	Shrub (scaled)	0.967	0.116	0.000
	Elevation (scaled)	-0.426	0.095	0.000
	Annual forbs & grass (scaled)	0.738	0.167	0.000
Summer-fall	Intercept	6.179	0.287	0.000
	Shrub (scaled)	1.328	0.212	0.000
	Annual forbs & grass (scaled)	0.657	0.249	0.008
	Elevation (scaled)	-0.075	0.132	0.569
	Bare ground (scaled)	-0.554	0.135	0.000
	Peren. forbs & grass (scaled)	-0.297	0.121	0.014

Winter	Intercept	5.116	0.414	0.000
	Shrub (scaled)	1.499	0.296	0.000
	Elevation (scaled)	-0.367	0.163	0.025

Although there was strong support for many topographic and vegetation cover variables across seasons, for some seasons, the ∆AIC was less than 2 between the top two models (Table 4), suggesting that both models may be informative (Burnham and Anderson 2002). During the nesting season, the second-best model (∆AIC = 0.8) also contained perennial forbs and grasses (Table 4). The small difference in ∆AIC suggests that sage-grouse hens in this population may consider perennial cover when selecting habitat during this season, or at least, that this relationship merits further exploration. During the brood-rearing season, the second-best model (∆AIC = 1.2) suggested possible weak evidence that sage-grouse hens select against tree cover, again due to the small difference in AIC among the two models. Drivers of summer-fall home range selection were clearer, with the majority of evidence supporting the top model, whereas the second-best winter model suggested sage-grouse may select for annual forb and grass cover as well (∆AIC = 0.5). (Table 4)

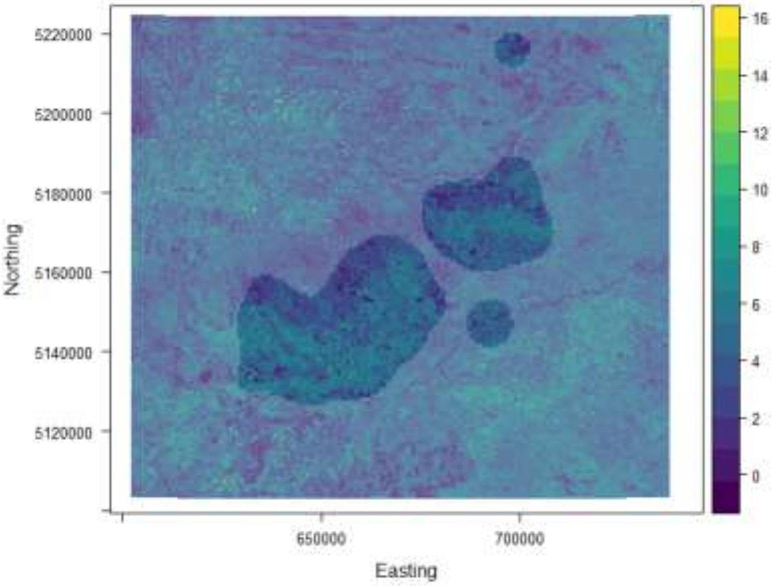
Table 4. The 5 most-supported models from a set of 13 candidate models describing female sage-grouse home range selection. All vegetation variable (shrub, annual forbs and grasses, or "annuals", bare ground, tree, perennial forbs and grasses, or "perennials", and litter) are measures of percent cover at the 30m^2 resolution. The top model for each season is highlighted in bold.

Season	Model	Resid. DF	Resid. Deviance	∆ AIC	AIC Weight
Nesting	**1. Shrub + Annuals + BareGround + Slope**	**9342**	**1009**	**0**	**0.482**
	2. Shrub + Annuals + BareGround + Slope + Perennials	9341	1008	0.8	0.323
	3. Shrub + Annuals + BareGround	9343	1013	1.9	0.186
	4. Shrub + Annuals	9344	1021	8.1	0.008
	5. Shrub	9345	1059	44.6	0

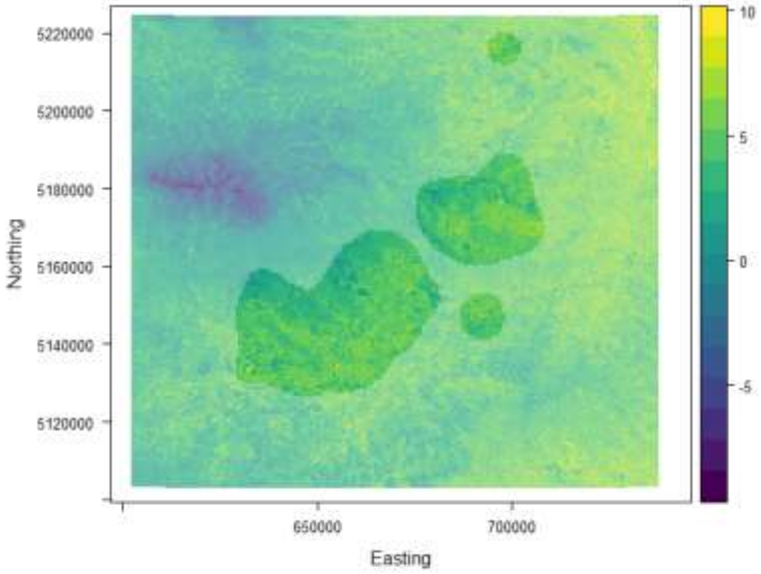
Brood-rearing	**1. Shrub + Elevation + Annuals**	**7579**	**841**	**0**	**0.541**
	2. Shrub + Elevation + Annuals + Tree	7578	840	1.2	0.297
	3. Shrub + Elevation + Annuals + Tree + Perennials	7577	840	2.4	0.163
	4. Shrub + Elevation	7580	868	25.3	0
	5. Shrub	7581	900	55.1	0
Summer-fall	**1. Shrub + Annuals + Elevation + BareGround + Perennials**	**7544**	**505**	**0**	**0.933**
	2. Shrub + Annuals + Elevation + BareGround	7545	513	5.3	0.066
	3. Shrub + Annuals	7545	526	14.6	0.001
	4. Shrub + Annuals + Elevation	7547	526	16.2	0
	5. Shrub	7546	555	41.9	0
Winter	**1. Shrub + Elevation**	**1265**	**184**	**0**	**0.392**
	2. Shrub + Elevation + Annuals	1264	183	0.5	0.306
	3. Shrub + Elevation + Annuals + Litter	1263	182	2	0.144
	4. Shrub	1266	189	2.7	0.102
	5. Shrub + Elevation + Annuals + Litter + Perennials	1262	182	3.9	0.056

Predictive maps of seasonal home range selection show where hens are expected to be based on the habitat components they select (identified using the previously-described RSFs) for their seasonal home ranges. Building this type of predictive model assumes that these seasonal habitat components remain in similar proportions to their distribution over the nine years of the study. These maps demonstrate minor differences in areas that we expect sage-grouse hens to select seasonally (Figures 12). The map of sage-grouse nesting season shows areas with a lower relative probability of use along the northern boundary of the annual population home range (in blue, Figures 12, top left), whereas areas north of the annual population home range have a higher relative probability of use (in yellow, Figures 12, top left). The map of the brood-rearing season shows strong selection against an area of high elevation northwest of the annual population home range (in purple, Figures 12, top right), but otherwise, looks similar to the nesting season. Summer-fall home range selection is more similar across the annual population home range, whereas winter selection is more variable, showing mixed areas of lower relative probability of use (in blue, Figures 12, bottom left and right).

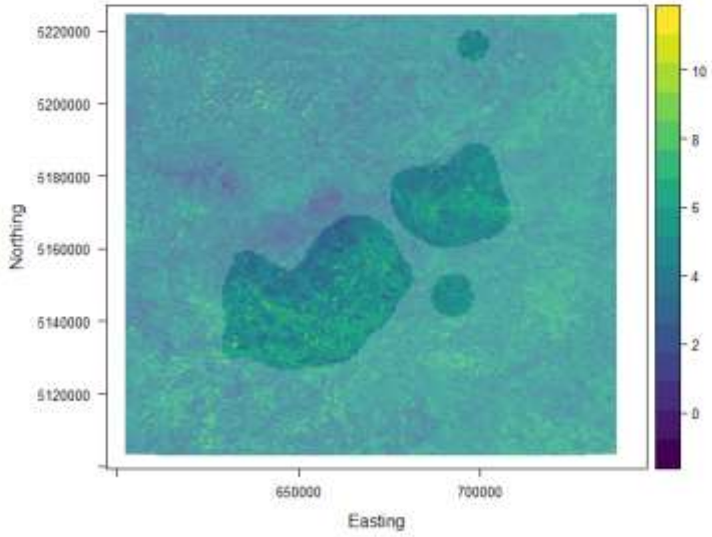
12A. Nesting season



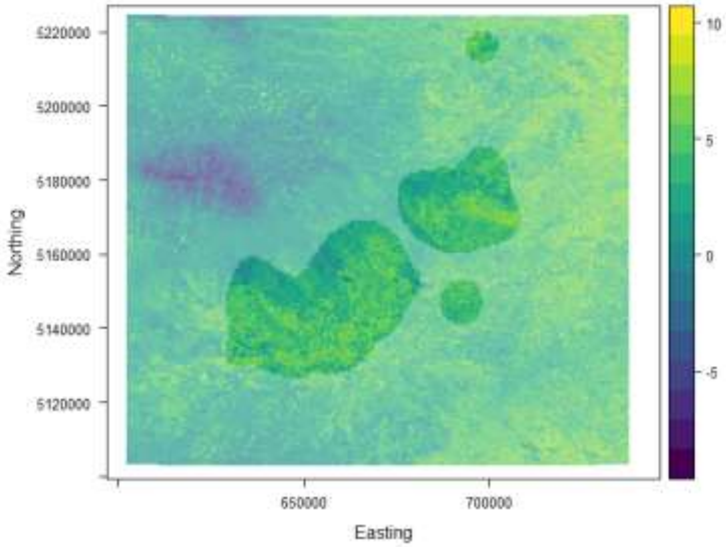
12B. Brood-rearing season



12C. Summer-fall season.



12D. Winter season.



Figures 12a-12d. Predictive maps of seasonal home ranges selected by sage-grouse hens. Maps depict the relative probability of use, ranging from low use (in purple) to high use (in yellow). The annual home range is depicted via the polygons in the center of each map, whereas the area around the annual home range is slightly grayed out to indicate that extrapolating outside the area where the data were collected is more uncertain.

Annual third-order selection

Female sage-grouse that were ever located within livestock grazing pastures (n = 407 hens) selected for higher shrub cover and higher levels of U-AUMs (Figure 13, Table 5, Table 6, Figure 14). Based on the coefficient estimate for shrub cover (Table 5), selection for shrub cover still dominated selection patterns at this scale. However, there was also evidence that they selected for U-AUMs, with a small positive coefficient effect (Table 5).

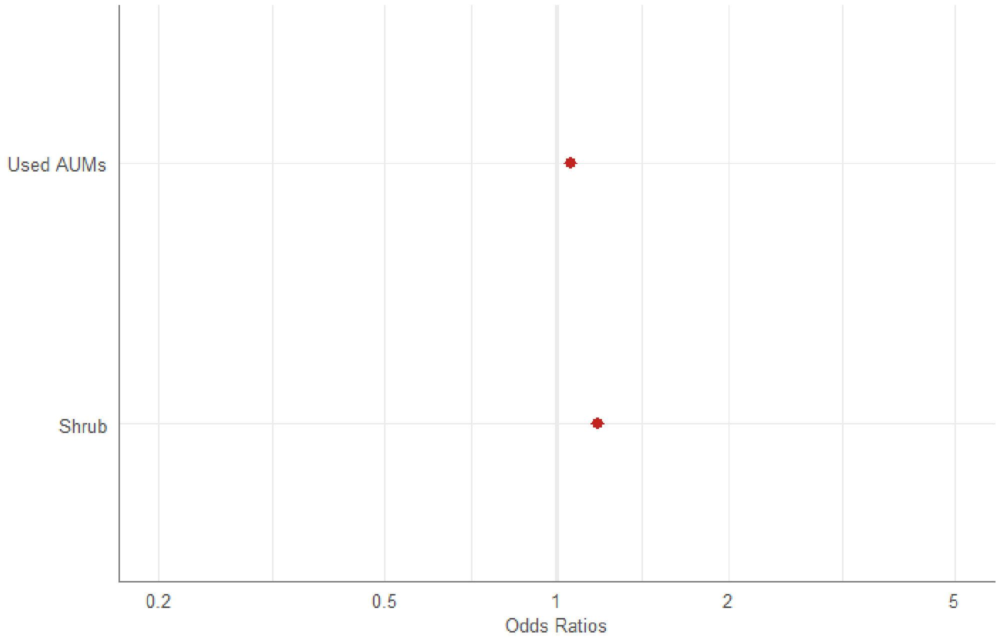


Figure 13. Odds ratios and 95% confidence intervals of the coefficients in the top model for habitat component selection. Confidence intervals are pictured on the graph, but they are very small, so are difficult to see. Coefficient effects in red are positive.

Table 5. Coefficient estimates from the top year-round, within-pasture habitat selection model.

Season	Covariate	Estimate	Standard error	Pr(>|z|)
All seasons together	Intercept	0.145	0.0138	0.000
	Used AUMs (scaled)	0.057	0.0139	0.000
	Shrub (scaled)	0.166	0.0141	0.000

Table 6. The 5 most-supported models from a set of 8 candidate models describing year-round, within-pasture habitat selection by sage-grouse hens.

Season	Model	Residual DF	Residual Deviance	ΔAIC	AIC Weight
All seasons together	1. Used AUMs + Shrub	21436	29425	0	1
	2. Used AUMs	21437	29564	137	0
	3. Days grazed	23460	32441	3014	0
	4. Shrub	44285	60765	31338	0
	5. Shrub + SGI	44284	60765	31340	0

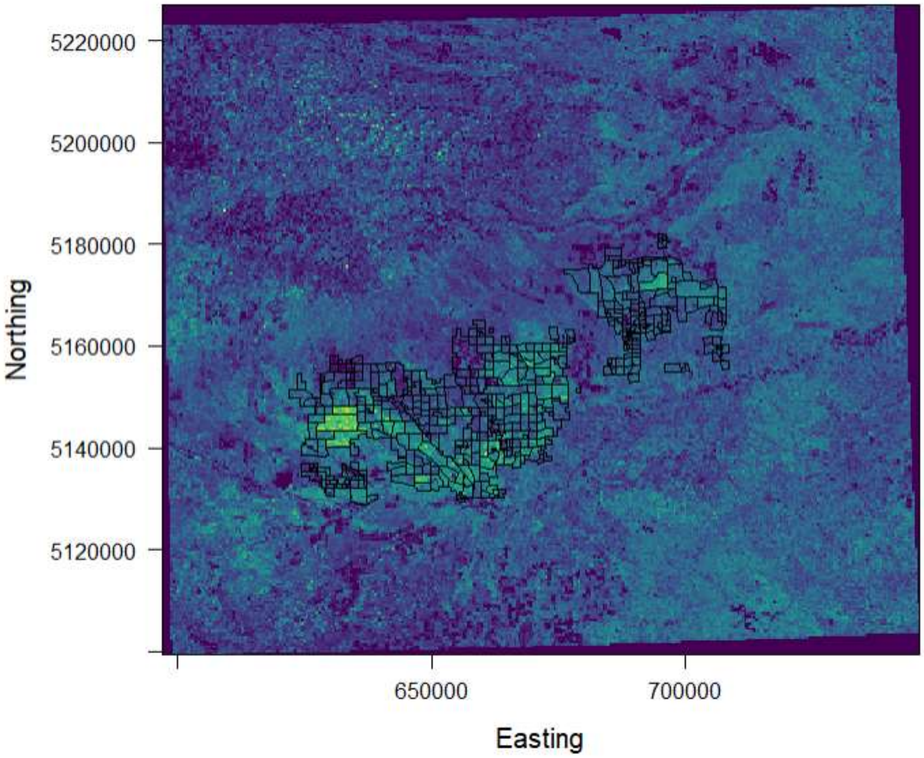


Figure 14. A predictive map of habitat within livestock pastures that was selected by sage-grouse hens. This map depicts the relative probability of use, ranging from low use (in purple) to high use (in yellow). Pasture boundaries are superimposed in black. The pasture boundaries were within the study area, but the pastures are displayed the center of

the map to show that shrub cover still affected habitat selection outside the pasture boundaries (i.e. where grazing data was unavailable).

