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Gelling, E. L. <u>Seasonal habitat selection and breeding ecology of greater sage-grouse in Carbon</u> <u>County, Montana</u>. M.S. Department of Ecosystem Science and Management, May 2022.

# ABSTRACT

Greater sage-grouse (Centrocercus urophasianus; hereafter 'sage-grouse') are the focus of much research and conservation efforts owing to their obligate relationship with sagebrush (Artemisia spp.) and dramatic population declines over the last 50 years. Sage-grouse are a partially migratory species with three main seasonal habitats during breeding, summer, and winter. Anthropogenic disturbances can impact habitat and areas used by sage-grouse during all three seasons. Sage-grouse also exhibit low productivity that is limited, in part, by nest and chick survival. As uniparental incubators, nesting can be energetically costly for female sage-grouse because they have limited mobility when their precocial chicks are young. In addition, habitat characteristics have been shown to differ between brood-rearing female sage-grouse and broodless females (i.e., females without broods). Therefore, to sustain sage-grouse populations, focus should be on increasing vital rates for adult females, chicks, and nests-the life stages that most influence population growth. Research is thus critical to better understand the relationships between life stages of sage-grouse and their seasonal habitats, particularly during breeding and summer brood-rearing. The focus of my thesis was to assess the influence of natural and anthropogenic features on sage-grouse seasonal habitat selection, assess factors influencing sagegrouse nest survival and attentiveness, and assess habitat selection and behavior between broodrearing and broodless female sage-grouse. By focusing on habitat selection across three seasons, during reproductive and non-reproductive states, and across second, third, and fourth-order habitat selection, wildlife managers will have better information to manage sage-grouse habitat to sustain or increase survival for adult females, broods, and nests. More specifically, this

information will inform areas to prioritize management, restoration, and conservation to benefit sage-grouse populations and add to the body of knowledge of basic sage-grouse breeding ecology.

In Chapter 1, I examined natural and anthropogenic landscape features that influence sagegrouse habitat selection during breeding, summer, and winter seasons. I used data from 85 GPStagged female sage-grouse in Carbon County, Montana and Park County, Wyoming spanning April 2018–April 2020. I found natural and anthropogenic features combined best explained sage-grouse habitat selection for all three seasons. Sage-grouse habitat selection differed between each season with sagebrush cover being important for breeding and agricultural fields being important in summer. In general, sage-grouse selected for sagebrush or shrub characteristics and lower slopes and avoided major roads, residential development, and oil and gas. However, anthropogenic disturbances were not always avoided and sometimes sage-grouse selected areas closer to these disturbances, such as agricultural fields during summer or roads during winter. I created predictive maps from resource selection function modeling to depict relative probability of use for each seasonal range to be used in wildlife management and conservation planning.

In Chapter 2, I focused on nest survival and attentiveness. Nest success is an important part of the breeding process that has implications for population growth. I described sage-grouse incubation behavior, examined whether sage-grouse incubation behavior influenced nest survival, and evaluated factors that influenced sage-grouse incubation behavior. For this chapter, I used data collected from my study area in Carbon County, Montana and Park County, Wyoming and a separate study area in the Red Desert of Carbon and Sweetwater counties,

Wyoming. I used 131 nests to describe sage-grouse incubation behavior and 118 nests to examine nest survival and average recess duration. I found nest survival was higher in Bridger compared to Red Desert. I found incubation constancy was higher and recesses shorter for adults compared to yearlings. I found nest survival was higher with increased minimum temperature and reduced with longer recesses. Recess duration was shorter with greater sagebrush cover within 30 m and recesses were longer with higher minimum temperature and day of incubation. Factors influencing nest survival and incubation patterns will be important for directing management to improve sage-grouse nest success and to clarify to researchers and managers our understanding of the basics of sage-grouse nesting biology.

In Chapter 3, I focused on habitat selection, activity patterns, and ranges of both brood-rearing and broodless females during the breeding season. I examined behavior and reproductive state influence on microhabitat selection, daily and seasonal range sizes, and daily activity levels for brood-rearing and broodless females. I sampled microhabitat for 36 females, estimated ranges for 38 females, and measured activity for 43 females. I found females with broods 0–2 weeks selected microhabitat characteristics when night roosting and females with broods 3–5 weeks selected microhabitat characteristics when foraging and night roosting. However, broodless females showed no selection for microhabitat based on behavior. I also found differences in activity levels for both brood-rearing and broodless females throughout the day. Broods 0–2 weeks had the smallest ranges while broods 3–5 weeks and broodless females had larger daily and seasonal ranges. Differences in habitat selection, range size, and behavior warrants management to conserve areas used by both brood-rearing and broodless female sage-grouse in a population, whereas most past efforts focused primarily on habitat used by brood-rearing

females. The *Wildlife Society Bulletin* has accepted this chapter for publication with Drs. Jeffrey Beck and Aaron Pratt as coauthors.

# SEASONAL HABITAT SELECTION AND BREEDING ECOLOGY OF GREATER SAGE-GROUSE IN CARBON COUNTY, MONTANA

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of the requirements for the degree of Master of Science

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# DEDICATION

I dedicate this thesis to my husband, Ryan, who saw the best but also had to endure through the worst while I worked to complete my thesis, and yet who continued to support me. I also dedicate this thesis to my family for their love and support and encouraging me to achieve my goals.

#### ACKNOWLEDGMENTS

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# CHAPTER ONE: Natural and anthropogenic landscape features influence greater sagegrouse seasonal habitat selection in Carbon County, Montana

In the format of manuscripts submitted to Journal of Wildlife Management

# ABSTRACT

Quantifying resource selection by animals assists wildlife and land managers in making habitat decisions that can be used for restoration and conservation planning. Greater sage-grouse (Centrocercus urophasianus; hereafter 'sage-grouse') are the focus of much research and conservation efforts owing to their obligate relationship with sagebrush (Artemisia spp.) and dramatic population declines over the last 50 years. Sage-grouse typically utilize different habitats during breeding, summer, and winter seasons. Our objectives were to: 1) evaluate sagegrouse habitat selection and anthropogenic disturbance effects at the individual and population scales of selection during breeding, summer, and winter seasons and 2) create predictive Resource Selection Function maps that can be used by wildlife managers for sage-grouse management and conservation. We used data from 85 GPS-tagged female sage-grouse in Carbon County, Montana and Park County, Wyoming from April 2018–2020. Natural and anthropogenic features combined best explained sage-grouse habitat selection for all seasons. During breeding, sage-grouse selected for moderate sagebrush cover and avoided residential development, major roads, and oil and gas. We found sage-grouse selected for sagebrush cover but avoided variability in sagebrush cover during the breeding season. In summer, sage-grouse selected for more variability in sagebrush cover but avoided steeper slopes. In summer, sage-grouse selected for areas close to agricultural fields but avoided major roads, residential development, and oil and gas. During winter, sage-grouse selected for shrub height, homogenous slopes, and areas closer to roads but avoided larger proportion of major roads and all disturbances. Understanding

habitat selection and anthropogenic disturbance effects on sage-grouse will aid in management and conservation planning.

# **INTRODUCTION**

Understanding habitat selection during critical life stages is essential for directing management and conservation efforts of vulnerable species. Wildlife managers often need to prioritize areas for restoration or management. However, habitat selection for a given species can differ depending on the scale (Chalfoun and Martin 2007, Doherty et al. 2010) or season (Marzluff et al. 1997, Doherty et al. 2010, Fedy et al. 2014). Focusing on a single life stage or season (e.g., breeding) risks exclusion of important areas or habitat features selected during other stages or seasons or along migration routes (Knick et al. 2003). Management policy, therefore, must include all seasonal habitats necessary to maintain populations (Sherry and Holmes 1995). Seasonal habitat selection maps are one tool that can aid management, restoration, and/or conservation decisions for sensitive species (Johnson et al. 2004, Aldridge and Boyce 2007, Doherty et al. 2008, Smith et al. 2014).

Animals use specific habitats seasonally that have the resources necessary to survive, reproduce, and persist (Hall et al. 1997). However, habitat loss is the leading threat to birds worldwide (Wilcove et al. 1998, Venter et al. 2006). Habitat can also be fragmented where a strong contrast occurs between vegetation patches and their surrounding areas and habitat can be degraded where vegetation structure is deteriorated (Fischer and Lindenmayer 2007). Habitat loss, fragmentation, and degradation can have negative effects on species (Fischer and Lindenmayer 2007) and these may be caused by landscape changes or anthropogenic disturbances.

Anthropogenic disturbances affecting animals may be caused by cropland conversion (Venter et al. 2006, Smith et al. 2016), oil and gas development (Hovick et al. 2014, Kirol et al. 2015, Reinking et al. 2019, Duchardt et al. 2020), wind energy infrastructure (LeBeau et al. 2017*a*, 2017*b*, Smith et al. 2020*b*), transmission and distribution lines (Beck et al. 2006, Pruett et al. 2009, Dinkins et al. 2014*a*, Kohl et al. 2019), and urbanization (Venter et al. 2006, Tomasevic and Marzluff 2018), including roads (Ciarniello et al. 2007, Fedy et al. 2014, Hovick et al. 2014, Reinking et al. 2019) and homes (Støen et al. 2010). Anthropogenic disturbance can have direct effects on species such as collisions and habitat loss or lead to avoidance of anthropogenic features (Dyer et al. 2001, Pruett et al. 2009, Sawyer 2009, Hovick et al. 2014) or other indirect effects, such as increased predation rates or reduced survival near anthropogenic features (Støen et al. 2010, Gilbert and Chalfoun 2011, Hovick et al. 2014, Pratt and Beck 2019). A better understanding of species responses to habitat features and disturbances aids wildlife management and conservation (Knick et al. 2003).

Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) is a species of conservation concern that has undergone significant range contraction and population decline (Schroeder et al. 2004, Nielson et al. 2015). Declines in populations and concern about habitat loss and degradation have prompted a considerable number of studies on sage-grouse. The sagebrush ecosystem faces numerous ecological threats (Knick et al. 2003), including conifer encroachment (Baruch-Mordo et al. 2013, Severson et al. 2017), invasive annual grasses (Lockyer et al. 2015, Chambers et al. 2016), alterations in fire regimes (Crawford et al. 2004, Lockyer et al. 2015, Chambers et al. 2016, Coates et al. 2016*b*), increased predator numbers (Coates et al. 2016*a*), and climate change (Chambers et al. 2016). Ecological changes coupled

with anthropogenic disturbance increases pressure on sage-grouse and other species living in the sagebrush ecosystem.

Sage-grouse populations employ different migration strategies, such that any one population may have up to three different migration strategies between two or three distinct seasonal ranges or have only one seasonal range throughout the year (Connelly et al. 2000). In addition, sage-grouse populations are often partially migratory (Fedy et al. 2012), with many grouse migrating to higher elevations to access resources during summer (Pratt et al. 2017). Sage-grouse show high fidelity to seasonal ranges, such as nesting areas (Fischer et al. 1993, Connelly et al. 2004). Habitat selection and response to disturbances can vary within each seasonal range. For example, sage-grouse feed almost exclusively on sagebrush during the winter but incorporate insects and forbs during breeding and summer seasons (Patterson 1952, Wallestad and Eng 1975). Summer and winter habitat are two seasonal habitats that are most unlike each other though breeding habitat is more like both summer and winter habitat (Pratt et al. 2019). Diversity in migration within populations and distinct seasonal habitats necessitates mapping habitat selection for each season for sage-grouse to better inform conservation needs. Disturbance effects on species are not uniform across seasons and scales (Heinrichs et al. 2019). Incorporating anthropogenic disturbance is necessary due to direct and indirect impacts to sage-grouse throughout breeding, summer, and/or winter seasons (e.g., Braun 1998, Walker et al. 2007, LeBeau et al. 2014, Pratt and Beck 2019). Though much research has been completed on sage-grouse seasonal habitat selection in response to disturbances such as energy development and roads (e.g., Aldridge and Boyce 2007, Holloran et al. 2015, Kirol et al. 2015, LeBeau et al. 2017), little research exists on

sage-grouse response to residential development (but see Aldridge et al. 2012) that was widespread in our study area.

Resource Selection Functions (RSFs) are powerful tools for understanding habitat selection that provide important insights for wildlife management and conservation planning (Boyce et al. 2002). We applied an RSF framework to model seasonal habitats for sage-grouse in our study area. Our primary objective was to evaluate sage-grouse habitat selection and anthropogenic disturbance effects at the individual and population scale of selection during breeding, summer, and winter seasons and our secondary objective was to create predictive RSF maps for use by wildlife managers to assist planning and conservation of sage-grouse. Evaluating seasonal habitat selection while considering anthropogenic disturbance to sage-grouse will aid wildlife managers in conservation and restoration projects and inform scientists and managers to better understand potential impacts to sage-grouse habitat and populations as threats continue in the future. We used data from 85 GPS-tagged female sage-grouse in Carbon County, Montana and Park County, Wyoming from April 2018–2020 to create RSFs for breeding, summer, and winter seasons at the individual and population scales of selection. We considered natural landscape features from remotely sensed data and identified anthropogenic features such as roads, oil and gas development, agriculture, and houses within multiple circular scales ranging from 100 m to 3200 m. For habitat selection, we predicted sage-grouse would select for herbaceous and sagebrush cover during breeding season (Doherty et al. 2010, Fedy et al. 2014), sagebrush cover during summer (Gregg et al. 1993, Fedy et al. 2014, Walker et al. 2016), and sagebrush cover and flatter terrain during winter (Beck 1977, Dzialak et al. 2012, Fedy et al. 2014, Smith et al. 2016). We predicted sage-grouse would use alfalfa (Medicago sativa) fields during the summer because of

the close proximity of these fields to leks in our study area and because they have been shown to be used by sage-grouse elsewhere (Fischer et al. 1996). We also predicted sage-grouse would avoid areas in close proximity to paved and high-use roads, oil and gas, and residential homes during all seasons (Aldridge and Boyce 2007, Dzialak et al. 2012, Fedy et al. 2014, Smith et al. 2014, LeBeau et al. 2017*b*).

# METHODS

# **Study Area**

Our study area consisted of approximately 2781 km<sup>2</sup> located in southern Carbon County, Montana and northern Park County, Wyoming (from 109°7'16.255"W 45°16'8.214"N to 108°46'13.734"W 44°48'52.390"N). Elevation ranged from 1110–1830 m above sea level with both sagebrush (*Artemisia* spp.) steppe and agricultural fields used by sage-grouse. Thirty-year averages from 1991–2020 for annual high temperature were 15.7° C, for average minimum temperature –5.7° C, and 47.1 cm for average precipitation (PRISM Climate Data; http://www.prism.oregonstate.edu). Residential development, cattle grazing, and recreational use all occurred within the study area. Anthropogenic development was mainly in the form of residential houses or agricultural buildings with little oil and gas infrastructure concentrated in the southeast. Public and private lands both occurred in the study area. Federal lands consisted of 1266 km<sup>2</sup> (45.5%), the majority of which was Bureau of Land Management administered-lands (1059.74 km<sup>2</sup>, 38.1%). State lands consisted of 143 km<sup>2</sup> (5.2%), private lands 1363 km<sup>2</sup> (49.0%), and lands under other ownership 7.78 km<sup>2</sup> (0.3%).