DISCUSSION

A recent meta-analysis questions whether the role of microhabitat-scale vegetation is overstated in current sage-grouse habitat management, suggesting that vegetation at the level of pastures or allotments may be sufficient to evaluate habitat relationships and more realistic for land managers to implement (Smith et al. 2020). We investigated drivers of habitat selection at two spatial scales, because the effects of habitat selection on fitness costs and benefits change with scale (Mayor et al. 2009).

Seasonal second-order selection

Although broad-scale seasonal habitat selection may be more apparent in migratory individuals, seasonal partitioning of habitat selection by sage-grouse occurs even in the absence of migration (Wallestad 1975, Fedy et al. 2012, Dinkins et al. 2017), depending on the scale at which selection is observed. We found that sage-grouse hens selected different vegetation variables during different seasons at the home range scale. Importantly, the main driver of home range selection – the percent of shrub cover – persisted across all seasons. This is unsurprising, since sage-grouse are a sagebrush obligate species, relying on sagebrush for food and cover throughout their annual cycle (Connelly et al. 2000). Selection for shrub cover aligns well with current management strategies, which emphasize maintaining shrub cover for nesting habitat (Connelly et al. 2004); this result goes further by providing evidence that shrub drives habitat selection during other seasons as well.

During the nesting season, sage-grouse selected most strongly for shrub cover, followed by annual forbs and grasses, and slope. Lastly, they selected against bare ground (Figure 8). Many studies at the microhabitat scale have shown that sage-grouse select for tall and broad nest shrubs (Holloran et al. 2005, Dinkins et al. 2016). Similar to past work (Smith et al. 2018b), our work shows that sage-grouse are also selecting for shrub cover at the home range scale, not just at the nest site (Smith et al. 2020). Although other studies suggest that annual forb and grass cover may be detrimental to sage-grouse due to its ability to outcompete native perennial plants, it is possible that hens selected for it during this season because it provided early-season nesting cover before perennials grew. Selection for steeper slopes is an interesting effect that is not corroborated by other studies. One study found that sage-grouse selected nest sites at moderate elevations on slopes (Gibson et al. 2016), but in contrast, another found that female sage-grouse selected nest sites with a lower terrain roughness index (Doherty et al. 2010); it is possible that in our study area sage-grouse selected areas on higher slopes so they could see oncoming predators. Finally, selection against bare ground during the nesting season makes sense, as spending time in open areas, or areas with less vegetative undergrowth, would make hens and their nests more vulnerable to predation due to a lack of cover.

During the brood-rearing season, sage-grouse hens again selected most strongly for shrub cover, followed by selection for annual forbs and grasses and then followed by selection against higher elevations (Figure 9). The mechanism behind selection for shrub and annual forb and grass cover is likely similar to that of the nesting season, as hens are predominantly focused on managing predation risk to their broods during this season, thus requiring ample vegetative cover. However, hens must manage trade-offs between predation risk and resource access. It is likely that selection for lower-elevation areas is correlated with selection of wetter areas, since hens are known to select more mesic areas during the brood-rearing season (Donnelly et al. 2016) due to arthropod availability in wetter areas. In the Great Plains, where our study is located, most mesic areas are found in lower-elevation depressions (Donnelly et al. 2018) such as wet meadows. We did not test for the effect of any mesic variables, but this could be an interesting variable to incorporate in future studies.

During the summer-fall season, sage-grouse selected for more diverse habitats, as evidenced by more variables being present in the top model. They retained their selection for shrub cover and annual forbs and grasses, but they selected against higher elevations, perennial forb and grass cover, and bare ground cover. Selection for shrub cover was slightly less than in the nesting and winter seasons (Figure 10), which aligns with the fact that sage-grouse use alternative sources of food during this season, weakening their association with shrub during this time. Some studies found that sage-grouse hens spend more time moving (Braun et al. 2005), and in some cases migrating (Dinkins et al. 2017) in the fall. In cases like that, fall habitat may take the form of movement corridors (Connelly et al. 2000, Crist et al. 2017). However, this does not hold true in our population of sage-grouse, which stayed within the study area for the duration of the year (Table 1), although we note that occasionally individuals may have left the population temporarily and were not possible to monitor during that time. Other studies suggest that sage-grouse move toward uplands in the fall, but our work demonstrated the opposite effect (Table 3), with sage-grouse selecting for lower elevations. It is possible that we identified sage-grouse selection for lower elevations in the summer-fall season because this season is so long (July through November), encompassing a multitude of temperature extremes. For example, in the early part of the season, hens are likely moving with their broods in more mesic lowlands. Selection against bare ground cover during this season is likely due to the birds seeking thermal cover during hot and dry weather, as well as avoiding predation risk when traveling with their broods.

Finally, we found that sage-grouse winter home range selection was dominated by selection for shrub and against high elevations (Figure 11). Selection for high shrub canopy cover during this season aligns with most winter habitat selection work (Wallestad and Pyrah 1974), given that sage-grouse use sagebrush for both food and cover during the winter season. As such, selection might be expected to be stronger in the winter when it is required for nearly all life history needs, and this was reinforced by our results (Figure 8, Figure 9, Figure 10, Figure 11). However, it is worth noting that smaller number of variables represented in the top model could be due to the smaller sample size of hens in the winter season sample, since hens telemetry locations were recorded less frequently during this season.

Other studies suggest that sage-grouse select gentle topography (Doherty et al. 2008) and sagebrush-grassland at intermediate elevations in winter (Walker et al. 2016). They avoid conifers, riparian areas, rugged areas (Doherty et al. 2008, Carpenter et al. 2010, Fedy et al. 2014), and high densities of coal-bed natural gas development (Doherty et al. 2008). It is plausible that sage-grouse select for lower elevations during the winter to avoid ridges and get out of inclement weather. Although we did not explore it in this study, we suggest that future work investigates the relationship of snow depth and duration to habitat selection, as it may affect sage-grouse behavior in the winter due to its effects on access to sagebrush for food and cover.

Overall, patterns of seasonal home range selection by sage-grouse hens largely followed patterns documented in other areas of their range. This is interesting, because different parts of sage-grouse range have different types of sagebrush, different vegetation, and different moisture and temperature patterns, slopes, and elevations, which we expected could lead to some different results in Montana, which is in the northern part of their range.

It is worth noting that these seasonal results are based on data that was sampled unevenly across seasons, meaning that models for some seasons (e.g. nesting and brood-rearing) were based on larger sample sizes than others (e.g. winter). These discrepancies could lead to underrepresentation of habitat selection patterns during the seasons smaller samples if birds using specific areas were omitted from the sample due to low numbers. As a result, we suggest interpreting results from the winter season with caution.

Annual third-order selection

Theory predicts that sage-grouse select habitat at smaller scales than some species (for example, predators, Mayor et al. 2009). As such, we were interested in whether differences in livestock grazing systems, duration, and intensity affected finer-scale habitat selection within a system of livestock pastures. We found that sage-grouse continued to select habitat based on areas of higher shrub cover at this finer resolution, but interestingly, they also selected areas with higher used AUMs, or areas that experienced more forage removed by livestock over the course of the year. This was a surprising result, given that sage-grouse tend to prioritize selecting cover during certain seasons such as while nesting. This seasonal selection for cover includes annual forb and grass cover during the nesting, brood-rearing, and summer-fall season, as well as selection for perennials during the summer-fall season (Figure 13, Figure 14). However, it is possible that at the seasonal scale the selection for these habitat components is associated with food or another aspect of habitat that is not cover.

It is possible that the mechanism underlying sage-grouse selection for higher used AUMs reflects sage-grouse preference for areas with more new growth, as grazing can stimulate plant growth. Additionally, it is possible that cattle presence could have a positive effect on sage-grouse demographic rates (Foster et al. 2014) as it does for sharp-tailed grouse (Kirby and Grosz 1995, Milligan et al. 2020). This effect is thought to be due to either grazing or human presence serving as a predator deterrent. This could cause hens to select habitat in areas that either have more cattle present or that are grazed longer, leading to more forage to be removed. Similarly, more livestock in an area is associated with more cow pats, which could be linked to a higher density of insects that sage-grouse eat (Goosey et al. 2019). However, it is also possible that this result is not biologically significant, and that it reflects the challenge of obtaining accurate grazing data in the field, as well as the challenge of identifying which grazing variables matter and disentangling effects from other sources of variation at the relevant spatiotemporal scale. Although estimates of used AUMs were derived from landowner-provided records containing livestock type, number, and duration grazed in different pastures, this type of data is difficult to collect and maintain. Furthermore, more AUMs on a pasture probably means that the pasture had more forage available in the first place, meaning that the U-AUMs metric could be a proxy for more vegetated pastures.

Another factor that could affect these finer-scale habitat selection estimates is that sage-grouse are highly patterned behaviorally, returning to the same area year after year. If sage-grouse return to the same pasture every year regardless of grazing system, it is possible that it could appear that they were selecting for pasture-specific grazing variables, when in fact they may simply be linked tightly to a particular area. This links to the challenges that have been acknowledged for decades relating to the difficulty of quantifying habitat selection from the perspective of the animal that is making decisions (Wiens 1976) and then linking the outcome of those decisions to available management tools. We suggest that future work further investigates this purported relationship between used AUMs and fine-scale habitat selection before adjusting grazing management recommendations.

Management implications

The study of habitat selection by animals and the link between habitat and demographic rates or population trends is a critical component of wildlife population management (Manly et al. 2002, Mayor et al. 2009). Studying drivers of habitat selection behavior can identify mechanisms that can help to implement better management. The results of this chapter identify areas that sage-grouse select for their habitat throughout their annual cycle, which provides a framework for adding additional protections for seasonal hen habitat if needed. We recommend continuing to conserve sagebrush shrublands, as sage-grouse select them across seasons. Prior to implementing grazing regimes that are specific to sage-grouse conservation, we suggest that future studies experimentally test sage-grouse habitat selection responses to livestock grazing timing, duration and intensity by controlling grazing intensity, rather than working within an observational framework. At present, this study of sage-grouse habitat selection supports priorities as they are currently laid out in sage-grouse management plans.

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CHAPTER 2. Evaluating livestock grazing as a management tool to support greater sage-grouse nest success on sagebrush rangelands in central Montana

ABSTRACT

Livestock grazing is a dominant land use in sagebrush habitat, leading to ongoing questions about the relationships between grazing and coexisting wildlife populations. We evaluated a rotational grazing system implemented through the United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) Sage Grouse Initiative (SGI) in central Montana that had the goal of encouraging sustainable ranching practices while supporting sage-grouse habitat. We collected data on livestock grazing and sage-grouse nests to investigate the effects of SGI grazing on nest success as part of a decade-long collaboration (2011-2020). Our results indicated that neither rotational grazing systems nor other indices of livestock use had measurable effects on nest success. Differences in nest success across years were mostly due to unexplained annual variation. Ultimately, the grazing metrics we used suggest that SGI grazing did not affect nest success.

INTRODUCTION

The greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse") is an imperiled bird species that relies on large, intact, sagebrush ecosystems (Aldridge et al. 2008). Historically, sage-grouse habitat heterogeneity and phenology were maintained by disturbances such as bison grazing (Geremia et al. 2019) and wildfire (Wrobleski and Kauffman 2003). However, the near-extirpation of bison by the late 19th century (Knapp et al. 1999) combined with wildfire suppression (Starns et al. 2019) led to livestock grazing serving as a primary disturbance process maintaining this system (Allred et al. 2011; Freilich et al. 2003; Connelly et al. 2004). Livestock grazing, a dominant land use in sage-grouse range (Connelly et al. 2004), can meet the competing needs of different rangeland stakeholders (Krausman et al. 2009). It can maintain intact ecosystems (Krausman et al. 2009) and provide wildlife habitat (Fuhlendorf and Engle 2001, Connelly et al. 2004, Krausman et al. 2009, Chambers et al. 2017). Grazing timing, duration, intensity, and length of rest can be modified (Frost and Launchbaugh 2003, Bailey et al. 2019) to achieve conservation and management goals. However, research is needed to identify how to implement grazing as a disturbance process to promote wildlife demographic rates. In this study, we investigate whether a sagebrush system supporting multiple uses, including livestock grazing, can also support sage-grouse nest success (i.e. the probability that a nest produces at least one individual, Converse et al. 2013), an important demographic driver of sage-grouse population growth (Taylor et al. 2012).

Recent studies have investigated the effects of grazing on prairie grouse nesting habitats (Smith et al. 2018b, Milligan et al. 2020b, 2020a), which include both herbaceous (i.e. forb and grass) and shrub components (Gregg et al. 1994, Gibson et al. 2016, Cutting et al. 2019). In the sagebrush steppe, moderate cattle and heavy sheep grazing decrease herbaceous vegetation cover (Harniss and Wright 1982, Davies et al. 2010), although effects are microclimate- and site-specific (Milchunas and Lauenroth 1993). In contrast, livestock grazing increases sagebrush growth by reducing competition with herbaceous plants during seedling growth phases (Davies et al. 2020). These opposing effects on sage-grouse nesting habitat (i.e. decreasing some vegetation types while increasing others) call for a clearer understanding of how to implement grazing to support nest success.

In addition to annually-varying environmental conditions, nest success depends on habitat components such as vegetation cover that conceal the nest from predation and temperature extremes (Morris 1989, Czaja et al. 2020). In ground-nesting birds, grasses often conceal nests, and thus livestock grazing may be implemented to affect nest success, although a recent study suggests that specific grazing programs may not lead to different nest success in thick-billed longspurs (*Rhynchophanes mccownii*) (Reintsma et al. 2022). However, some aspects of livestock grazing systems that are separate from grazing pressure may affect sage-grouse nest success. For example, fences that delineate grazed pastures can provide perches for avian predators, thereby decreasing sage-grouse nest success in nearby nests (Cutting et al. 2019).

Studies measure grazing in many ways, particularly when direct information on grazing intensity, timing, and duration are unavailable. Vegetation height and cover can indicate the cumulative effects of the intensity, duration, and timing of grazing (Davies et al. 2020; Gillen and Sims 2006) on nest success. The proportion of grazed grass tufts in a pasture can serve as an index of grazing intensity (Smith et al. 2018a), and the height of senesced grass can indicate areas that were allowed to accumulate more residual vegetation, which can support sage-grouse nest success (Lockyer et al. 2015). Livestock presence may also be indexed by counting and aging cow patties in a pasture (Smith et al. 2018a). Although a short-term study found that several of these variables were not strong drivers of nest success (Smith et al. 2018a, 2018b), more work is needed to investigate if there are longer-term effects of these variables. Herein we explore how livestock grazing can be implemented to benefit sage-grouse nest success over approximately a decade.

In 2011, the NRCS implemented the Sage Grouse Initiative (SGI), a voluntary rest-rotation or deferred grazing system that NRCS staff tailored to ranches containing potential sage-grouse habitat. This program was intended to simultaneously maintain livestock production, rangeland health, and sage-grouse habitat (Natural Resources Conservation Service 2011). It involved maintaining moderate stocking rates, shifting grazing timing each year, and limiting grazing durations (Natural Resources Conservation Service 2012, Smith et al. 2018a). We evaluated the SGI program by comparing it to other grazing systems that ranged from continuous grazing throughout the year to rotational grazing systems not enrolled in SGI. Specifically, our primary objectives were to: 1) investigate the relationship between livestock grazing and nest success in central Montana, and 2) evaluate the effects of the NRCS SGI grazing program in central Montana on sage-grouse nest success. Our study provides information about how to implement grazing that enables livestock production to coexist with the habitat requirements of sage-grouse populations.

METHODS

Study area

We conducted this study in central Montana from 2011-2020 (elevation: 980m), in an area spanning >1,500km^2 in Musselshell, Golden Valley, and Petroleum counties. The area is a mosaic of private and public rangeland dominated by Wyoming big sagebrush (*Artemisia tridentata*), greasewood (*Sarcobatus vermiculatus*), silver sagebrush (*Artemisia cana*), saltbush (*Atriplex spp.*), and rabbitbrush (*Chrysothamnus spp.*). The average annual temperature in Roundup, the central town, is 6.8º C (44.2º F), and the average annual precipitation is 38.4 cm, most of which falls in May (6.1 cm) and June (7.6 cm) (National Centers for Environmental Information 2021). During the sage-grouse nesting period (April-June), the average monthly temperature is lowest in April (41.8º F) and highest in June (60.6º F) (National Centers for Environmental Information 2021). As one of Montana's sage-grouse "core areas", this area supports some of Montana's highest sage-grouse density (United States Fish and Wildlife Service 2015), yielding an aggregation of sage-grouse nests that is ideal for conducting a nesting study due to the relatively large sample size (Figure 15).

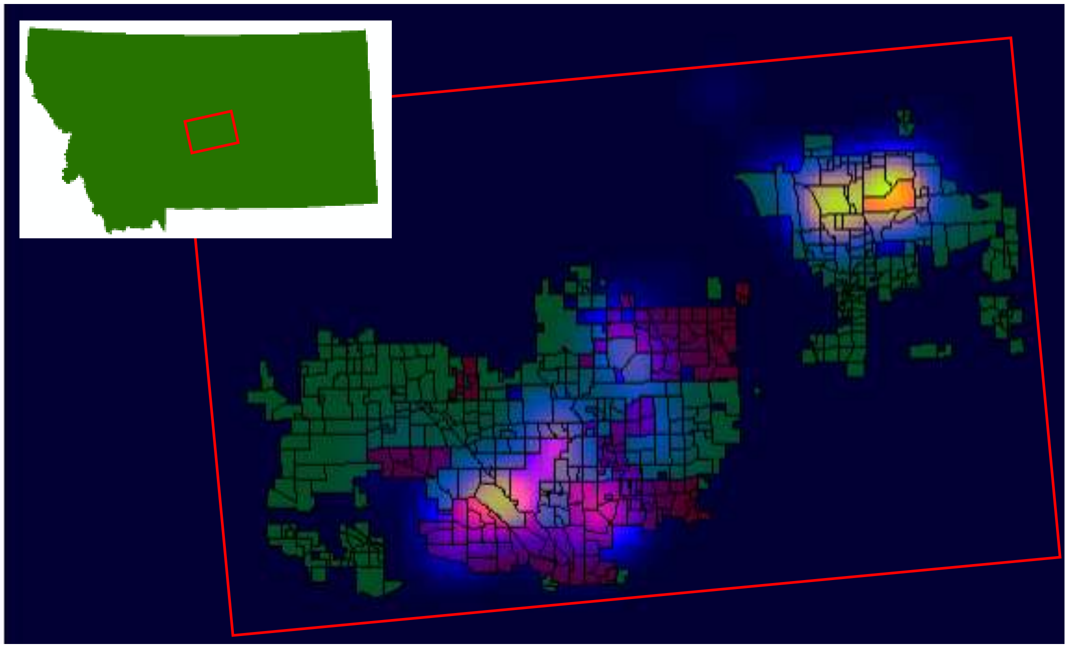

Figure 15. The study area in central Montana is represented by a red rectangle in the inset map in the top left; the same red rectangle is duplicated around the main map. In the main map, livestock pastures are pictured in green (not enrolled in SGI) and red (enrolled in SGI) for the year 2014 (where the year 2014 was selected to simplify the pasture visualization, because pasture enrollment in SGI changes depending on the year). A 99% kernel density estimate (KDE) of the area used by nesting sage-grouse is superimposed to

show the pastures used most frequently by nesting sage-grouse. Yellow portions of the KDE indicate the highest density of nesting sage-grouse, pink indicates moderate density, and blue indicates lower density.

Sage-grouse nesting data: Field methods

We collected nesting activity data on sage-grouse hens (adult females). We attached radio transmitters to hens located near known active leks at the onset of each breeding season (March-April) after capturing hens using nighttime spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992). We located sage-grouse nests and monitored them based on movements of radio-marked hens. We marked nests with natural markers 10-20m from the nest. We monitored the activity status of nests ≥2 times per week from ≥100m away until the hen departed. We classified nests as either failed (eggs were either destroyed or missing) or successful (≥1 hatched egg had a detached membrane, Wallestad and Pyrah 1974). Capturing and handling of sage-grouse hens was approved by the University of Montana's Institutional Animal Care and Use Committee (AUP 009-18VDWB-031418; AUP 011-14DNWB-031914).

Covariates

We investigated the effects of five grazing-related covariates on sage-grouse nest success: SGI enrollment (measured at the pasture resolution), nearest fence distance (measured from the point), number of cow patties (measured in the $30m^2$ around the nest site), proportion of plants grazed ($30m^2$), and senesced grass height ($30m^2$). Each of these grazing covariates was associated with a nest location. We also accounted for the known effect of annual variation on sage-grouse nest success (Sika 2006, Moynahan et al. 2007, Lockyer et al. 2015), where we defined each year as beginning on April 1 and ending on

March 31 of the next calendar year to align with the sage-grouse annual cycle. We identified these covariates based on previously-published studies about drivers of sage-grouse nest success in similar habitat types (Lockyer et al. 2015, Smith et al. 2018b, 2018a, Cutting et al. 2019). Pairwise correlations among the covariates were not significant (all $r^2 \leq 0.4$). Prior to inclusion in models, we centered and scaled variables by subtracting the mean value of the variable and dividing by the variable's standard deviation.

We defined SGI enrollment as a binary variable. If a nest was in the first category (SGI = 1, or "SGI pastures"), this meant that the pasture where the nest was located was enrolled in an SGI grazing program at some point. This categorization encompassed nests in pastures that were previously enrolled in the SGI grazing regime (any time prior to nest initiation) as well as nests initiated in pastures that were concurrently enrolled in a three-year SGI grazing regime at the time of nesting. The second category (SGI = 0, or "non-SGI pastures") indicated that a nest was in a pasture that had never been enrolled in an SGI grazing regime at the time of nesting.

We defined the distance to the nearest fence as the distance (in meters) between the nest point and the nearest point on the fenced pasture boundary. We calculated this distance using the "Near" tool in ArcMap 10.8, which minimized the distance between the nest point and a polygon shapefile of pasture boundaries. We constructed this pasture boundaries shapefile based on detailed conversations with landowners, which were held while reviewing and highlighting printed-out aerial photos and maps.

We defined cow patties as the count of cow patties around the nest site that were produced during the concurrent nesting season. We calculated this index of concurrent livestock presence during the nesting season by counting all cow patties in the $30m^2$ around the nest site and ageing them as either fresh (i.e. produced during the concurrent nesting season) or older based on signs of decomposition and oxidation (Smith et al. 2018a).

We estimated the proportion of plants around the nest site that were grazed by livestock by sampling herbaceous plants around the nest site. We approximated random sampling by walking around the nest site in an ad-hoc manner and recording whether the plant at every fifth step was grazed. We conducted this sampling in each of the four quadrants of the $30m^2$ plot around the nest, and we recorded the status (grazed or ungrazed) of 25 herbaceous plants in each quadrant, yielding 100 plants sampled per nest, to estimate the proportion of plants grazed. Last, we defined senesced grass height as the maximum vertical height of senesced grass on the plant that was nearest to the nest, excluding inflorescences (Smith et al. 2018a).

Hypotheses

First, we hypothesized that there would be no difference in nest success between pastures that were ever enrolled in SGI grazing systems and pastures that were not enrolled. We assumed that if nest success varied as a result of indirect (i.e. vegetation-mediated) effects of the grazing system, then differences in vegetation height and cover would be a precursor to differences in nest success. Smith et al. (2018a, 2018b) found very little difference in vegetation height and cover across these grazing systems in our study area, providing the foundation for our hypothesis. Alternatively, we hypothesized that nest success was different between pastures that were ever enrolled in SGI grazing systems and pastures that were not enrolled. We anticipated that our decadal dataset might capture longer-term effects of grazing systems that were not possible to measure during shorter-term studies such as those previously conducted in our study area (e.g., Smith et al. 2018a, 2018b).

Second, we hypothesized that nests initiated closer to fences would have lower success, based on previous work suggesting that fences increased rates of nest predation (Cutting et al. 2019), likely due to perching avian predators and terrestrial predator use of fences as travel corridors. This relationship is important for grazing management, because a negative relationship between fence distance and nest success could affect recommendations about where fencing is placed on the landscape in relation to nesting habitat. Our alternative hypothesis stated that nest success would be similar in areas that are different distances from fences, which would mean that fence proximity is not an important driver of nest success in our study area.

Third, we hypothesized that the number of cow patties around a nest would not be related to nest success. We included this variable because cow patty counts are easy to conduct. As such, if this metric was tied to nest success, it would be helpful for predicting effects of grazing intensity. However, previous work in our study area did not find an effect of cow patties on nest success (Smith et al. 2018a, 2018b), so we expected similar results. Our alternative hypothesis stated that nest success would be different among pastures with higher cow patty counts, which would reflect an effect of livestock presence and duration (as indexed by cow patties) on nest success (e.g. Milligan et al. 2020b).

Fourth, we hypothesized that the proportion of plants grazed would not have a strong relationship with nest success. Similar to cow patties, previous work in our study area (Smith et al. 2018a, 2018b) provided the foundation for our hypothesis of no effect. Our alternative hypothesis stated that nest success would be different in areas that experienced higher or lower grazing pressure (as estimated by the proportion of plants grazed) via the mechanism of reduced cover at the nest site.

Fifth, we hypothesized that taller senesced grass (i.e. dead, standing grass from the previous year's growth) at the nest site would be associated with higher nest success (Lockyer et al. 2015) due to its function as hiding cover. Our alternative hypothesis stated that senesced grass would be associated with reduced survival (e.g. Cutting et al. 2019).

Nest success analysis

We tested our hypotheses using a logistic exposure nest survival model in a Bayesian framework (e.g. Smith et al. 2018b; Specht et al. 2020; Schmidt et al. 2010) to estimate the effects of grazing-related covariates on sage-grouse nest success (i.e. the probability that a nest produces at least one individual, Converse et al. 2013). We also included a random effect to encompass year-to-year variation. This model assumes that survival is homogenous within and among nests, except for as described by the covariates, and that all nests fail independently.

We coded encounter histories for each nest following Schmidt et al. (2010), where nest fates were recorded as either successful or failed. The exposure period for failed nests was unknown and the endpoint of the exposure period was defined based on evidence at the nest, ranging from the day prior to the last visit to the midpoint of the last two visits. We right-truncated nest encounter histories for failed nests at the estimated hatch date to avoid negatively biasing the data (Stanley 2004, Specht et al. 2020).

We estimated the daily survival probability *S* (the probability that a nest survives until the next day) as a function of covariates as follows:

$$\text{logit}(S_{i,t}) = B_0 + \sum_{j=1}^{P} B_j x_{i,j,t} + \alpha_k$$

where $S_{i,t}$ is daily survival probability *S* at nest *i* and time *t*, $B_j x_{i,j,t}$ is the effect of covariate *j* at nest *i* in time *t*, and $\alpha_{k[i]}$ is a random effect for year *k* at nest *i*. We then exponentiated the estimated daily survival probability across the 37-day laying and incubation period (Schroeder et al. 1999, Smith et al. 2018a) to estimate sage-grouse nest success. We performed all analyses in program R v. 4.0.3 (R Core Team 2020) and JAGS v. 4.3.1 (Plummer 2003).

RESULTS

Sage-grouse nesting data

From 2011-2020, we monitored 779 nests from 470 radio-marked sage-grouse hens. We omitted 10 nests monitored in 2020 due to the low sample size in that year. Of the remaining nests (2011-2019), 736 (94%) had sufficient data for analysis (i.e. at least two monitoring visits to a known-location nest with an incubation status, Specht et al. 2020).

Among the 397 nests with reported causes of failure, 348 (88%) failed due to predation (Table 7). Predators were often unknown, but common nest predators in the area were coyotes (*Canis latrans),* bobcats (*Lynx rufus*), badgers (*Taxidea taxus*), common ravens (*Corvus corax*), red fox (*Vulpes vulpes*), small mammals, and snakes. Of the remaining failed nests, 31 (8.9%) had an unknown cause, and four (1.1%) failed due to investigator disturbance when hens did not return after being accidentally flushed off nests while technicians were initially locating the nest. Two nests (0.6%) were assumed to have failed due to livestock presence (i.e. nests were intact but abandoned with evidence of cattle nearby), and one (0.3%) failed due to a hail storm.

Table 7. The total number of nests in each SGI status for each year compared to the number of nests with documented nest predation events for each year and SGI status. "Percentage of failed nests predated" is the percentage of failed nests with the cause of failure reported as predation during a given year and SGI enrollment status.