The landscape was dominated by basin big sagebrush (*Artemisia tridentata tridentata*) and Wyoming big sagebrush (*A. t. wyomingensis*). Other common shrubs in the study area included black sagebrush (*A. nova*), broom snakeweed (*Gutierrezia sarothrae*), Gardner's saltbush (*A. gardneri*), greasewood (*Sacrobatus vermiculatus*), rubber rabbitbrush (*Ericameria nauseosa*), shadscale saltbush (*Atriplex confertifolia*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*). Isolated stands of juniper (*Juniperus spp.*) were found on steeper hillsides or higher elevation. Dominant perennial grasses included blue grama (*Bouteloua gracilis*), Indian ricegrass (*Achnatherum hymenoides*), needle-and-thread (*Hesperostipa comata*), and Sandberg bluegrass (*Poa secunda*). The invasive annual, cheatgrass (*Bromus tectorum*), was abundant throughout the study area and field brome (*Bromus arvensis*) occurred less frequently but was still prevalent.

## **Data Collection**

We captured female sage-grouse in Montana in 2018 and 2019 across 7 leks during spring or near GPS-tagged birds in summer. We fit sage-grouse with solar-powered, rump-mounted transmitters (15g-Bird Solar tag, e-obs GmbH, Grunwald, Germany with attached 6g-VHF tag, Holohil, Ontario, Canada; total weight ~30g) with locations at 0700, 1100, 1500, 1800, 2300 MDT during breeding and summer (approx. Apr to Oct) and 0900, 1200, 1500, 2300 MST during winter (approx. Nov to Mar) to obtain both day and night sage-grouse locations. We determined female age (i.e., yearling or adult) by examining primary wing feathers (Braun and Schroeder 2015). We monitored females by downloading their locations with an antenna either on the ground or via fixed-wing aircraft from April 2018 through April 2020 to obtain two breeding, summer, and winter seasons. We retrieved transmitters as soon as possible after death;

however, this was not always possible, therefore cause of death was unknown. All capture, handling, and post-release monitoring of sage-grouse followed protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (protocol #20180102JB00289-01 and #20180102JB00289-02) and Montana Fish Wildlife and Parks Scientific Collector's Permit (#2018-072-W and #2019-039-W).

## **Data Analysis**

We delineated locations for each season and individual sage-grouse by examining sage-grouse locations within a 95% utilization distribution and net squared displacement graphs (adehabitatLT R package, Bunnefeld et al. 2011; R Core Team 2021). We defined the start of each season as the first full day each sage-grouse stayed in that seasonal range longer than outside the seasonal range and the end of the season as the last full day spent in that seasonal range before spending more time outside that seasonal range. We allowed seasonal ranges to shift by year as defined by grouse movements. For females whose seasonal ranges were the same, we used the average start or end date of all females for that year and seasonal range to determine the start or end date of each season per year. Therefore, in our analysis, each female had its own unique start and end date for each season per year depending on their movements. We excluded inter-seasonal movements. Based on our observations of grouse movements, we excluded the day of and the day following capture while sage-grouse were adjusting to transmitters and excluded day of mortality because transmitters may have been carried by predators and recorded locations after the grouse had already died.

We implemented Design II (population scale) and Design III (individual scale) study designs to examine sage-grouse habitat selection for breeding, summer, and winter seasons (Manly et al.

2002). We employed a use/availability design through the development of RSFs (Boyce et al. 2002, Manly et al. 2002) to examine the effect of landscape features on sage-grouse seasonal habitat selection. We modeled RSFs from a 99% dynamic Brownian Bridge Movement Model (BBMM; move R package, Kranstauber et al. 2012; R Core Team 2021) for each grouse-seasonyear with 30-m resolution to match the grid cell size of each raster used as predictor variables. We used a window size of 9 locations and a margin of 3 locations to create the dynamic BBMM (Pratt et al. 2017). We created a ratio of 15:1 random locations for each used location for the RSF. We determined the use/availability ratio by testing samples of 5, 10, 15, and 20 available locations per used locations until the coefficient estimates converged for each season; this was necessary because an adequate number of available locations must be used to compare to animal use locations in a RSF (Northrup et al. 2015). We confined random locations to inside a minimum convex polygon of either the seasonal home range for a grouse or a pooled home range across all grouse per season. We examined selection at the home range scale for each female during each season (i.e., individual scale) and the population scale where the BBMM's for each grouse were pooled across all grouse for each season and year (Manly et al. 2002, Kirol et al. 2015). The population scale, therefore, was an aggregate of the birds from the individual scale. For the population scale, we excluded four grouse during breeding and three grouse during summer whose seasonal ranges were well outside ( $\sim 20 \text{ km}$ ) of the study area because including them would include a vast area of unoccupied habitat. We excluded these females from the population level but included them in the individual scale analyses. Extensive unoccupied habitat at the population scale was not an issue for winter, so no grouse were removed from winter analyses. All grouse were included in the individual scale analysis for breeding, summer, and winter seasons.

We included biologically relevant variables that have been shown in the literature to be important for sage-grouse during each season, including natural (landscape and vegetation) and anthropogenic variables (Table 1). We digitized anthropogenic disturbance using World Imagery basemap (0.3 m resolution) within ArcGIS 10.7 (Environmental Systems Research Institute 2011). We followed the Wyoming Density Disturbance Calculation Tool (DDCT) to digitize and categorize each disturbance variable (https://ddct.wygisc.org/; accessed 14 Oct 2019). Cultivated agricultural fields were treated separately from other agricultural disturbances because grouse used agricultural fields during the summer in our study area. Agricultural structures included out buildings and general disturbance from feed lots or haystacks. Oil and gas structures included wells and general oil and gas infrastructure. We did not distinguish between oil and gas wells that were active or inactive because the priority of our study was to assess general anthropogenic disturbance on sage-grouse not specific forms or activity levels of disturbances on sage-grouse habitat selection. Major roads included paved, county gravel roads, other improved gravel roads, oil and gas access roads, railroads, and aircraft landing strips (Dinkins et al. 2014a). All roads included major roads and unimproved roads. We ignored primitive roads (i.e., two-tracks) and trails because research has shown positive associations between sage-grouse and primitive roads (Aldridge and Boyce 2007, Fedy et al. 2014, Kirol et al. 2015) possibly due to abundance of nonnative forbs (e.g., common dandelion [*Taraxacum officinale*]; Aldridge and Boyce 2007). We calculated a distance decay function at every circular scale in the form  $e^{-d/\alpha}$ , where d was the distance in meters from each pixel to every anthropogenic feature (Aldridge et al. 2012). The distance decay function scaled each variable between 0 and 1, with the highest values close to the feature of interest and allowed for nonlinearity in effects of distance to landscape features

feature (Aldridge et al. 2012). We calculated proportion of anthropogenic features within the radii for each circular scale we assessed.