SGI status	Year	Total # nests	# failed	# of failed nests predated	% of failed nests predated
Yes	2011	17	13	13	100
No	2011	81	54	39	72
Yes	2012	26	15	13	87
No	2012	66	28	25	89
Yes	2013	26	15	12	80
No	2013	57	35	32	91
Yes	2014	28	10	9	90
No	2014	46	17	16	94
Yes	2015	33	15	9	60
No	2015	43	22	21	95
Yes	2016	44	31	31	100
No	2016	40	22	21	95
Yes	2017	54	33	31	94
No	2017	49	24	20	83
Yes	2018	31	19	17	89
No	2018	37	21	18	86
Yes	2019	20	6	6	100
No	2019	38	11	9	82

Grazing covariates

First, we summarized grazing covariates at each nest during each year to show the average variation in grazing covariates across years (Table 8). Across all years, 37% of nests were located in SGI pastures, whereas 63% were in non-SGI pastures. During seven of the nine years of the study, most nests were located in non-SGI pastures. There were exceptions during 2016 and 2017, when more nests were located in SGI pastures. However, of note, far more pastures were not enrolled in SGI systems each year (Table 10). When averaged across years, the mean distance between a nest and the nearest fence was 441m (range: 354m – 504m), but the within-year standard deviation was high, indicating that there was substantial within-year variation in nest-to-fence distance. Both cow patties and the proportion of plants grazed showed little variation in the mean estimates across years, but within-year standard deviation was higher than the mean estimates in both cases, again suggesting within-year variation in both metrics. Senesced grass height demonstrated more among-year variation than the other variables, ranging from a mean of 9.1 cm in 2011 to a mean of 23.6 cm in 2019 (Table 8).

Table 8. The number of hens in the sample at the onset of the nesting period and the number of nests in the sample per year with covariate summaries. In cases where there are more nests than hens, some hens made multiple nesting attempts. Sample sizes of nests in categorical covariates and ranges of continuous covariates are provided. Unstandardized values are provided for continuous covariates but were standardized for the nest success analysis.

Year	# Hens	# Nests	SGI nests (#)	Fence Dist. (m)	Patties (#)	Proportion grazed	Senesced Grass (cm)
2011	101	98	Yes: 17 No: 81	Mean: 354 SD: 324	Mean: 1.35 SD: 5.18	Mean: 0.05 SD: 0.12	Mean: 9.10 SD: 5.81
2012	108	92	Yes: 26 No: 66	Mean: 501 SD: 410	Mean: 2.46 SD: 4.68	Mean: 0.03 SD: 0.07	Mean: 18.0 SD: 5.12
2013	90	83	Yes: 26 No: 57	Mean: 504 SD: 441	Mean: 2.94 SD: 5.61	Mean: 0.02 SD: 0.10	Mean: 9.47 SD: 3.25
2014	91	74	Yes: 28	Mean: 452	Mean: 3.18	Mean: 0.07	Mean: 13.6

			No: 46	SD: 438	SD: 7.22	SD: 0.13	SD: 3.84
2015	102	76	Yes: 33 No: 43	Mean: 485 SD: 460	Mean: 3.45 SD: 7.08	Mean: 0.07 SD: 0.13	Mean: 18.3 SD: 6.09
2016	95	84	Yes: 44 No: 40	Mean: 384 SD: 356	Mean: 1.87 SD: 5.59	Mean: 0.04 SD: 0.10	Mean: 17.2 SD: 5.74
2017	101	103	Yes: 54 No: 49	Mean: 407 SD: 377	Mean: 0.67 SD: 3.51	Mean: 0.01 SD: 0.04	Mean: 13.1 SD: 8.31
2018	73	68	Yes: 31 No: 37	Mean: 467 SD: 412	Mean: 1.01 SD: 4.24	Mean: 0.02 SD: 0.05	Mean: 9.95 SD: 7.45
2019	81	58	Yes: 20 No: 38	Mean: 412 SD: 436	Mean: 1.31 SD: 3.21	Mean: 0.02 SD: 0.03	Mean: 23.6 SD: 9.49

Second, we summarized grazing covariates at each nest across the two SGI categories and during each year to show the average variation in grazing covariates across both years and SGI status (Table 9). In all years but one, the average distance between nests and fences was smaller for nests located in SGI-enrolled pastures, indicating that these nests were closer to fences. However, the standard deviation was large, indicating high variation in nest-to-fence distance both within years and among SGI status designations. Mean cow patty counts were variable across both SGI categories and years, and these means did not display any pattern. The proportion of plants grazed was low and less variable across both SGI categories and years. Senesced grass height varied among years but displayed less variation across SGI categories within years (Table 9).

Table 9. Covariate ranges and sample sizes of nests across SGI grazing categories. For each SGI status (ever enrolled in an SGI grazing program vs. not enrolled) and year, we present the number of nests in the category, as well as the mean and standard deviation of the remaining four grazing covariates included in the nest success model.

SGI status	Year	Nests (#)	Fence dist. (m): Mean (SD)	Cow patties: # Mean (SD)	Prop. grazed: Mean (SD)	Senesced grass: Mean (SD)
Yes	2011	17	416 (367)	5.12 (11.2)	0.06 (0.06)	11.10 (4.90)
No	2011	81	341 (316)	0.56 (1.95)	0.04 (0.13)	8.69 (5.93)
Yes	2012	26	426 (294)	1.00 (2.40)	0.03 (0.06)	18.10 (5.29)
No	2012	66	531 (446)	3.03 (5.22)	0.03 (0.08)	18.0 (5.10)
Yes	2013	26	398 (275)	1.38 (3.93)	0.00 (0.02)	9.59 (3.38)

No	2013	57	552 (494)	3.65 (6.12)	0.03 (0.12)	9.42 (3.22)
Yes	2014	28	309 (242)	3.68 (8.44)	0.08 (0.16)	14.60 (3.56)
No	2014	46	539 (505)	2.87 (6.45)	0.06 (0.10)	13.10 (3.92)
Yes	2015	33	417 (286)	1.39 (5.23)	0.02 (0.03)	16.70 (6.90)
No	2015	43	538 (555)	5.02 (7.39)	0.11 (0.16)	19.40 (5.16)
Yes	2016	44	335 (300)	2.50 (6.69)	0.06 (0.13)	17.90 (6.13)
No	2016	40	438 (406)	1.18 (4.03)	0.02 (0.04)	16.40 (5.25)
Yes	2017	54	335 (281)	1.07 (4.77)	0.01 (0.04)	12.80 (10.2)
No	2017	49	485 (451)	0.22 (0.83)	0.01 (0.04)	13.40 (5.72)
Yes	2018	31	337 (300)	1.42 (5.52)	0.02 (0.04)	8.04 (6.59)
No	2018	37	576 (463)	0.68 (2.79)	0.03 (0.06)	11.50 (7.84)
Yes	2019	20	315 (269)	1.75 (4.06)	0.02 (0.02)	26.60 (7.78)
No	2019	38	462 (498)	1.08 (2.69)	0.02 (0.03)	22.00 (10.00)

In addition to the covariates included in our nest success model (Table 8, Table 9), we also summarized other grazing-related variables across SGI and non-SGI categories to describe similarities and differences among the SGI and non-SGI grazing systems (Table 10) to assist with interpretation. These covariates were not included in the nest success model because they were only available for a small fraction of pastures. Overall, fewer pastures were enrolled in SGI grazing systems, and thus there was a smaller area enrolled in SGI (Table 10). Mean estimates of used animal unit months (AUMs, a measure of grazing pressure) varied by year and SGI status, but no patterns were evident. The mean duration of grazing was substantially lower in SGI pastures, and the mean first turn-in date was nearly two months later in SGI-enrolled pastures than in non-SGI pastures (Table 10).

Table 10. Grazing metrics across SGI status. The number of pastures and the pasture area refer to the number of distinct pastures and the pasture area in the specified SGI grazing category for a given year. The mean used AUMs refers to the mean animal unit months (a measure of grazing pressure) used by livestock in the pastures in the specified SGI grazing category for a given year. The mean duration refers to the total number of days a pasture was grazed during a given year, which may be a sum across multiple grazed

periods. The mean first turn-in date is the mean of the first dates when livestock were put out to pasture in a given year (which is measured April 1 – March 31).

SGI status	**Year**	**Number of pastures**	**Pasture area (km^2)**	**Mean used AUMs**	**Mean duration (days)**	**Mean first turn-in date**
Yes	2011	52	138.15	139.74 (sd=106)	27.73 (sd=16d, n=30)	July 24 (sd=90d, n=30)
No	2011	458	1378.16	138.04 (sd=193)	59.21 (sd=67d, n=80)	June 15 (sd=102d, n=81)
Yes	2012	128	361.39	122.07 (sd=97)	27.26 (sd=17d, n=86)	August 2 (sd=77d, n=87)
No	2012	388	1159.77	136.52 (sd=221)	83.48 (sd=76d, n=50)	May 24 (sd=116d, n=51)
Yes	2013	152	394.68	123.85 (sd=109)	32.72 (sd=23d, n=76)	July 3 (sd=84d, n=80)
No	2013	369	1121.70	185.78 (sd=515)	68.86 (sd=68d, n=69)	May 12 (sd=104d, n=69)
Yes	2014	181	514.18	131.67 (sd=131)	32.54 (sd=21d, n=100)	July 2 (sd=101d, n=101)
No	2014	342	1002.19	122.85 (sd=240)	76.78 (sd=73d, n=58)	May 2 (sd=95d, n=58)
Yes	2015	189	536.27	184.34 (sd=160)	35.18 (sd=27d, n=78)	July 2 (sd=101d, n=80)
No	2015	334	978.79	170.48 (sd=252)	77.40 (sd=66d, n=93)	May 2 (sd=93d, n=93)
Yes	2016	233	582.72	162.78 (sd=175)	37.50 (sd=26d, n=109)	July 11 (sd=70d, n=110)
No	2016	292	934.66	187.65 (sd=244)	80.27 (sd=67d, n=116)	May 27 (sd=99d, n=121)
Yes	2017	231	575.03	159.05 (sd=151)	37.56 (sd=30d, n=104)	July 8 (sd=78d, n=108)
No	2017	298	941.33	203.46 (sd=296)	80.39 (sd=75d, n=104)	May 21 (sd=90d, n=111)
Yes	2018	231	575.02	153.44 (sd=181)	49.84 (sd=42d, n=100)	July 6 (sd=85d, n=100)
No	2018	298	941.36	212.25 (sd=327)	77.26 (sd=72d, n=136)	May 19 (sd=82d, n=138)
Yes	2019	229	574.97	No data	40.97 (sd=27d, n=66)	July 10 (sd=72d, n=66)
No	2019	300	941.66	216.07	77.33	December 31

	(sd=287)	(sd=65d, n=123)	(sd=111d, n=123)

Nest success

Overall, annual variation demonstrated the strongest effect on sage-grouse nest success (Figure 16, Table 11). Although the 95% credible intervals for the year-specific intercepts overlapped zero for eight of the nine years, the random effects for 2014 and 2019 were strongly positive, while the random effect for 2016 was strongly negative (Figure 16, Table 11).

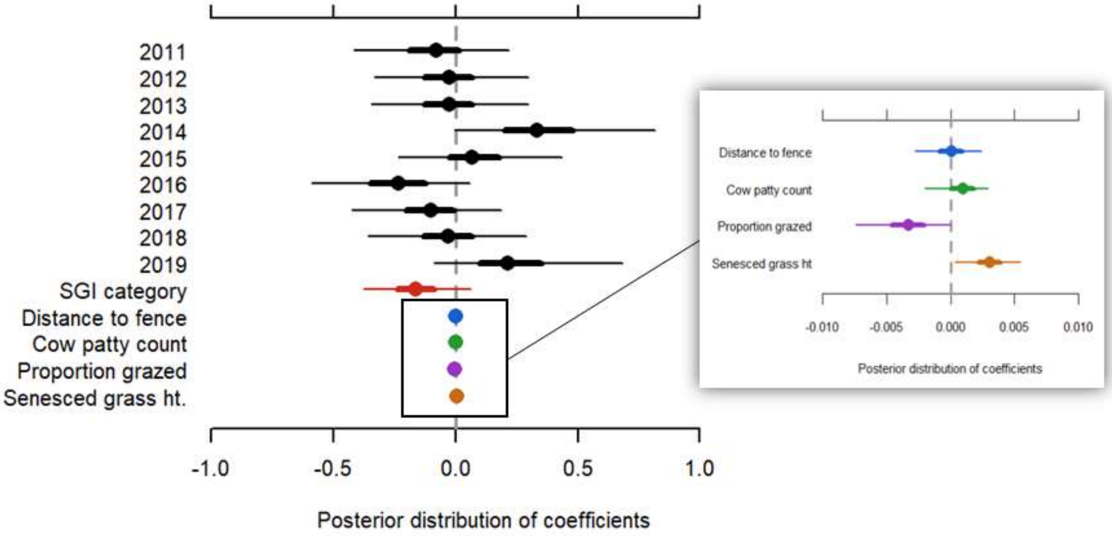

Figure 16. Caterpillar plots showing the 95% credible intervals of the posterior distributions for the random effects for each year (in black) and the fixed effects of the five grazing covariates of interest (in color). The inset caterpillar plot shows the 95% credible intervals of the posterior distributions for the four covariates whose effects were small compared to the effect of year.

Table 11. The mean and 95% credible intervals of the posterior distributions for the random effects for each year and the fixed effects of the five grazing covariates of interest. Rhat values indicated model convergence for all variables.

Variable	**Lower 95% CRI**	**Median (50% CRI)**	**Upper 95% CRI**	**Rhat**
Intercept	3.344	3.597	3.835	1.001
Intercept[2011]	-0.415	-0.081	0.220	1.000
Intercept[2012]	-0.332	-0.027	0.296	1.001
Intercept[2013]	-0.344	-0.027	0.298	1.000
Intercept[2014]	-0.002	0.334	0.816	1.000
Intercept[2015]	-0.235	0.068	0.435	1.000
Intercept[2016]	-0.588	-0.237	0.060	1.000
Intercept[2017]	-0.424	-0.102	0.186	1.000
Intercept[2018]	-0.358	-0.030	0.287	1.001
Intercept[2019]	-0.088	0.213	0.685	1.000
SGI category	-0.378	-0.163	0.061	1.000
Distance to fence	-0.003	0.000	0.002	1.000
Cow patty count	-0.002	0.001	0.003	1.000
Proportion grazed	-0.007	-0.003	0.000	1.001
Senesced grass height	-0.000	0.003	0.005	1.000

We found weak to no evidence for an effect of SGI grazing systems on sage-grouse nest success in central Montana. Although the median nest success of nests in non-SGI pastures was slightly higher than the median nest success in SGI-enrolled pastures, the 95% credible interval of the coefficient for SGI grazing overlapped zero (Figure 16, Table 11) and the predicted posterior distributions had considerable overlap (Figure 17).