We calculated soil-adjusted vegetation index (SAVI; Qi et al. 1994), which represents vegetation "greenness" from a median surface reflectance image (30-m resolution, Landsat 7 Enhanced Thematic Mapper Plus, Earth Explorer 2018). We chose imagery with less than 20% cloud cover during June 2018 and 2019 for use in breeding season analyses and August 2018 and 2019 for use in summer season analyses. This resulted in images on 8 June and 11 August 2018 and on 27 June and 14 August 2019; therefore, there were two images per season. We averaged the two June images together and the two August images together, resulting in one image to be used for breeding and summer seasons, respectively.

The scale at which variables are examined may influence the effect they have on the species being studied (Weins 1989). Therefore, we considered all variables at multiple spatial scales based on previous literature because each variable differs in the scale that's most informative for sage-grouse habitat selection (Boyce 2006). Using variables at the scale at which they make the highest contribution can produce better model results, as each variable explains species occurrence at different scales (Graf et al. 2005). These scales included circular analysis regions within 100, 200, 400, 800, 1000, 1600, and 3200 m radii (Aldridge and Boyce 2007, Fedy et al. 2014, Pratt et al. 2019, Kirol et al. 2020).

We examined the mean and standard deviation of each variable at each scale separately. We initially compared singe-variable models against a null model to evaluate individual variable

support (Pratt et al. 2019). Any variable with an Akaike's Information Criterion (AIC, Burnham and Anderson 2002) lower than that of the null model moved forward in analyses; any variable where the null model had a lower AIC was not brought forward and was no longer considered for further analysis. We also examined quadratic relationships for suitable variables where appropriate (e.g., sagebrush cover) during this step to detect any non-linear relationships that may otherwise go undetected (Doherty et al. 2010, Aldridge et al. 2012).

We checked the remaining variables for correlation, however, variables do not need to be completely independent, and multiple regression models will produce the best linear estimates of coefficients even if independent variables are correlated (McCullagh and Nelder 1989). When two variables were highly correlated (r > |6|), we chose the most predictive of the variables (i.e., the variable with the lowest AIC<sub>c</sub> in a single variable model) or the one that was most biologically relevant. Consequently, during summer, we chose sagebrush cover (SD) instead of bare ground cover (SD) because of the importance of sagebrush to sage-grouse during summer (Aldridge and Boyce 2007, Fedy et al. 2014, Kirol et al. 2015, Walker et al. 2016). During winter, we chose big sagebrush (M) and sagebrush (SD) over bare ground (M and SD, respectively) because of the importance of sagebrush cover to sage-grouse during winter (Dzialak et al. 2012, Fedy et al. 2014, Smith et al. 2016, Walker et al. 2016).

We fit a generalized linear mixed effects model (lme4 R package, Bates et al. 2015; R Core Team 2021) for each season at the individual and population scales. The response variable was binary (used or not-used) and bird-year was used as the random effect. We assessed variables independently for the natural model (vegetation and topography), anthropogenic model, and combined model (natural and anthropogenic) for each season for individual and population scales of selection. We used forward stepwise selection to assess variables in models, selecting top models based on the lowest AIC scores. We compared the top natural, anthropogenic, and combined models first. Then we compared those models together with a null model to obtain a final model for each season and scale of selection. We tested the predictive accuracy of our final occurrence models using a five-fold cross-validation for each season and scale of selection (Boyce et al. 2002). We used cross-validation to interpret the predictive ability of each RSF and to create a more reliable tool for wildlife managers (Boyce et al. 2002). Finally, we generated predictive map surfaces based on the best RSF model for each season at the population scale (e.g., Kirol et al. 2015). These maps will provide managers a means to prioritize future conservation for sage-grouse in the study area. We conducted all analyses using Program R (R Core Team 2021). We set significance at  $\alpha = 0.5$ .

# RESULTS

We monitored 82 (39 in 2018, 43 in 2019) female sage-grouse during breeding, 78 (37 in 2018, 41 in 2019) in summer, and 73 (33 in 2018, 40 in 2019) in winter. There were 69 and 54 unique bird-year combinations for the individual and population scales for breeding season, respectively. We removed 4 females resulting in 5 unique bird-year combinations from the breeding season population scale analysis because they nested far outside the study area (~20 km) and any available locations would have occurred in a large area of unsuitable habitat. There were 73 unique bird-year combinations for both individual and population scales for summer season. There were 67 unique bird-year combinations for both individual and population scales for summer season. We used 5,857, 4,192, and 9,227 days of bird locations for analyses for breeding, summer, and winter seasons, respectively. Of the 36 sage-grouse that we monitored for

3 seasons, 10 (27.8%) sage-grouse used the same winter and breeding range, 3 (8.3%) used the same summer and winter ranges, and 2 (5.6%) used the same breeding and summer ranges. One sage-grouse (2.7%) used the same range for all three seasons, 15 (41.7%) used two distinct seasonal ranges, and 20 (55.6%) used three distinct seasonal ranges.

## **Breeding Season Habitat Selection**

For breeding season, the combined model (containing natural and anthropogenic variables) outcompeted the natural, anthropogenic, and null models at both individual and population scales of selection (Table 2). Likewise, for both scales of selection, the natural model had a lower AIC<sub>c</sub> score than the anthropogenic model. The individual and population scales had similar results for variables, scales of variables, coefficient estimates and odds ratios, except that the population scale included the addition of agricultural fields (DD) at 800 m. Results of *k*-fold cross-validation indicated the averaged coefficients from breeding season models performed well at predicting selection. The Spearman's-rank correlation coefficients ( $r_s$ ) for folds k1-k5 had a mean of 0.95 for the individual scale and mean of 0.99 for the population scale, indicating these RSFs were strong, positive predictors of sage-grouse breeding season habitat selection. The predictive RSF map based on the population scale illustrated the patchiness of high and moderately high sage-grouse probability of selection during the breeding season (Figure 1).

At the population scale during the breeding season, sage-grouse selected for moderate variability in sagebrush cover. For every 1% increase in the variability in sagebrush cover, sage-grouse use decreased by 31% within 1000 m. Sage-grouse avoided bare ground, HLI, and variability in annual herbaceous cover, CTI, slope, and vegetation "greenness" (SAVI; Table 3). Odds of

selection indicated that for every 1% increase in the variability of slope, sage-grouse selection decreased by 61% within 400 m. At the population scale, for every 1% increase in the variability of annual herbaceous cover, odds of sage-grouse selection decreased by 34% within 3200 m. Sage-grouse avoided residential development, major roads and greater proportion of oil and gas and residential development during breeding (Table 3). At the population scale, the odds ratio indicated sage-grouse were 16% less likely to select an area adjacent to major roads. However, sage-grouse selected for areas closer to oil and gas and all disturbances, such that the odds ratio indicated they increased use by 22% in areas adjacent to all disturbances (within 100 m) compared to areas away from all disturbances. Individual sage-grouse were more likely to select areas closer to disturbances than the population as a whole. The odds of selection suggest that a 1% increase in the proportion of residential development decreased sage-grouse use by 38% within 3200 m and the detrimental effect of residential development on sage-grouse use was strongest during the breeding season (Figure 2).

#### **Summer Habitat Selection**

For summer, the combined model best explained sage-grouse habitat use at the individual and population scales (Table 2). The individual and population scales for summer had similar results for variables, scales of variables, coefficient estimates, and odds ratios. The Spearman's-rank correlation coefficients for folds k1-k5 had a mean of 0.95 for the individual scale and mean of 0.96 for the population scale, indicating the RSF was a strong, positive predictor of summer sage-grouse habitat selection. The predictive RSF map based on the population scale illustrated high and moderately high sage-grouse probability of selection in concentrated areas during the summer season (Figure 3).