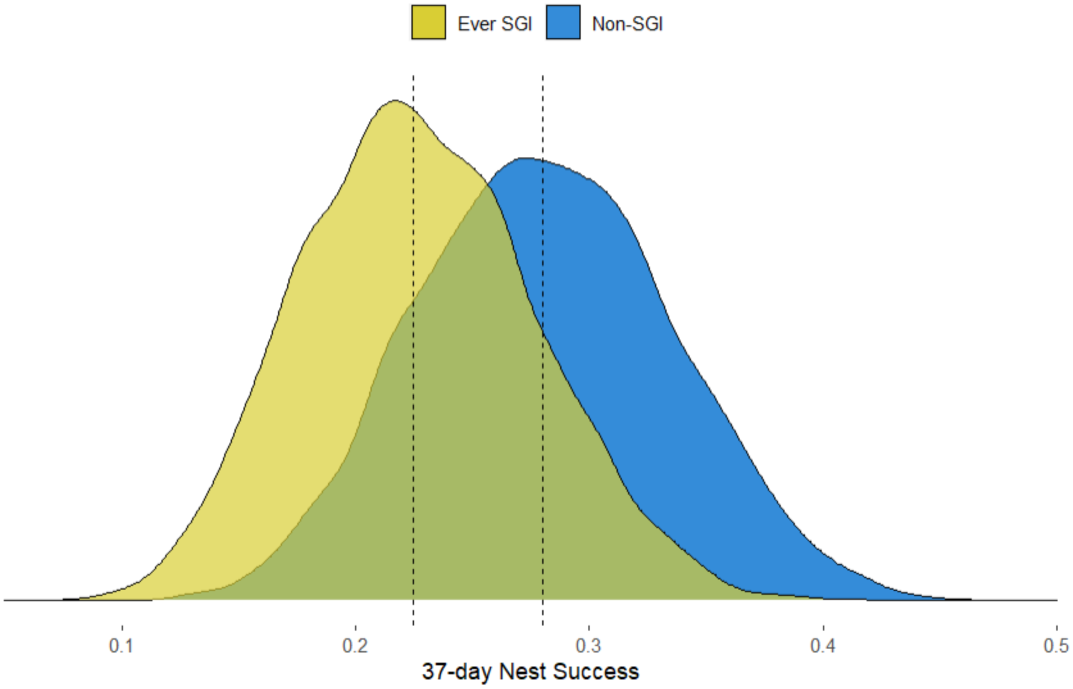

Figure 17. Predicted posterior distributions of 37-day nest success in SGI- and non-SGI pastures, where SGI pastures are either currently or were previously enrolled. The dotted lines correspond to the median posterior estimate of the coefficient for nest success in the category: 0.28 for pre- or non-SGI nests, and 0.22 for during- or post-SGI nests.

We did not find evidence for an effect of the nearest distance to fences or the number of cow patties on nest success. The posterior distributions of these two covariates overlapped zero (Figure 16, Table 11). However, there was weak evidence for a relationship between senesced grass height and nest success, as well as weak evidence for a relationship between the proportion of vegetation grazed and nest success, as evidenced by the 95% credible intervals of the coefficients not overlapping zero (Figure 16). However, in both cases, the median coefficient estimate is very small and the 95% credible intervals touch zero, emphasizing that these effects are not strong.

DISCUSSION

Overall, sage-grouse nest success was most strongly influenced by inter-annual variation. This result aligns with many other demographic studies of grouse species. For example, nest success is highly variable among years in ruffed grouse (Pollentier et al. 2021). For sage-grouse, annual variation in nest success can likely be attributed to precipitation and temperature differences across years. Additionally, other differences among years, such as vegetation growth and human use patterns, might contribute to annual variation. Nest success was also influenced by intra-annual variation, likely driven by individual characteristics of nesting hens such as age and body condition.

The first objective of this project was to investigate the relationship between livestock grazing and sage-grouse nest success in central Montana. We expected that livestock grazing systems would support sage-grouse nesting habitat by maintaining vegetation heterogeneity, similar to the historical effects of bison grazing and fire (Allred et al. 2011; Freilich et al. 2003; Connelly et al. 2004). For example, grazing maintains habitat heterogeneity for lesser prairie chickens (Kraft et al. 2021, Londe et al. 2019), and it improves forage nutrition, quality, and accessibility for bobwhite quail (*Colinus virginianus*), mule deer (*Odocoileus hemionus*), and elk (*Cervus Canadensis*) (Alpe et al. 1999). However, it is worth noting that a rest-rotation grazing system did not influence habitat heterogeneity for sharp-tailed grouse (*Tympanuchus phasianellus*) (Milligan et al. 2020b). In grasslands, grazing can be used to manage habitat for grassland-obligate songbirds under certain precipitation and soil conditions (Lipsey and Naugle 2017). In mixed sagebrush-grassland habitat, grazing regimes influence grassland-associated bird abundance for thick-billed longspurs (*Rhynchophanes mccownii*) (Golding and Dreitz

2017). As such, it was reasonable to believe that using SGI grazing as a management tool could support sage-grouse nest success as well, by maintaining varying heights of grasses and forbs via adjusting the timing and duration. However, in comparison with the dramatic annual variation in our study area, the smaller variation among SGI and non-SGI grazing systems made it difficult to separate out an effect of grazing on nest success from natural variation occurring on the landscape (Table 9). In this region, grazing occurs at similar AUMs used across years and grazing regimes (i.e. SGI grazing status) (Table 10). As such, annual variables including precipitation and temperature likely cause more variation than differences in grazing pressure.

The second objective of this project was to evaluate the effectiveness of the Sage-Grouse Initiative (SGI) grazing program as a tool that benefits sage-grouse nest success. The SGI grazing plans include implementing grazing utilization rates at ≤50% of key forage species growth, annually-shifted grazing timing (≥20 days), and limited grazing durations within a given pasture (≤45 days at a time) (Natural Resources Conservation Service 2012, Smith et al. 2018a). Our findings suggest that the use of the SGI grazing program has little to no effect on sage-grouse nest success, or if anything, the effect was negative. This is likely due in part to the temporal variation in grazing pressure on a given pasture, even within a 3-year SGI grazing categorization, because some of that time is dedicated to pasture rest or deferment. This meant that the timing and duration of grazing pressure was not constant, making it difficult to determine a program-wide effect. Ranch-specific approaches under SGI may include changes to pasture rest, the number of animal units, fencing, and water sources (NRCS 2017), all of which can affect patterns of grazing within pastures, including potentially homogenizing vegetation by reducing areas of lower and/or higher grazing pressure. In addition, variation in nest success across grazing systems is likely overshadowed by temporal variation in weather, plant growth, and other factors. This finding supports the conclusions of previous studies in our study area conducted from 2011-2016 (Smith et al. 2018a).

Our study design was based on previous work in our study area, and our data relied on data that were initially analyzed during that work (Smith et al. 2018b, 2018a), with some differences. We included many of the same nests, but we added 3 years of data. Although the study areas were similar, the study area expanded slightly throughout the study depending on where sage-grouse nested. Our modeling framework was similar, but we explored slightly different covariates to investigate the effects of grazing from a different perspective. This included categorizing SGI grazing slightly differently to explore longer-term effects of SGI grazing systems that might occur as a result of the cumulative effect of the different aspects of a 3-year grazing regime over time.

Each 3-year SGI grazing system was designed to shift grazing each year, making every SGI grazing plan slightly different depending on the ranch and the local conditions. For example, for a single pasture, a SGI plan might defer grazing until after seed-set in one year, graze in early spring in the next year (a seasonal change), and then rest the pasture completely during the third year. On another pasture, the order could be completely different. The intention of changing the timing of grazing each year was to allow vegetation to recover between rotations, benefiting nesting habitat. However, the variation on the ground of how these SGI grazing systems actually operated at a given time makes it very difficult to obtain a workable sample size of any particular condition during a particular year.

We were interested in the distance between nests and fences because rest-rotation grazing may put more fencing on the landscape, creating perches for avian predators that depredate sage-grouse nests (Dinkins et al. 2016). Additionally, sage-grouse collisions with fences are more frequent near high activity sage-grouse areas, such as leks (Stevens 2011). Other studies have documented a negative relationship between fence distance and nest success in sage-grouse (Cutting et al. 2019). However, our work did not demonstrate an effect of distance to fences on sage-grouse nest success. It is possible that this lack of a response is due to the fact that nests are generally similar distances from fences across years (Table 8, Table 9), likely resulting from similar pasture sizes across years.

We also investigated the effects of senesced grass height at the nest site, expecting that quality sage-grouse nesting habitat would be best supported by livestock grazing management that leaves some senesced grass cover in the fall for use as cover during nesting the following spring, and that avoids heavy grazing during the growing season to maintain forbs and perennial grasses for nesting habitat. Additionally, some studies have hypothesized that sage-grouse select nest-sites before grass starts growing in the spring, meaning that senesced grass is particularly important for early-season nest cover. Although we saw slight evidence for an effect, this is likely not biologically relevant, as the coefficient estimate is very small and translates to millimeters of difference in senesced grass height, which is not feasible to be manipulated by managers to support nesting sage-grouse (Figure 18). Similar to our results, senesced grass at the nest site was positively related to nest success in other studies (Smith et al. 2018a), although it was not biologically significant and it was unclear how to manage this variable using livestock grazing.

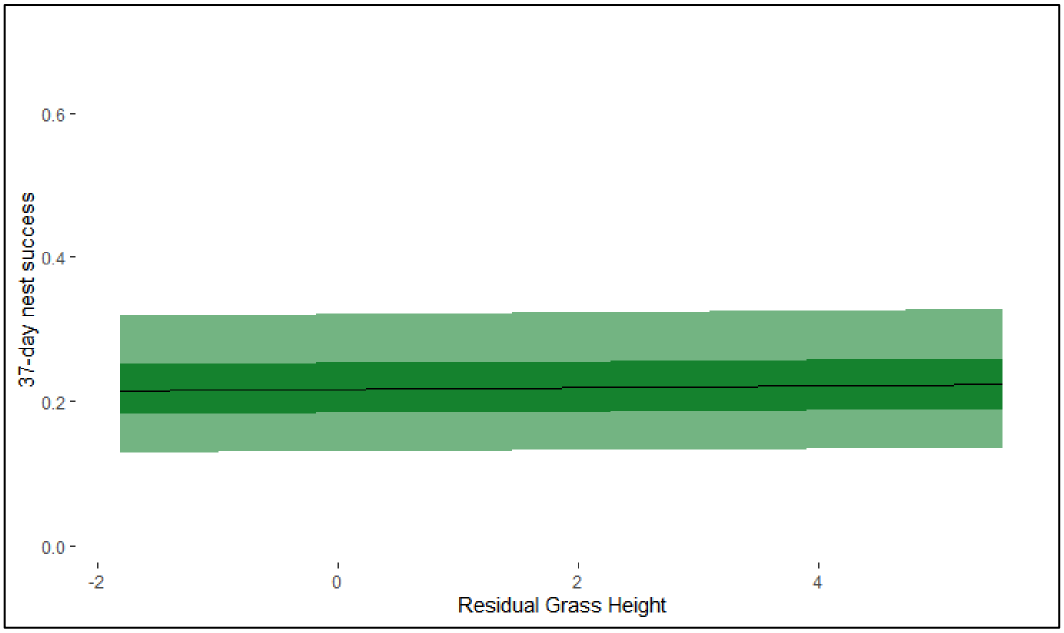

Figure 18. The effect of residual (i.e. senesced) grass height (mm) on nest success. The 50% credible interval ribbon is shown in dark green, and the 95% credible interval ribbon is shown in light green. The nearly-flat slope indicates that there is only a very small effect of grass height on nest success.

Since livestock grazing is a dominant land use, managing grazing to support an at-risk species would be a win-win situation for both ranchers and wildlife managers. We aimed to use information about the effects of grazing on sage-grouse to make recommendations on best grazing management practices to support sage-grouse nest success. However, to make strong inference about different grazing regimes would likely require experimenting (rather than an observational study) with the timing of grazing and different stocking rates to obtain large enough sample sizes to investigate the multitude of grazing variables that interact to affect a rangeland. During our observational study, we found no evidence that rotational livestock grazing supported sage-grouse nest success either directly or indirectly through vegetation. Overall, despite this lack of evidence for an effect of grazing, our estimate of sage-grouse nesting success in central Montana was very similar to the estimate from previous work in our study area (Smith et al. 2018b). Our estimate also aligned with range-wide estimates for other sage-grouse populations (Smith et al. 2020), further suggesting that there is no effect of grazing on sage-grouse nesting success in central Montana.

In addition to grazing, nest success in many regions varies in relation to environmental conditions and intrinsic conditions specific to the nesting female, which can lead to dramatic inter- and intra-annual variation. For example, nest success may be lower in years with heavy precipitation coinciding with low temperatures. Similarly, if a hailstorm occurs during the nesting season one year, it has the potential to decrease nest success during that year. Within a single year, nest success may vary in relation to female age or body condition, which can create a range of within-year variation in nest success as well. This inter- and intra-annual variation can be difficult to explain since it can be driven by a multitude of different variables that are region-specific.

As mentioned earlier, inter-annual variation in nest success is likely primarily driven by variation in temperature, precipitation, and other environmental factors. In sharp-tailed grouse, production of young was affected by average temperatures in May and June, as well as cumulative precipitation over a longer time period (Flanders-Wann et al. 2010). In Columbian sharp-tailed grouse, one study also documented a weak positive effect of post-hatch precipitation on some reproductive vital rates (Proett et al. 2022). Although we did not specifically investigate the effects of these variables in this study, it is helpful to consider how they may affect nest success in the future or in different settings. For example, if this study was conducted over a broader area, there would be a greater range of variation in environmental and weather variables, likely yielding more variation in nest success in response. The timing of precipitation can be important depending on the region, as rainy nesting season in the desert may have a positive effect on reproductive vital rates, whereas a rainy nesting season in colder climates can negatively affect survival. These differences are especially important in the context of climate change, in which extreme temperatures and weather events are becoming more extreme. As such, it is critical to investigate the effects of weather on nest success in future work, particularly as it relates to the conservation and management of habitat that may serve as thermal refugia such as sagebrush.

Ultimately, we found that annual variation had a much stronger influence on sage-grouse nest success than any measurable effects of grazing-related variables in our study area. Of the grazing-related variables we hypothesized would affect nest success, we found that the proportion of plants grazed and senesced grass height at the nest had the most evidence for an effect, but these effects were weak. In light of our results, we recommend preventing further reduction and fragmentation (Smith et al. 2018b) in sage-grouse habitat and employing a variety of grazing management strategies focused on sustainable range management (Golding and Dreitz 2017). This may provide adequate habitat for nesting sage-grouse (Smith et al. 2018b) without the need for choosing a specific grazing system.

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CHAPTER 3. Estimating greater sage-grouse population growth rate in central Montana: A comparison of methods with implications for future monitoring

ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus)* have a history of population declines across their range due to habitat loss, degradation, and fragmentation. However these declines are difficult to measure due to cryptic behavior, monitoring challenges, and the cyclic nature of grouse population abundance. As such, it is useful to compare population growth rates using disparate datasets and multiple methods to determine if trend estimates align. We used twenty years of male-based lek count data to calculate the average annual population growth rate in central Montana. We then compared this trend to annual growth rates derived from a female-based matrix population model based on demographic data collected from the same study area. We found that the population growth rate from the lek counts was more variable than that from the matrix model, but that the lek counts suggested an increasing trend while the matrix model suggested a decreasing trend. We caution the use of lek counts to make management decisions due to the possibility that they could overestimate the population growth rate.

INTRODUCTION

Over the last century, the range of the greater sage-grouse (*Centrocercus urophasianus*, hereafter “sage-grouse”) has declined due to habitat loss, habitat degradation, and land use changes (Connelly and Braun 1997, Braun 1998, Schroeder et al. 2004). The sage-grouse was petitioned for listing under the Endangered Species Act several times (United States Fish and Wildlife Service 2010, 2015), thereby focusing research attention on drivers of demographic rates (Taylor et al. 2012), habitat selection (Fedy et al. 2012), and population dynamics (McCaffery and Lukacs 2016). However, due to the cyclic nature of grouse population abundance (Fedy and Aldridge 2011), variation in abundance estimates easily masks population trajectories (Coates et al. 2021), despite long-term data collection throughout the range. Abundance estimates are further complicated by crypsis, clustered distributions, and limited monitoring budgets, despite advances in surveying and modeling techniques (Buckland et al. 2001, Specht et al. 2017, Henderson 2020). As such, comparing estimates of population growth rate (lambda, or λ) derived from different datasets enables better understanding of sources of uncertainty and variation (Dahlgren et al. 2016). Here, we compare population growth rates derived from the standard abundance survey method, male-based lek counts, to an estimate of population growth rate derived from a female-based matrix population model (following Dahlgren et al. 2016) to investigate whether these growth rates follow similar trends.