During summer, sage-grouse selected for HLI and more variability in sagebrush cover and shrub height but avoided bare ground and steeper slopes (Table 4). At the population scale, for every 1% increase in the variability of sagebrush cover, sage-grouse selection increased by 86% within 1000 m and for every 1% increase in variability of shrub height, sage-grouse selection increased by 73% within 1600 m. During summer, sage-grouse avoided areas with a greater proportion of major roads, residential development, and agricultural fields (Table 4). At the population scale, for every 1% increase in proportion of agricultural fields, sage-grouse selection decreased by 12% within 400 m. However, as distance to agricultural fields decreased, sage-grouse probability of selection more than doubled within 3200 m (Figure 2). Sage-grouse were 22% less likely to select areas within 100 m of major roads and half as likely to select areas within 800 m of oil and gas. For every 1% increase in proportion of residential development, sage-grouse were 28% less likely to use the area within 400 m.

# Winter Habitat Selection

Similar to breeding and summer, the combined model best explained sage-grouse winter habitat selection at both the individual and population scales (Table 2). The individual and population scales for winter had similar results for variables, scales of variables, coefficient estimates and odds ratios. The Spearman's-rank correlation coefficients for folds k1-k5 had a mean of 1.00 for the individual scale and mean of 1.00 for population scale, indicating the RSF performed perfectly at predicting winter sage-grouse habitat selection. The predictive RSF map based on the population scale illustrated high and moderately high sage-grouse probability of selection concentrated in some areas and patchy in other areas during winter (Figure 4).

During winter, sage-grouse selected for shrub height and homogenous slopes and avoided variability in sagebrush cover (Table 5). For every 1% increase in variability of sagebrush cover, probability of use decreased by 28% within 100 m. During winter, sage-grouse avoided moderate shrub heights and variability in shrub heights but selected for taller shrubs. For every 1 cm increase in shrub height, sage-grouse were 2.5 times more likely to select the area within 1600 m in winter. In winter, sage-grouse selected areas closer to all roads but avoided areas with a larger proportion of major roads and all disturbances (Table 5). For every 1% increase in proportion of major roads, sage-grouse probability of use decreased by 43% within 400 m. For every 1% increase in proportion of all disturbances, sage-grouse were 7 times less likely to select the area within 800 m. Sage-grouse avoided areas closer to oil and gas and avoided areas with a high proportion of oil and gas. For every 1% increase in proportion of residential development, probability of use decreased by 27% within 400 m. However, sage-grouse were 42% more likely to select areas closer to residential development within 3200 m, indicating sage-grouse selected for areas closer to residential development than away from it but avoided areas with a higher proportion of residential development.

# DISCUSSION

Understanding habitat selection and influence of anthropogenic disturbances to sage-grouse aids wildlife managers in management and conservation planning. Resource selection functions are one tool that has been successfully used to map habitat use by sage-grouse and other species that can facilitate conservation planning (Johnson et al. 2004, Walker et al. 2016). Our primary objective was to use RSFs to model breeding, summer, and winter habitat for individual sage-
grouse as well as at the population scale. Individual and population scales were similar in natural features and anthropogenic disturbance effects on sage-grouse across all three seasons. We detected differences in habitat selection by female sage-grouse for natural and anthropogenic features during breeding, summer, and winter seasons (Doherty et al. 2010, Fedy et al. 2014). Sage-grouse have high fidelity to seasonal ranges (Berry and Eng 1985, Fischer et al. 1993) and may exhibit different types of seasonal migratory patterns (Connelly et al. 2000). Sage-grouse in our study area were partially migratory and showed fidelity to one, two, and three distinct seasonal ranges. Natural and anthropogenic variables combined showed the greatest support during all seasons and at both individual and population scales (Boyce 2006, Doherty et al. 2008). Our second objective was to create predictive probability of selection maps for each season highlighting areas of low to high probability of use. These predictive maps showed differences and similarities in areas used for each season. Knowledge about sage-grouse habitat selection during each season and the availability of probability of selection maps will aid sage-grouse habitat management.

### **Breeding Season Habitat Selection**

Sagebrush is important for sage-grouse during the breeding season for nesting and brood-rearing (Aldridge and Boyce 2007, Fedy et al. 2014, Smith et al. 2020*a*). Though sage-grouse select areas with intermediate sagebrush cover, they choose areas with heterogeneous sagebrush or shrub cover (Aldridge and Boyce 2007), avoiding dense sagebrush during the breeding season (Kirol et al. 2015). Previous studies have shown nest failure can be reduced in areas with patchy distribution of shrub cover (Aldridge and Boyce 2007) and lower variability in shrub height (LeBeau et al. 2014). However, Kirol et al. (2015) found nest survival increased with an increase

in shrub height variability. We found sage-grouse selected areas with moderate variability in sagebrush cover and selection decreased as sagebrush variability increased during the breeding season, suggesting sage-grouse selected for large areas of moderate sagebrush cover. Sagegrouse also select for areas with herbaceous cover when breeding (Aldridge and Boyce 2007, Fedy et al. 2014, Kirol et al. 2015). However, herbaceous cover did not appear in our top models because it was highly correlated with sagebrush cover, indicating the areas sage-grouse selected during the breeding season have both adequate sagebrush and herbaceous cover. Sage-grouse avoid nesting in areas with cheatgrass present and increased cheatgrass abundance (Kirol et al. 2012, Lockyer et al. 2015). Cheatgrass, an invasive annual grass, was widespread throughout our study area and contributes to habitat degradation. We found that an increase in the variability of annual grasses decreased sage-grouse probability of selection during the breeding season but annual herbaceous cover did not appear in our top model for summer or winter seasons. Mean annual herbaceous cover was highly positively correlated with sagebrush cover during the breeding season, indicating sage-grouse may be selecting areas during breeding with cheatgrass because they are selecting for other habitat characteristics. We also found sage-grouse selected areas with homogenous slopes during the breeding season, corroborating previous studies that have shown sage-grouse avoid rugged terrain and steep slopes on breeding range (Doherty et al. 2010, Fedy et al. 2014, Kirol et al. 2015, Walker et al. 2016).

Anthropogenic disturbances can influence sage-grouse breeding habitat selection through habitat loss, degradation, and fragmentation. Sage-grouse avoid areas with greater anthropogenic edge habitats during breeding and broods avoid habitats near high density urban developments (Aldridge and Boyce 2007). Sage-grouse also avoid areas near active mining disturbance (Pratt and Beck 2019) and surface disturbance from wind energy infrastructure (LeBeau et al. 2017a). Sage-grouse risk of nest failure gradually increases and brood survival decreases with increased press disturbance (Kirol et al. 2020). We found sage-grouse avoided residential development and major roads but selected areas closer to oil and gas and all disturbances during the breeding season. Most likely, sage-grouse were not selecting to be closer to these anthropogenic disturbances but instead were selecting for habitat without regard to nearby disturbances or because of the high level of habitat fragmentation, sage-grouse were not able to move far from these disturbances. Sage-grouse broods in Wyoming selected areas closer to rural homes (Dinkins et al. 2014b), though we found sage-grouse avoid residential development. Oil and gas disturbance in our study area was minimal compared to the residential development and may not have contributed to as much habitat loss and fragmentation nor have had as much of an impact on sage-grouse breeding habitat selection as did residential development. However, though sagegrouse selected for areas closer to some disturbances, these areas could be riskier leading to indirect habitat loss related to avoidance behavior of sage-grouse. Adult sage-grouse mortality increases with more disturbance from major roads during the breeding season (Pratt and Beck 2021). Aldridge and Boyce (2007) found over half of the attractive nesting habitat in their study area was considered risky and would not result in successful nests. Additionally, nests may become subjected to increased depredation near residential or urban development (Støen et al. 2010). Anthropogenic development such as powerlines provide perches and nesting sites for predators (e.g., common ravens [Corvus corax]; Steenhof et al. 1993) that can influence sagegrouse nesting and brood-rearing habitat (Dinkins et al. 2014b). Therefore, selection for all disturbances by sage-grouse during the breeding season does not indicate success or survival, though we did not estimate survival for sage-grouse in our study area.