Lek counts provide an easy and economical way to collect long-term datasets, as it is convenient to survey areas where birds return annually during the mating season. Sage-grouse leks are somewhat spatially distinct, sparsely-vegetated areas with high inter-annual site fidelity (Connelly et al. 2000), where breeding sage-grouse congregate early each spring to engage in highly detectable mating displays (Knick and Connelly 2011). Lek counts involve counting males (or occasionally both males and females) on specified leks at least once per year, often within 30 minutes of sunrise (Walsh et al. 2004, Newell 2016), and up to 90 minutes after sunrise (Monroe et al. 2016), when male attendance is highest. Lek counts are typically conducted from a vehicle or blind using binoculars or a spotting scope, within 50m of the lek when possible without disturbance (Walsh et al. 2004). Managers adopted lek counts decades ago as the primary survey method across sage-grouse range (Emmons and Braun 1984, Knick and Connelly 2011) to use in setting harvest limits (Walsh et al. 2004). However, as early as 1980, researchers began raising questions about the accuracy of using lek counts as an index of sage-grouse population abundance (Beck and Braun 1980, in Knick and Connelly 2011).

Concerns about the accuracy of lek counts are rooted in sampling methods and assumption violations that affect population-level inference, leading managers to apply corrections and explore other abundance estimation methods. Sampling-related concerns include: 1) the relationship of monitored leks to all leks is unknown due to convenience sampling (Walsh et al. 2004), including considerations like leks being more accessible for counting on public than private land; 2) leks are often only counted once per season, whereas multiple counts per season would offer more information about detection probability (McCaffery et al. 2016); 3) male lek attendance varies through time and peaks later for sub-adults than males (Wann et al. 2019); and 4) the proportion of males that attend leks is low (Walsh et al. 2004) and often unknown (Blomberg et al. 2013), making the link to overall abundance more uncertain. Concerns about assumption violations include: 1) imperfect detection probability of birds on leks (Monroe et al. 2016); 2) movement of birds among leks resulting in double-counting (Fremgen et al. 2017); 3) volatility of leks, which may change, move or disappear each year (Jahner et al. 2016, Spence et al. 2017); 4) challenges delineating leks when they are close together (Gibson 1996, Cayuela et al. 2021); and 5) unknown sex ratio on leks when only males are counted (McCaffery et al. 2016, Hagen et al. 2018). These concerns have gained increasing attention over the last decade, leading to a number of lek count methodological improvements (Coates et al. 2019, Wann et al. 2019).

These corrections to the lek count method have increased confidence in the approach, but the data required to complete them can be difficult to obtain, leading to interest in comparing lek counts to abundance estimates derived from other data sources. For example, sightability models adjust counts for different detection probabilities (Coates et al. 2019), but this type of model requires independent data streams. N-mixture models are also promising, but they are most accurate when at least 75% of leks are surveyed at least once per year, and approximately 60% of those leks are surveyed multiple times per year (McCaffery et al. 2016). Given that these conditions are not upheld across the sage-grouse range, we employ an alternative, comparative approach rather than a correction. We estimate long-term trends from male-based lek counts and investigate whether they are corroborated by population growth rate estimates derived from ten years of demographic data used to construct a matrix population model (Dahlgren et al. 2016).

Matrix population models (hereafter, “population models”) are useful tools that describe the life cycle of an organism by using demographic rates, thereby using observations from individuals to estimate population dynamics (Caswell 2001). Population models are commonly used to estimate population growth rate (λ) and extinction probability (e.g. via population viability analysis, Morris et al. 1999), identify demographic rates that have the strongest effect on population growth (e.g. via sensitivity analysis, Taylor et al. 2012), and prioritize conservation actions for species of concern (Hines and Nichols 2002, Dahlgren et al. 2016). Empirical models of specific populations often draw on long-term datasets collected while monitoring individuals throughout their lifetime. This may include metrics that are hypothesized to influence population growth rate, such as differences in demographic rates among sexes, ages, or stages. However, when these data are unavailable, estimates from other populations may be substituted, particularly in the case of range-wide analyses (e.g. Taylor et al. 2012). Population models are subject to different types of errors than count-based estimators, such as uncertainty in estimates of key demographic rates that are difficult to measure or that may be subject to limited data availability. However, the differences in data types and sources of variation between estimates from lek counts and population models provide the opportunity to validate the use of lek counts as an index for sage-grouse population growth rate, since it may be helpful to investigate whether parallel trends are derived from independent datasets.

This study also presented an opportunity to produce an empirical population model for a specific population of sage-grouse, which has been identified as a need by several studies (Taylor et al. 2012, Dahlgren et al. 2016). Population-specific models are more location-specific than more general, range-wide population models that have the potential to confound spatial and temporal variation (Morris et al. 1999, Taylor et al. 2012, Koons et al. 2017), which is important when identifying which vital rates drive population dynamics. For example, in sage-grouse, a range-wide population model identified three demographic rates – nest success, chick survival, and hen survival – as primarily important to population stability across the range, rather than other demographic rates such as nest initiation rate, clutch size, and juvenile survival (Taylor et al. 2012). However, this relationship may not apply to individual populations. An empirical study in Utah that compared a matrix model to lek counts found that while population growth rate trends matched, nest survival was not as important as post-fledging (i.e. juvenile, yearling, and adult) survival (Dahlgren et al. 2016). We address this knowledge gap for central Montana by developing an empirical population model using demographic rates estimated in our study area and comparing it to lek counts following Dahlgren et al. (2016).

Overall, our objectives are twofold. First, we draw on ten years of intensive demographic data to compare population growth rate estimates to lek counts, thereby assessing trend similarity and considering whether lek counts can be used as an index for population abundance. Second, we aim to provide recommendations for future monitoring of sage-grouse populations in central Montana. These results will also apply to other areas in sage-grouse range with similar vegetative habitats and patterns of land use, leading to a better understanding of sage-grouse population dynamics in similar areas of the range.

METHODS

Study area

We conducted this study in central Montana from 2011-2020, outside the town of Roundup (elevation: 980m), in an area spanning >1,500km^2 in Musselshell, Golden Valley, and Petroleum counties. The study area is a mosaic of private and public rangeland dominated by Wyoming big sagebrush (*Artemisia tridentata*), greasewood (*Sarcobatus vermiculatus*), silver sagebrush (*Artemisia cana*), saltbush (*Atriplex spp.*), and rabbitbrush (*Chrysothamnus spp.*). The average annual temperature in Roundup

(1991-2020) is 6.8º C (44.2º F), and the average annual precipitation is 38.4 cm, most of which falls in May (6.1 cm) and June (7.6 cm) (National Centers for Environmental Information 2021).

Field methods

In March and April from 2011-2019, we captured hens from a non-migratory population on or near leks using night-time spotlighting (Giesen et al. 1982, Wakkinen et al. 1992). We fit hens with either a 25-g necklace style VHF transmitter (Model A4060, Advanced Telemetry Systems, Isanti, MN) or a 25 g solar GPS PTT (2018-2020 only). After capturing an initial sample of 100 hens (2011), we captured hens annually to replace lost or dead hens. When possible, we replaced two-year-old transmitters prior to failure to increase each hen's monitoring duration. Capturing and handling of sage-grouse hens was approved by the University of Montana's Institutional Animal Care and Use Committee protocols (AUP 009-18VDWB-031418; AUP 011-14DNWB-031914).

Research staff monitored VHF-marked hens via ground surveys 3x/week (nesting and brood-rearing seasons) and via aerial telemetry 1x/month (summer-fall and winter). We monitored GPS-marked hens via an online platform (Woods Hole Group, Inc., Bourne, MA, USA) where satellite-transmitted locations uploaded on a pre-programmed schedule designed to maximize locations based on seasonal solar charging capacity (8x/day during nesting, 10x/day during brood-rearing, 6x/day during summer-fall, and 4x/day during winter). Hens with GPS transmitters also had VHF piggybacks that enabled technicians to nest-search, although technical issues with the VHF transmitter precluded this in some cases.

We monitored chicks from near hatching to independence from the brood hen, up to 125 days post-hatch. We captured chicks 1-10 days after hatch and affixed a 1.3g backpack VHF radio transmitter (Model A1065, Advanced Telemetry Systems, Isanti, MN) on up to four randomly selected chicks per brood via two small sutures on the lower back. Transmitters lasted 75-125 days. We monitored chicks every other day for the first two weeks when mortality rates were typically highest, and ≥2 times per week thereafter until the chicks died, their tags expired, we lost their signals, or they were recaptured and fitted with a larger transmitter. Chicks found dead and intact near the capture site were excluded from analyses due to the possibility that their mortality was human-induced and could thus bias their survival estimate.

We aged birds following standard protocols for sage-grouse (Braun and Schroeder 2015) that are based on the plumage in the season of capture (Table 12).

Table 12. Descriptions of sage-grouse female life stages during different seasons, and the associated differences in plumage that enable technicians to accurately age birds at capture.

Year of life	Months	Stage	Plumage type	Capture type
Year 1	Mar-May	Eggs	None	None
	Jun-July	Chick	Distinctive	Chicks are tagged (~2 per brood)
	Aug-Oct	Juvenile	Distinctive	Juveniles previously captured as chicks are recaptured and collared
Year 2 (“Second year” or “SY”)	Mar-May	Yearling (SY)	Distinctive	Hens captured (initial)
	Jun-July	Yearling (SY)	Distinctive	None
	Aug-Oct	Yearling (SY)	Distinctive until late fall	Hens occasionally recaptured (if needing a new collar)
Year 3+ (“After second year” or “ASY”)	Mar-May	Adult (ASY)	Distinctive	Hens captured (initial)
	Jun-July	Adult (ASY)	Distinctive	None
	Aug-Oct	Adult (ASY)	Distinctive	Hens occasionally recaptured (if needing a new collar)

We obtained lek count data (1959-2022) from Montana Fish, Wildlife and Parks (FWP). Attendance of male sage-grouse at leks was counted by observers affiliated with FWP, non-governmental organizations, and federal agencies. Leks were counted 1-3 times each year, but not all leks were counted every year (Montana Fish Wildlife and Parks 2020). Observers visited leks around sunrise and counted birds from either vehicles or nearby observation points.

Demographic rate estimation

We defined nest initiation probability (I) as the probability that a marked female initiated a nest that was subsequently detected; we calculated this value as the ratio of the number of nests initiated per number of hens under observation on April 1 of each year. We defined clutch size (C) as the minimum number of eggs in each clutch, which was recorded in a single count conducted by technicians after nest completion. Clutch size is a minimum count because it is not possible to count eggs while hens are incubating due to the risk of hens abandoning their nests. We defined nest success (N) as the probability that at least one chick left the nest after a 37-day laying and incubation period (Smith et al. 2018), and we modeled nest success using a logit link and a binomial distribution (Chapter 2). We used nest success rather than hatching rate in this model because it is not possible to count eggs during the sage-grouse nesting season due to the female's tendency to abandon the nest if disturbed. This definition assumes that if a nest is predated, all eggs are destroyed.

We defined chick survival (K) as the probability that a hatched chick survived to 42 days. Lorelle Berkeley led the effort to model chick survival using a mixed-effects

Cox proportional hazards model with a correlated frailty random effect for brood dependence (Dahlgren et al. 2016, Berkeley et al. 2021, Berkeley et al. in prep). We used an estimate of juvenile survival from a range-wide study of sage-grouse demographic rates (Taylor et al. 2012) due to a lack of available data in our study area. Given that we combined our juvenile survival across nest attempts, and that the juvenile survival estimate extended from 35 days (rather than the 42-day endpoint of the chick survival study) until the start of the next breeding season (April 1), we selected the lower range-wide juvenile survival estimate associated with second and third nest attempts to be conservative. David Messmer led the effort to estimate annual hen survival (HS) for each April 1 – March 31 survival year using a known fate model (David Messmer, unpublished analysis). For hen survival estimation, we combined data from second-year (SY) and after-second-year (ASY) hens, because there is no difference in hen survival among SY and ASY females (Figure 19), potentially because these birds flock together and are exposed to similar conditions. We also combined data across stages for the other demographic rates due to sample size constraints. We fit all models in Program R (R Core Team 2020); Cox proportional hazards models were fit using package "survival" (Therneau 2015), and known-fate models were fit using package "RMark" (Laake 2013).

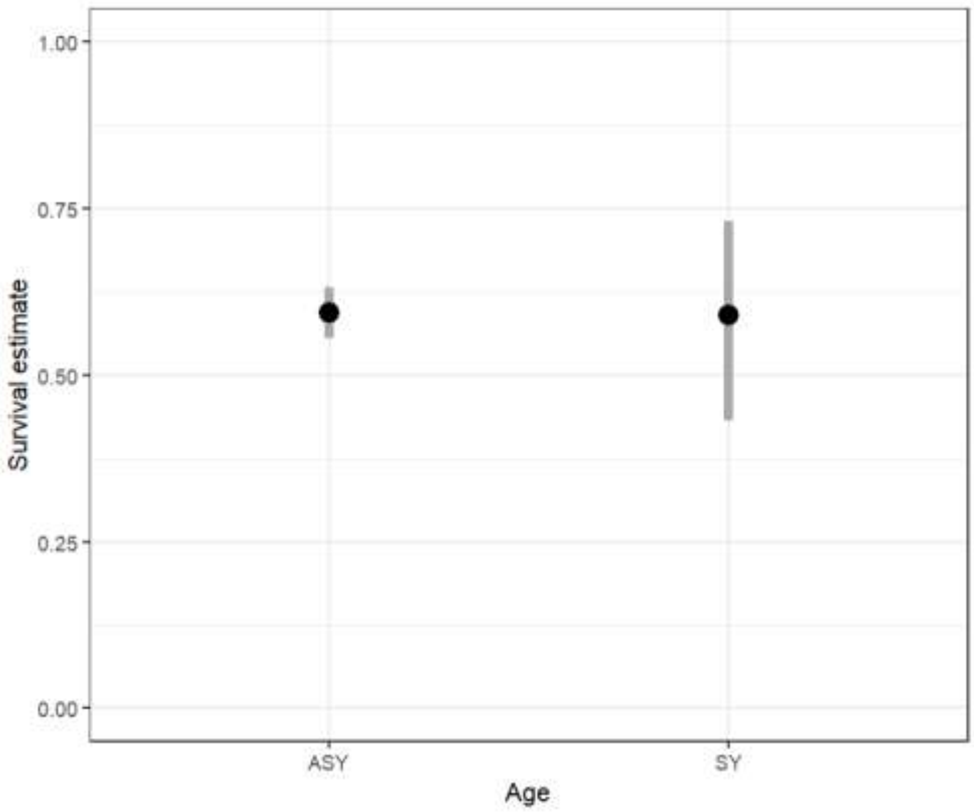

Figure 19. A comparison of second-year and after-second-year hen survival for our population of sage-grouse in central Montana derived from a known-fate analysis incorporating a “stage” effect. Estimates were very similar, although there was more variability in the estimate for the second-year hens, likely due to the smaller sample size. Figure created by David Messmer.

Female-based population model

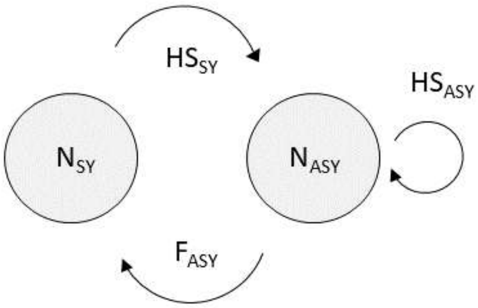

Figure 20. A diagram of the two-stage female-based population model. N = sample size, HS = hen survival, and F = fertility (which we define further below). SY = second-year hen, and ASY = after-second-year hen.

Following the methods described in Dahlgren et al. (2016), we used estimated demographic rates to construct a life table (Table 14) that we used to build a two-stage, female-based matrix population model (Caswell 2001). We used a one-year projection interval, a pre-breeding census, and a birth-pulse reproduction format (Caswell et al. 2001):

$$A = \begin{bmatrix} F_{SY} & F_{ASY} \\ HS_{SY} & HS_{ASY} \end{bmatrix}$$

where F = fertility, HS = hen survival, SY = second-year, and ASY = after-second-year, where SY and ASY birds were combined. Again, following Dahlgren et al. (2016), we defined fertility as the number of females recruited to breeding age in year *t+1* per breeding female of stage *x* in year *t* (Dahlgren et al. 2016). We calculated fertility as follows:

$$F = \frac{(I * N * C * K * J)}{2}$$

where for each stage, I = nest initiation probability, N = nest survival probability, C = clutch size, K = chick survival probability, and J = juvenile survival probability. We then estimated the asymptotic finite population growth rate across all years by calculating the mean demographic rates across all years and using them to construct a mean matrix model. We hard-coded the population model in Program R and retroactively checked estimates of lambda (λ) using package “popbio” (Stubben et al. 2020).

We estimated the precision of our annual population growth estimates using Monte Carlo simulation. We simulated 10,000 uncorrelated sets of year-specific vital rates using the mean and standard deviation of each year-specific estimate (Taylor et al. 2012, Dahlgren et al. 2016). We then constructed 10,000 2x2 matrices for each vital rate within each year, and estimated precision from the resulting distribution of 10,000 estimates of year-specific population growth rate. We repeated this process for each year of the study.

Male-based lek count analysis

After compiling lek count data from 180 leks in and around our study area (i.e. within a rectangular polygon encompassing the study area), we identified the maximum male lek count for each lek in each year. For example, if a lek was counted three times in one year, we selected the highest count of the three to represent that lek in that year. Given that some leks were not counted every year, for every year pair (year t and year t+1), we omitted leks that were not counted in both years. We then summed the maximum counts at each lek in each year across all leks remaining in the dataset. Next, we estimated the population growth rate for each year of the study (Dahlgren et al. 2016):

$$\lambda(t) = \frac{\sum_{i=1}^{n} M_i(t+1)}{\sum_{i=1}^{n} M_i(t)}$$

Where λ = the population growth rate, M_i = the maximum number of males counted during a given year on lek *i*, *t* = the year during which the maximum count occurred, and *n* = the number of leks surveyed during years *t* and *t*+1. We estimated the variance of the annual population growth rate estimates using a standard ratio estimator (Dahlgren et al. 2016).

RESULTS

Demographic rate estimation

Nest initiation began in mid-April, peaked in mid-May, and tapered off by mid-June, with a median overall "found date" of May 8. We defined nest initiation rate as the proportion of hens that initiated a first nest attempt, where nest attempt refers to the number of times (typically 1, 2, or 3 for sage-grouse) that a hen tries to initiate a nest, only moving to a later attempt if the first fails. The average nest initiation rate across the study was 0.70, ranging from a low of 0.57 in 2015 to a high of 0.73 in 2012 (Table 14. Sample sizes and estimated demographic rates for sage-grouse in central Montana that were used in a female-based population model. I = nest initiation rate, C = clutch size, N = nest success, K = chick survival, J = juvenile survival, and HS = hen survival.). Across the ten years of the study, most hens nested at least once (N = 183 hens) or twice (N = 108 hens), but some initiated nests in three (N = 42), four (N = 13), or five (N = 2) distinct years.

The mean clutch size was 7.16 eggs, and clutch sizes were slightly larger and more variable for first nest attempts than for second attempts (Table 13). Very few hens made three nest attempts (Table 13), and no instances of double brooding were detected (i.e. no hen initiated another nest after successfully hatching a nest in a given year). Reported clutch sizes are minimum values as they are based on eggs and egg remnants observed after the nest hatches.

Table 13. Mean clutch sizes and variability across first, second, and third nest attempts of sage-grouse hens in central Montana during 2011-2020. Clutch sizes are reported only for successful nests (i.e. clutch size ≥ 1).

Nest attempt	**Mean clutch size**	**SD**	**Range**	**Sample size**
First	7.16 eggs	2.02 eggs	1 – 11 eggs	517 nests
Second	6.10 eggs	2.02 eggs	1-10 eggs	99 nests
Third	8 eggs	1.41 eggs	7-9 eggs	2 nests
Overall	***7.00 eggs***	***2.05 eggs***	***1-11 eggs***	***619 nests***

Median nest survival probability across the study duration was 0.36, with substantial variation among years (Helm et al. in prep, Table 14). Chick survival probability ranged from 0.24 to 0.6, with variation by year as well (Berkeley et al. in prep, Table 14). Hen survival was variable to a lesser degree among years (Table 14).

Female-based population model

We constructed a life table for the ten years of the study (Table 14) using estimated year- and age-specific demographic rates, which shows differences in estimated demographic rates among years. Although annual population growth rates from the matrix ($\lambda_{\text{female, yr}}$) visually appear to fluctuate around a stable growth rate of $\lambda_{\text{female,}}$=1 (Figure 21. Annual population growth rates from a ten-year female-based matrix population model (purple dashed line) and twenty years of male lek counts (blue dashed line), plotted together. Error ribbons represent 95% confidence intervals around each annual estimate of population growth rate., Table 15), the geometric mean of the annual population growth rate estimates (λ_{female}) was 0.904.

Table 14. Sample sizes and estimated demographic rates for sage-grouse in central Montana that were used in a female-based population model. I = nest initiation rate, C = clutch size, N = nest success, K = chick survival, J = juvenile survival, and HS = hen survival.

Year	**Sample size**	**I**	**C**	**N**	**K**	**J**	**HS**
2011	100	0.72	6.89	0.34	0.44	0.73	0.54
2012	130	0.73	7.54	0.6	0.19	0.73	0.71
2013	100	0.67	6.97	0.36	0.41	0.73	0.74
2014	120	0.72	7.52	0.49	0.40	0.73	0.70
2015	140	0.57	6.83	0.39	0.56	0.73	0.84
2016	100	0.68	6.47	0.28	0.33	0.73	0.69
2017	95	0.71	6.92	0.33	0.47	0.73	0.51
2018	85	0.71	6.67	0.36	0.24	0.73	0.44
2019	46	0.67	7.51	0.44	0.60	0.73	0.64

Male-based lek count analysis

Estimates of annual population growth rate derived from lek counts ($\lambda_{male,\ yr}$) suggested substantial variation in male abundance on leks across years, although the trend appeared relatively stable over the duration of the study (Figure 21). The geometric mean of lek-derived annual population growth rates across all years was 1.156, suggesting that the population grew by nearly 16% over the ten-year study. The lowest $\lambda_{lek,yr}$ occurred in 2018 ($\lambda_{lek,2018}$ =0.063), whereas the highest occurred in 2019 ($\lambda_{lek,2019}$ =2.04). We included estimates of $\lambda_{lek,yr}$ both before (2001-2010) and after (2021-2022) our study duration to provide broader context for our $\lambda_{lek,yr}$ estimates (Figure 21).

Of the 180 leks monitored in the study area from 2011-2022, a mean of 68.2 leks were included in the sample used to estimate $\lambda_{lek,yr}$, due to intermittent gaps in counts at some leks in some years. Approximately 13% of leks (n = 23) were counted at least once per year during all ten years of the study. Of those 23 leks, 100% were typically counted at least two times per year. However, when considering all 180 leks, each one was counted during only 5 of the 10 years, on average.

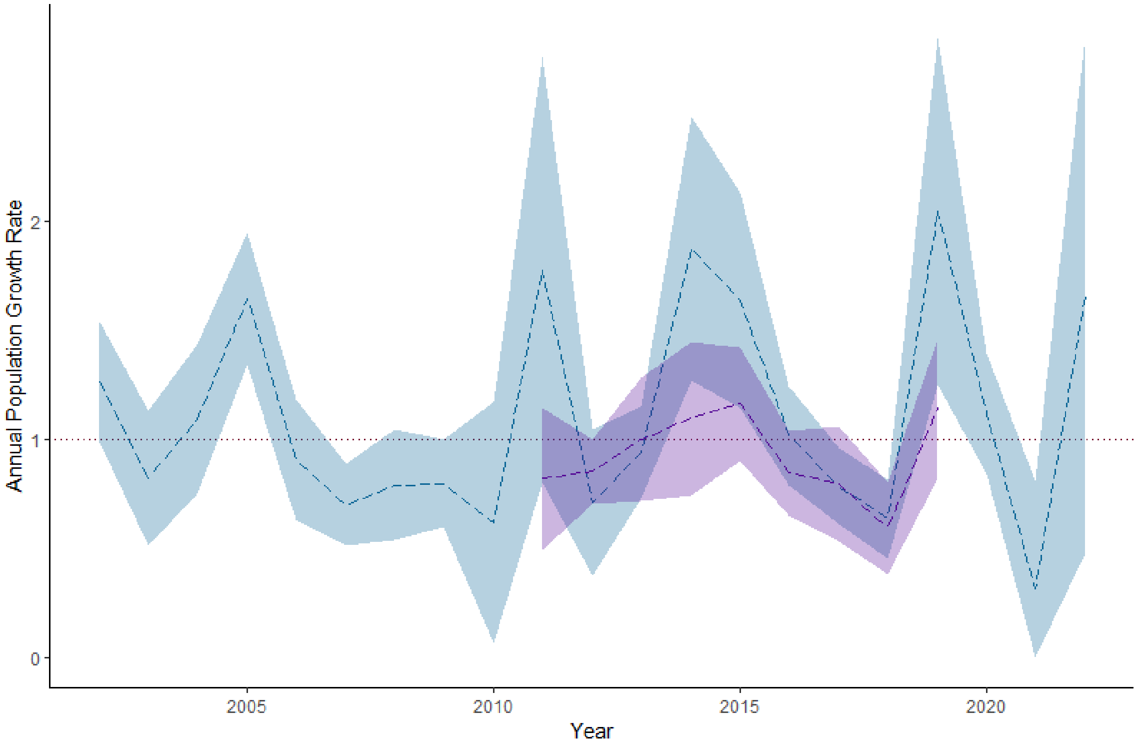

Figure 21. Annual population growth rates from a ten-year female-based matrix population model (purple dashed line) and twenty years of male lek counts (blue dashed line), plotted together. Error ribbons represent 95% confidence intervals around each annual estimate of population growth rate.

Table 15. Annual population growth rates and standard deviations derived from a female-based population model compared to growth rates derived from high male lek

counts. Note that values are only included for 2011-2019 to match the lek count data to the duration of the demographic data.

	Population model		**Lek counts**	
Year	**λ**	**SD**	**λ**	**SD**
2011	0.817	0.163	1.780	0.489
2012	0.850	0.074	0.706	0.168
2013	1.000	0.139	0.937	0.106
2014	1.098	0.181	1.870	0.302
2015	1.162	0.130	1.640	0.247
2016	0.843	0.095	1.010	0.112
2017	0.797	0.129	0.784	0.087
2018	0.594	0.108	0.634	0.091
2019	1.143	0.163	2.04	0.398
Geometric mean	**0.904**		**1.156**	

We estimated the sensitivity of λ to each matrix element and found that population growth rate was most sensitive to ASY hen survival (Table 16). It was second-most sensitive to ASY nest success, and ASY chick survival came in third. Overall, λ was more sensitive to ASY demographic rates than SY rates (Table 16), despite the fact that they were combined in the data used to parameterize the model.

Table 16. Sensitivity of demographic rates incorporated into female-based matrix model. The top three demographic rates to which λ is most sensitive are highlighted in bold.

Demographic rate	**Sensitivity**	**Sensitivity rank**
HS SY	0.297	4
HS ASY	0.703	**1**
NS SY	0.218	7
NS ASY	0.515	**2**
NI SY	0.118	9
NI ASY	0.279	5
CS SY	0.200	8
CS ASY	0.474	**3**
ECS SY	0.012	12
ECS ASY	0.027	11
JS SY	0.108	10
JS ASY	0.256	6

DISCUSSION

We investigated whether lek counts, a standard population trend estimator, reflect population growth rate estimates derived from an independent, ten-year demographic dataset. We found that although annual population growth rate estimates derived from a female-based matrix population model generally followed a similar trend as the annual growth rate estimates derived from lek counts (Figure 21), the geometric mean of the annual population growth rates from the two different analyses over the ten-year study suggested opposite trends (Table 15), posing a serious obstacle for managers making decisions about habitat conservation and harvest quotas.

Female-based population model

The matrix model suggested that there was moderate fluctuation in annual $\lambda_{female,yr}$ across the duration of the study. The lowest estimate occurred in 2018 ($\lambda = 0.594$, sd = 0.108, Table 15), and this was a substantial outlier. The next lowest λ occurred in 2017 ($\lambda = 0.797$, sd = 0.129, Table 15). Although we did not include covariates in this modeling effort, so we cannot comment definitively on causes of this variation, it is still instructive to consider why this variation exists. One potential reason for low growth rates in 2017 and 2018 could be due to direct and lagged effects of a severe drought that affected central Montana. Although female adult survival is not thought to be particularly sensitive to weather, it is possible that the severity of this weather event influenced the component vital rates underlying the fertility term in the population model. For example, the 2017 nest success estimate was on the lower side of average (NS = 0.33, Table 14), whereas the 2018 chick survival estimate was the second-lowest reported during the study (K = 0.24, Table 14). Given the high sensitivity of our model to both nest success and chick survival (Table 16), it is plausible that these vital rates pulled the growth rate down during these years. Given that chicks rely on new, green growth and associated insects for food, it is plausible that a major drought could have affected food availability during the critical brood-rearing period. In contrast, the highest annual population growth rate estimate occurred in 2019 ($\lambda = 1.143$, sd = 0.163, Table 15). Although we are not aware of any environmental explanatory variables that could explain this, it is noteworthy that the sample size of hens monitored in 2019 was only half of what was monitored in many of the other years (Table 14). Additionally, the chick survival probability reported during 2019 was a high outlier, which likely drove up the annual growth rate.