### **Summer Habitat Selection**

During summer, many sage-grouse shift from areas dominated by sagebrush to mesic meadows with adequate forb cover (Drut et al. 1994). We found the selection of sagebrush by sage-grouse shifted from breeding to summer habitat. During breeding, sage-grouse avoided areas with greater variability in sagebrush cover and shrub height, but in summer, sage-grouse selected for these same characteristics. Female sage-grouse survival has been shown to increase with variability in shrub height (Kirol et al. 2015). Our results indicated different habitat selection during breeding and summer seasons, though other populations have shown similarity between breeding and summer habitat (Pratt et al. 2019). Sage-grouse abundance increases near mesic areas (Donnelly et al. 2016) and sage-grouse select for more mesic areas during the summer (Aldridge and Boyce 2007, Schreiber et al. 2015). Female sage-grouse and broods eat a variety of insects but forage mostly on forbs during summer (Wallestad and Eng 1975, Smith et al. 2019) and may move to summer range as vegetation dries and senesces (Fischer et al. 1996). During late brood-rearing, sage-grouse in some regions may use agricultural fields (Patterson 1952, Wallestad 1975, Connelly 1988). During summer, our results indicated sage-grouse selected for agricultural fields or areas adjacent to agricultural fields, though sage-grouse did show avoidance of areas with a greater proportion of agricultural fields and residential development. Avoiding large expanses of agricultural fields but selecting areas closer to them indicated sage-grouse were selecting agricultural fields in small quantities or near the edges. Cropland conversion occurred in the valley bottom throughout the study area and sage-grouse used these fields during the summer. Many of the agricultural fields in our study area were planted in alfalfa, indicating alfalfa fields may be important sage-grouse summer habitat in this area. However, sage-grouse also avoid anthropogenic disturbances such as areas of urban or

residential development and areas close to cultivated cropland (Aldridge and Boyce 2007, Aldridge et al. 2012, Fedy et al. 2014). Urban or residential development within sagebrushdominated areas could result in habitat loss and fragmentation. Avoidance of urban development may explain why sage-grouse avoided major roads and areas with large expanses of agricultural fields and major roads that were also associated with increased residential development. Similar to breeding season, sage-grouse avoid oil and gas or other energy infrastructure and associated surface disturbance during the summer (Kirol et al. 2015, LeBeau et al. 2017*b*) and these disturbances reduce brood survival (Kirol et al. 2020). We found sage-grouse were half as likely to use areas adjacent to oil and gas during summer as areas without oil and gas.

### Winter Habitat Selection

Sage-grouse select for sagebrush cover during the winter (Beck 1977, Robertson 1991, Fedy et al. 2014, Smith et al. 2014) as they feed almost exclusively on sagebrush leaves (Patterson 1952, Wallestad et al. 1975). We found sage-grouse avoided moderate shrub heights and variability in shrub heights indicating sage-grouse were choosing areas with taller shrubs in winter (Fedy et al. 2014, Holloran et al. 2015). Habitats with greater heterogeneity in shrub cover are considered riskier for female sage-grouse in winter (Smith et al. 2014), though sage-grouse select for less risky areas in winter (Pratt and Beck 2021). We found sage-grouse avoided variability in sagebrush cover, selecting for more homogenous sagebrush stands. Snow cover can be a major factor in determining the areas sage-grouse use during winter because of the availability of sagebrush above the snow (Beck 1977). Though we did not examine the effects of snow on sage-grouse winter habitat selection, the selection of taller shrubs indicates sage-grouse were selecting areas where sagebrush remained available above snow. Sage-grouse also select for areas with

lower slope in winter (Smith et al. 2016) and avoid rough terrain (Carpenter et al. 2010, Walker et al. 2016). We found sage-grouse selected for more homogenous slopes during all seasons but especially in summer and winter.

During winter, sage-grouse avoid areas with greater anthropogenic disturbances including roads (Carpenter et al. 2010, Dzialak et al. 2012, Fedy et al. 2014, Smith et al. 2014). We found sagegrouse decreased selection as proportion of major roads increased, indicating roads resulted in loss and fragmentation of winter habitat. Sage-grouse have also been shown to avoid energy development such that it can greatly reduce the amount of functioning habitat (Carpenter et al. 2010, Fedy et al. 2014). Loss of winter habitat within a relatively small area can cause a large decline in sage-grouse numbers (Swenson 1987). Avoidance of energy development may be a factor of high anthropogenic activity levels such that sage-grouse would spend less time near infrastructure with higher levels of activity (Holloran et al. 2015). We found sage-grouse in winter avoided areas with a high proportion of oil and gas and avoided areas closer to these wells; even though oil and gas was not a major anthropogenic disturbance in our study area. However, we found sage-grouse selected areas closer to residential development and all roads but avoided high proportions of all disturbances. Residential development and roads may have been fragmenting habitat such that residential development was close to good sage-grouse winter habitat thus sage-grouse could not avoid these anthropogenic features. Sage-grouse have relatively high survival in winter and select habitat conducive to winter survival (Dinkins et al. 2017). Though anthropogenic disturbances may not affect female survival, sage-grouse show avoidance of highly disturbed areas (Smith et al. 2014). Avoidance by sage-grouse to high

proportions of all disturbances during winter indicates anthropogenic disturbance may lead to significant winter habitat loss and fragmentation.

## Conclusion

We found sage-grouse habitat selection to be similar at the individual and population scales but differed for breeding, summer, and winter seasons. By examining each variable at several circular scales, we identified the scale for each variable that best explained sage-grouse seasonal habitat selection (Weins 1989). We considered both natural and anthropogenic features that best described sage-grouse habitat selection for all three seasons. In general, we found sage-grouse selected for low slopes and sagebrush and shrub cover variability but avoided anthropogenic disturbances such as residential development and roads, depending on the season. Sage-grouse habitat in our study area experienced loss, fragmentation, and degradation from residential development, oil and gas, cropland conversion, wildfire, invasion of non-native weeds and grasses, and other land use changes. The main form of anthropogenic disturbance in our study area was residential and agricultural development that included roads, houses, agricultural fields and associated buildings that have caused fragmentation and degradation of sage-grouse habitat. Invasive weeds, conifer encroachment, cattle grazing, and other landscape changes have contributed to habitat degradation in our study area. Our results highlighted the importance of sagebrush and shrub cover and variability, low slopes, and herbaceous cover for seasonal sagegrouse habitats. Our results highlighted the avoidance of many anthropogenic features, such as residential development, major roads and agriculture during breeding; major roads and oil and gas during summer; and oil and gas and all disturbances during winter. If development continues, sage-grouse habitat will undergo more fragmentation and loss and potentially degradation that

may have negative consequences for this population. Understanding the effect of anthropogenic disturbances on sage-grouse will be vital for conservation and management of this species in our study area.

### MANAGEMENT IMPLICATIONS

Habitat selection for sage-grouse differed by season, highlighting the need for wildlife managers to manage for diverse sagebrush habitats to meet sage-grouse requirements during breeding, summer, and winter. Large contiguous sagebrush landscapes are the most critical component of sage-grouse habitats owing to the obligate relationship between sage-grouse and this foundational shrub species. Our research indicated managers should strive to provide variability in sagebrush cover during the breeding season as well as taller sagebrush for wintering sagegrouse. Our study also confirmed at least some female sage-grouse used agricultural fields during the summer, supporting the importance of carefully implementing agricultural practices such as having and use of pesticides (Blus et al. 1989) in areas where sage-grouse access agricultural lands. Sage-grouse avoidance of anthropogenic disturbances such as major roads (Carpenter et al. 2010, Dzialak et al. 2012, Fedy et al. 2014), indicates roads should be minimized within sage-grouse breeding and winter habitat. Our study was unique among studies on greater sage-grouse (but see Aldridge et al.'s 2012 findings relative to Gunnison sage-grouse [C. minimus]) in identifying the influence of residential development on sage-grouse during breeding and summer season. In particular, sage-grouse showed the steepest drop in probability of selection for residential disturbance during the breeding season (52% decrease in use within 400 m at the individual scale), suggesting residential development may be affecting grouse during the critical nesting stage. Avoidance by sage-grouse for most anthropogenic disturbances during each season suggests the need to conserve large sections of sagebrush habitat and

minimize any future disturbances that may further reduce functional sage-grouse seasonal habitat.

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# TABLES & FIGURES

**Table 1.1.** Predictor variables used in modeling resource selection functions for greater sagegrouse during breeding, summer, and winter seasons at the individual and landscape scales in southern Montana and northern Wyoming, USA 2018–2019. Every variable was calculated at multiple circular scales within a radius of 100, 200, 400, 800, 1,000, 1,600, and 3,200 m of sagegrouse locations.

Variable	Description	Reference
Topographic		
Slope (%) <sup>a</sup>	Calculated from	Doherty et al. 2010, Fedy et al. 2014,
	<b>Digital Elevation</b>	Smith et al. 2016
	Model	
Heat load index <sup>a</sup>	Calculated from	McCune and Keon 2002
	Digital Elevation	
	Model	
Compound topographic	Calculated from	Gessler et al. 1995, Walker et al. 2016
index <sup>a</sup>	Digital Elevation	
	Model	
Vegetation		
Herbaceous or ground		
Annual grass cover (%) <sup>a</sup>	From NLCD	Kirol et al. 2012
Bare ground (%) <sup>a</sup>	From NLCD	
Herbaceous cover (%) <sup>a</sup>	From NLCD	Doherty et al. 2010, Fedy et al. 2014,
		Kirol et al. 2015
Litter cover (%) <sup>a</sup>	From NLCD	
Shrub		
Big sagebrush cover (%)"	From NLCD	D 1 1077 A11:1 1D 2007
Sagebrush cover (%) <sup>a</sup>	From NLCD	Beck 19/7, Aldridge and Boyce 2007,
Casebrack haight (ang)	Erom NI CD	Fedy et al. 2014, Donerty et al. 2010
Shrub cover (%) <sup>a</sup>	FIOIII NLCD	Fody at al. 2014 Smith at al. 2014
Shrub beight $(\%)$	FIOIII NLCD	Deherty et al. 2014, Sinth et al. 2014
Vegetation index	FIOIII NLCD	Donerty et al. 2010
Seasonal (breading	June or August	$\Omega_{i}$ at al 100/
summer) soil-adjusted	June of August Landsat 7	Qi et al. 1994
vegetation index <sup>a</sup>	reflectance image	
Anthropogenic	Terrectance infage	
Major roads <sup>b</sup>	Digitized (payed	Dzialak et al 2012 Fedy et al 2014
ingoi ioudo	and county gravel	Kirol et al. 2015
	roads)	

All roads <sup>b</sup>	Digitized	Dzialak et al. 2012, Dinkins et al. 2014,
		Fedy et al. 2014
Agricultural fields	s <sup>b</sup> Digitized	Fischer et al. 1996, Fedy et al. 2014
Oil and gas <sup>b</sup>	Digitized	Fedy et al. 2014, Kirol et al. 2015
Residential develo	opment <sup>b</sup> Digitized	Aldridge and Boyce 2007
All disturbances <sup>b</sup>	Digitized	Carpenter et al. 2010, LeBeau et al.
		2017a

<sup>a</sup> Calculated as mean and standard deviation at every circular scale. <sup>b</sup> Calculated as proportion of area and as a distance decay function at every circular scale.

**Table 1.2.** Final models predictive for resource selection for breeding, summer, and winter seasons at the individual and landscape scales for greater sage-grouse. We reported number of parameters (*K*), AIC<sub>c</sub> scores,  $\Delta$ AIC<sub>c</sub> and model weight (*w<sub>i</sub>*). Every model had bird ID as a random effect. Resource selection was modelled using a resource selection function based on female sage-grouse locations collected in Carbon County, Montana and Park County, Wyoming, USA 2018–2019.

Season and Scale and Model	K	AICc	ΔAIC <sub>c</sub>	Wi
Breeding				
Individual				
Combined	17	146258.3	0.00	1.000
Natural	11	150990.8	4732.47	0.000
Anthropogenic	8	165291.4	19033.05	0.000
Null	2	179084.7	32826.33	0.000
Population				
Combined	17	145953.0	0.00	1.000
Natural	11	150163.2	4210.21	0.000
Anthropogenic	8	165198.8	19245.76	0.000
Null	2	179084.7	33131.65	0.000
Summer				
Individual				
Combined	17	146258.3	0.00	1.000
Natural	11	150990.8	4732.47	0.000
Anthropogenic	8	165291.4	19033.05	0.000
Null	2	179084.7	32826.33	0.000
Population				
Combined	18	111138.3	0.00	1.000
Natural	11	121951.0	10812.67	0.000
Anthropogenic	10	125059.7	13921.32	0.000
Null	2	140256.5	29118.21	0.000
Winter				
Individual				
Combined	17	163786.9	0.00	1.000
Natural	11	177199.7	13412.79	0.000
Anthropogenic	9	199242.8	35455.91	0.000
Null	2	220419.0	56632.10	0.000
Population				
Combined	17	163727.7	0.00	1.000
Natural	10	178256.2	14528.50	0.000
Anthropogenic	9	199245.1	35517.40	0.000
Null	2	220419.0	56691.30	0.000

**Table 1.3.** Spatial variables for the top model predictive of breeding season resource selection at

 individual and population scales. Results based on a resource selection function using female

 sage-grouse locations collected in Carbon County, Montana and Park County, Wyoming, USA

 2018–2019.