The overall geometric mean of the annual population growth rates (mean = 0.904) suggests that despite the years that experienced positive growth, this population declined by 10% over the course of the study period. However, it is possible that these population model estimates are influenced by observation error, and are not due solely to process noise. One possible source of observation error is the particular methods that we used to estimate the demographic rates that we input into the population model. For example, we used nest success along with clutch size, rather than incorporating an estimate of hatching rate, since we were unable to collect those data, thereby assuming that if a nest was predated, all of the eggs failed, whereas if it succeeded, then all of the eggs survived. Additionally, the use of a range-wide juvenile survival rate as a proxy for a study-area-specific estimate could introduce some bias. Finally, another possible source of observation error is individual random variation. This could be at least partially addressed through the inclusion of a random effect to vital rate estimates, so we recommend that future studies incorporate this.

Male-based lek count analysis

Past research on the accuracy of lek counts as an index for population abundance and growth rate is mixed. A recent study assessed the use of lek counts to guide local-scale sage-grouse habitat management, and found that it was a promising method, with the caveat that male detection probability was confounded with the effects of habitat management when sample sizes were small (Blomberg and Hagen 2020). Similarly, another recent study found that lek counts were biased because only some birds were present, but that repeated counts can address detection challenges (Coates et al. 2019). Our results are most similar to those of Dahlgren et al. (2016), showing more variation in annual population growth rates estimated from lek counts than from matrix models.

Our male-based lek count analysis suggested that there was much more dramatic variation in population growth rate among years than the matrix model indicated. The lowest $\lambda_{lek,yr}$ occurred in 2018 ($\lambda_{lek,2018} = 0.63$), suggesting a nearly 40% decline between 2017 and 2018. In contrast, the highest occurred in 2019 ($\lambda_{lek,2019} = 2.04$), suggesting that the population nearly doubled between 2018 and 2019. This dramatic increase between two adjacent periods is substantial enough that it seems likely to be due to observation error rather than underlying process variation. Several of the sources of possible observation error were described earlier (refer to introduction), and fall into the categories of sampling-related error and assumption violations. In addition to the challenges already mentioned, another source of potential observation error is the fact that leks can occasionally shift their location slightly, and smaller “satellite” leks may shift across years. We did not account for these types of changes, which could affect our results.

The overall geometric mean of the lek-derived annual population growth rates ($\lambda = 1.156$) suggested that the population was growing by approximately 16% per year. This apparent increase over time is visible in Figure 21, where it is clear that more years have positive population growth rates (above the dotted line denoting $\lambda = 1$), and that the positive population growth rates have a greater absolute value than the negative population growth rates.

Conclusions

Overall, while we found that while the population growth rates derived from the two methods tracked each other to some degree (Figure 21), the geometric means derived from the two different analyses over the ten-year study suggested opposite trends (Table 15). This lack of correlation of estimates across the study duration is clearly visible in a simple linear regression of λ_{male} against λ_{female} (Figure 22) where a 1:1 slope line plotted in gray does not track the estimates (paired by year) from each method ($R^2 = 0.53$).

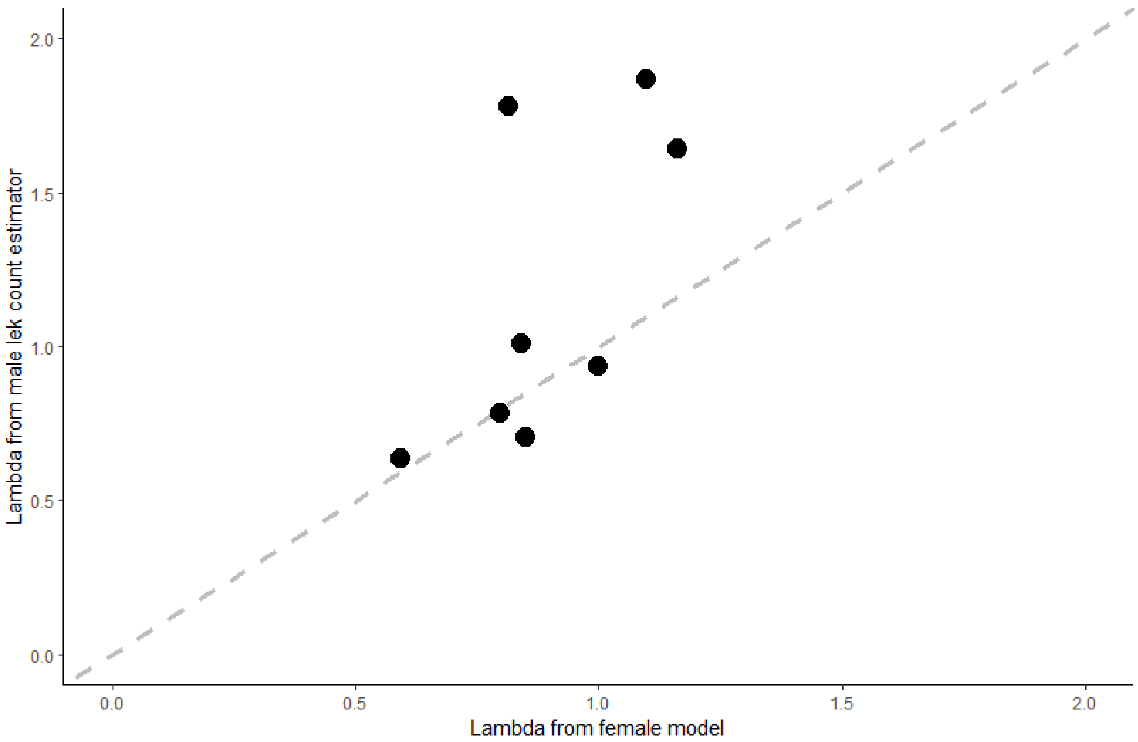

Figure 22. A linear regression of population growth rates (paired by year) derived from the two different methods shows a lack of correlation.

This plot shows two interesting pieces of information. First, it is clear that on average, λ_{male} is higher than λ_{female}. Regardless of which estimate is more accurate, this is a key piece of information for managers, because it means that managers may be less likely to detect declines than they would using the matrix method. The second interesting point from this plot is that estimates from certain years match very well (i.e. are plotted close to the 1:1 line), but certain years are dramatically different (i.e. far from the line with the lek count estimate being higher than the matrix estimate). The three points far from the line in Figure 22 are from 2011, 2014, and 2019. It is difficult to know what drove these serious differences in estimates during these particular years, but one possible explanation is that observation error in the lek counts biases them high. This could result from detectability issues that arise during different weather conditions, given that there tends to be lower lek attendance on rainy days. While this may be mediated to some degree by survey protocols that encourage lek counting on days with good visibility, different conditions in different years could affect underlying processes such as lek attendance and vegetation growth (that could obstruct lek viewing) as well as the observation process.

Many studies have shown that raw lek counts may be associated with sampling bias (e.g. Walsh et al. 2004). As such, it is important to view any trends derived from that survey type with caution. On the matrix model side, assumptions must be made in terms of model structure, and these can influence results. For example, although the decision to combine demographic rates for SY and ASY birds was based on study area-specific evidence (Figure 19), it is possible that this could influence results if the smaller sample size of SY birds was biased.

Managers aiming to use this information to make decisions that depend on population growth rates (e.g. adjusting harvest) have a few options. First, they could choose either of these two estimators, and use the output to make their decision. If a manager went this route, the estimates from the population model are likely a better option. These estimates demonstrate less inter-annual variation that could be due to males moving from lek to lek, and they are also more conservative estimates on average. However, we suggest that the best option for managers moving forward is to produce an integrated population model that incorporates both the demographic data and the count data. Combining these different datasets will make it more intuitive for managers to identify thresholds beyond which a management action is needed, such as reducing harvest, as it is difficult to recommend a threshold based on these two divergent model outputs. The current guidance that several states implement looking for a multi-year decrease in abundance is a good starting place, but based on the high bias of lek counts relative to the matrix model, it is possible that this is not conservative enough to capture small decreases in population growth that could still lead to local extinction through stochastic processes if not caught early enough.

Accurate population trend estimates are necessary to monitor and protect wildlife populations (United States Fish and Wildlife Service 2015). It is especially helpful if this information is available at the scale at which management is occurring. This information is valuable to stakeholders engaged in wildlife habitat conservation efforts and population management, such as conservation organizations, private land owners, and land management agencies. Use of trend estimates includes assessing wildlife responses to habitat changes and setting harvest seasons and limits; additionally, federal agencies use estimates of population trends to develop their management plans. Furthermore, if sage-grouse are petitioned for listing under the Endangered Species Act again, regulators will need up-to-date estimates of population trends to make a listing decision. As such, states within sage-grouse range are required by law to document and report sage-grouse population trends (State of Montana Office of the Governor 2014). This work provides information in service of this goal.

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Table 17. Estimates of precision associated with annual estimates of demographic rates used to construct female based matrix population models.

Year	**sd(I)***	**sd(C)**	**sd(N)**	**SE(K)****	**sd(J)*****	**sd(H)**
2011	0.049	2.34	0.06	0.16	0.04	0.05
2012	0.049	1.55	0.06	0.05	0.04	0.05
2013	0.049	1.96	0.06	0.11	0.04	0.08
2014	0.049	2.06	0.06	0.10	0.04	0.07
2015	0.049	1.80	0.06	0.08	0.04	0.06
2016	0.049	2.13	0.06	0.08	0.04	0.06
2017	0.049	2.06	0.06	0.07	0.04	0.06
2018	0.049	2.54	0.06	0.07	0.04	0.07
2019	0.049	1.29	0.06	0.07	0.04	0.09

*standard deviation of nest initiation rate (I) was estimated based on the distribution of annual estimates. ** standard error was converted to standard deviation for simulation. *** standard deviation was derived from confidence intervals reported in Taylor et al. 2012.

OVERALL CONCLUSIONS

Greater sage-grouse (*Centrocercus urophasianus)* abundance has declined across the species' range due to habitat loss, degradation, and fragmentation. To address this decline, information is needed to guide habitat conservation priorities and population management efforts. This includes information about patterns of habitat selection at multiple spatial scales, habitat and land use variables that affect demographic rates, and population trend estimates. We collected ten years of data (2011-2020) on sage-grouse demographic rates and habitat selection, vegetation, and livestock grazing patterns to address these topics. Specifically, we investigated effects of a rotational grazing system implemented through the United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) Sage Grouse Initiative (SGI). In this dissertation, we aimed to capitalize on a ten-year dataset to explore three primary aspects of greater sage-grouse ecology: their habitat selection patterns in relation to livestock grazing, their nest success, and their population dynamics. As part of this work, we were able to characterize several previously undescribed aspects of a sage-grouse population in an important area that is critical to the long-term health of the species.

In Chapter 1, we investigated whether sage-grouse hens select seasonal home ranges based on topographic and vegetation variables. We found that hens select for shrub cover across all seasons, with seasonal differences in other variables. We also found that sage-grouse located within livestock pastures select for areas with higher used AUMs in addition to shrub cover. In Chapter 2, we evaluated the effects of the SGI rotational grazing system on sage-grouse nest success. We found that neither SGI rotational grazing systems nor other indices of livestock use had measurable effects on nest success, but we saw a very minor positive effect of senesced grass height. Annual variation was the strongest predictor of nest success, and although we did not test the environmental drivers of annual variation in this study, we believe that this variation is likely due to inter-annual variation in temperature, precipitation, and other environmental variables.

Taken together, these results lead us to some specific recommendations for future sage-grouse research and management. Overall, this study demonstrates the critical importance of long-term data collection when assessing population-level responses to habitat-related variables, particularly in settings where there is a large amount of annual variation. Although we were able to draw on data from our ten-year study to answer some questions that were challenging given the study design, such as assessing seasonal habitat selection using a long revisit window, we found that a ten-year dataset was still not long enough to disentangle the effects of habitat- and grazing-related variables from the effects of annual variation in most cases. As such, this study offers strong evidence that longer-term studies with larger sample sizes are necessary to parse out these different sources of variation. This is especially important in studies investigating the effects of climate change on different wildlife population and habitat selection parameters, because climate change operates on a time-scale that is typically longer than the ten years of the study.

The second overall conclusion we can draw from this study is that sage-grouse habitat conservation is critical, particularly in the context of a grazed landscape within a changing climate. We saw that sage-grouse in central Montana were primarily selecting for shrub cover, which is unsurprising given that they are a sagebrush obligate species. However, it was more surprising that sage-grouse were selecting for areas that had higher "used AUMs," or areas where larger amounts of forage were grazed by livestock. Further complicating matters, sage-grouse nest success was slightly higher in areas with higher senesced grass, or areas with higher amounts of grass left over after the grazing season to remain as standing cover for the next nesting season. At first glance, this result might seem to be counter to the finding that they select areas with more grazing pressure. However, in this study area, none of pastures that sage-grouse used for which we had grazing data demonstrated high grazing pressure; rather, grazing was very moderate across all grazing systems. This likely means that even in pastures grazed at the highest grazing intensities, there is still adequate senesced grass to support a healthy population. Similarly, there is far less sagebrush cover in this area of sage-grouse range than in other regions. This means that it is possible for pastures to contain both high proportions of sagebrush and high proportions of senesced grass. Taken together, these results suggest that continuing to conserve intact ranches and working lands is a good way to protect these populations, as long as the range of grazing intensity experienced on these ranches is within the range observed in this study.

The third overall conclusion we can draw from this study is that more experimental research is needed to tease apart the complex relationships between livestock grazing and wildlife population dynamics. Although we were lucky to have a well-designed observational study to investigate longer-term effects of two grazing systems on sage-grouse habitat selection and nest success, our inference was limited by the lack of difference in the systems among the metrics that we investigated. For example, although the timing of grazing varied somewhat between the rotational SGI grazing systems and the other grazing systems implemented in our study area, we did not detect meaningful differences among other vegetative metrics across study areas, including senesced grass height, distance to fence, and used AUMs. While the resulting finding that there was no difference among grazing systems is hopeful for sage-grouse management in that many different types of grazing may be satisfactory to maintain healthy sage-grouse populations, this was challenging because it meant that we could not speak to whether different vegetation metrics drove sage-grouse demographic rate trends in this population. We suggest that future studies experimentally manipulate vegetation and grazing to enable finer-resolution drivers of variation in sage-grouse population parameters.

Fourth, we can draw some conclusions from Chapter 3, in which we compared two methods of estimating sage-grouse population growth rate, using two different datasets. In this chapter, we found that the population growth rate from annual lek counts was more variable than the growth rate estimated using a matrix model. Additionally, we found that although the annual population growth rates tended to track each other across the study, the geometric mean of the rates across the study indicated an increasing trend from the lek count estimator in contrast to a decreasing trend. This pair of results, in particular, poses challenges to managers seeking to make decisions using these sources of information.

We suggest that managers aiming to use this information to make decisions that depend on population growth rates (e.g. adjusting harvest) follow estimates from matrix models over lek counts when those data are available, acknowledging that this is rarely the case. Matrix model-derived estimates demonstrate less inter-annual variation that could be due to males moving from lek to lek, and they are also more conservative estimates on average. In the long run, we suggest that if demographic data exists for a population, it would be helpful to produce an integrated population model that incorporates both the female-based demographic data and the male-based count data. This would streamline managers’ decision-making process by making it more intuitive for managers to identify thresholds beyond which a management action is needed.

Overall, the outlook for sage-grouse in central Montana seems optimistic, particularly if grazing continues at a similar level to that seen over the last ten years, and if wildlife managers keep a close eye on the population growth rate to ensure that long-term declines are not missed. We encourage the ongoing conservation of intact sagebrush habitat for the long-term health of this species.