	Scale		95% CI		Odds	95% CI	
Model and Variables <sup>b</sup>	(m) <sup>a</sup>	Estimate	Lower	Upper	Ratio	Lower	Upper
Individual							
Slope (SD)	400	-0.921	-0.899	-0.943	0.398	0.377	0.420
CTI (SD)	1000	-0.254	-0.232	-0.276	0.776	0.754	0.797
HLI (M)	1000	-0.298	-0.280	-0.316	0.742	0.725	0.760
SAVI- June (SD)	400	-0.413	-0.456	-0.370	0.662	0.705	0.619
Annual herbaceous (SD)	3200	-0.537	-0.513	-0.561	0.584	0.561	0.608
Bare ground (M)	1600	-0.589	-0.552	-0.626	0.555	0.518	0.592
Sagebrush (SD)	1000	-0.369	-0.326	-0.412	0.691	0.648	0.735
Sagebrush- quad (SD)	1000	0.135	0.168	0.102	1.145	1.111	1.178
Shrub height (SD)	800	-0.025	-0.001	-0.049	0.975	0.952	0.999
Major roads (DD)	800	-0.169	-0.151	-0.187	0.845	0.827	0.862
Oil and gas (P)	3200	-0.624	-0.567	-0.681	0.536	0.479	0.593
Oil and gas (DD)	3200	0.333	0.358	0.308	1.395	1.370	1.421
Residential develop (P)	3200	-0.527	-0.486	-0.568	0.590	0.549	0.632
Residential develop (DD)	400	-0.643	-0.606	-0.680	0.526	0.488	0.563
All disturbances (DD)	100	0.638	0.732	0.544	1.893	1.799	1.987
Population							
Slope (SD)	400	-0.961	-0.939	-0.983	0.383	0.361	0.404
CTI (SD)	1000	-0.252	-0.230	-0.274	0.777	0.756	0.799
HLI (M)	1000	-0.297	-0.279	-0.315	0.743	0.725	0.761
SAVI- June (SD)	400	-0.383	-0.338	-0.428	0.682	0.637	0.727
Annual herbaceous (SD)	3200	-0.409	-0.383	-0.434	0.664	0.639	0.690
Bare ground (M)	1600	-0.456	-0.419	-0.493	0.634	0.597	0.671
Sagebrush (SD)	1000	-0.173	-0.136	-0.210	0.841	0.804	0.878
Shrub height (SD)	800	-0.029	-0.005	-0.053	0.971	0.948	0.995
Agricultural field (DD)	800	-0.750	-0.685	-0.815	0.472	0.408	0.537
Major roads (DD)	800	-0.168	-0.150	-0.186	0.845	0.828	0.863
Oil and gas (P)	3200	-0.675	-0.618	-0.732	0.509	0.452	0.566
Oil and gas (DD)	3200	0.331	0.356	0.306	1.392	1.367	1.418
Residential develop (P)	3200	-0.472	-0.431	-0.513	0.624	0.583	0.665
Residential develop (DD)	400	-0.545	-0.508	-0.582	0.580	0.543	0.617
All disturbances (DD)	100	0.204	0.231	0.177	1.226	1.199	1.254

<sup>a</sup> Radius of circular scale for which the variable was calculated.

<sup>b</sup> Variable types were mean (M), standard deviation (SD), distance decay (DD), or proportion (P).

**Table 1.4.** Spatial variables for the top model predictive of summer resource selection at the

 individual and population scales. Results based on a resource selection function using female

 sage-grouse locations collected in Carbon County, Montana and Park County, Wyoming, USA

 2018–2019.

	Scale		95% CI		Odds 95% Cl		5 CI
Model and variables <sup>b</sup>	(m) <sup>a</sup>	Estimate	Lower	Upper	Ratio	Lower	Upper
Individual							
Slope (M)	200	-1.215	-1.250	-1.179	0.297	0.261	0.332
HLI (M)	3200	0.448	-0.477	-0.419	1.565	0.609	0.668
Bare ground (M)	3200	-0.464	-0.486	-0.442	0.629	0.607	0.650
Sagebrush (SD)	1000	0.550	-0.581	-0.519	0.577	0.546	0.608
Sagebrush- quad (SD)	1000	-0.409	0.385	0.433	1.505	1.482	1.529
Shrub height (SD)	1600	0.458	-0.476	-0.440	0.633	0.615	0.650
Agricultural fields (P)	400	-0.325	-0.342	-0.307	0.723	0.705	0.740
Agricultural field (DD)	3200	0.748	-0.781	-0.715	0.473	0.439	0.507
Major roads (P)	1000	-1.068	-1.103	-1.033	0.344	0.308	0.379
Major roads (DD)	100	-0.120	-0.144	-0.096	0.887	0.863	0.910
Oil and gas (P)	3200	0.116	0.091	0.141	1.123	1.098	1.148
Oil and gas (DD)	800	-0.539	-0.584	-0.494	0.583	0.538	0.628
Residential develop (P)	400	-0.327	-0.384	-0.270	0.721	0.664	0.778
All disturbances (DD)	1600	0.199	0.168	0.230	1.220	1.189	1.252
Population							
Slope (M)	200	-1.239	-1.274	-1.204	0.290	0.254	0.325
HLI (M)	3200	0.501	0.472	0.530	1.650	1.621	1.680
Bare ground (M)	3200	-0.339	-0.361	-0.317	0.712	0.691	0.734
Sagebrush (SD)	1000	0.621	0.590	0.652	1.861	1.829	1.892
Sagebrush- quad (SD)	1000	-0.439	-0.463	-0.415	0.645	0.621	0.668
Shrub height (SD)	1600	0.551	0.533	0.569	1.735	1.717	1.753
Agricultural fields (P)	400	-0.122	-0.140	-0.104	0.885	0.868	0.903
Agricultural field (DD)	3200	0.793	-0.826	-0.760	2.210	2.177	2.243
Major roads (P)	1000	-0.979	-1.014	-0.944	0.376	0.340	0.411
Major roads (DD)	100	-0.119	-0.143	-0.095	0.888	0.864	0.911
Oil and gas (P)	3200	0.127	0.102	0.152	1.135	1.110	1.161
Oil and gas (DD)	800	-0.617	-0.662	-0.572	0.540	0.494	0.585
Residential develop (P)	400	-0.316	-0.373	-0.259	0.729	0.672	0.786
All disturbances (DD)	1600	0.159	0.128	0.190	1.172	1.141	1.204

<sup>a</sup> Radius of circular scale for which the variable was calculated.

<sup>b</sup> Variable types were mean (M), standard deviation (SD), distance decay (DD), or proportion (P).

**Table 1.5.** Spatial variables for the top model predictive of winter resource selection at the

 individual and population scales. Results based on a resource selection function using female

 sage-grouse locations collected in Carbon County, Montana and Park County, Wyoming, USA

 2018–2019.

Model and variables <sup>b</sup>	Scale	Estimate	95% CI		Odds	95% CI	
	(m) <sup>a</sup>		Lower	Upper	Ratio	Lower	Upper
Individual							
Slope (SD)	200	-1.339	-1.366	-1.312	0.262	0.235	0.289
CTI (SD)	1600	0.179	0.161	0.197	1.196	1.178	1.214
HLI (M)	1600	-0.203	-0.489	0.083	0.816	0.530	1.102
Sagebrush (SD)	100	-0.324	-0.350	-0.298	0.723	0.697	0.749
Shrub height (M)	1600	0.922	0.904	0.939	2.514	2.497	2.532
Shrub height-quad (M)	1600	-0.282	-0.304	-0.260	0.754	0.733	0.776
Shrub height (SD)	200	-0.451	-0.476	-0.426	0.637	0.612	0.662
Shrub height-quad (SD)	200	-0.314	-0.326	-0.302	0.731	0.719	0.742
All roads (DD)	3200	0.494	0.470	0.518	1.639	1.615	1.662
Major roads (P)	400	-0.561	-0.579	-0.543	0.571	0.553	0.588
Oil and gas (P)	800	-0.147	-0.237	-0.057	0.863	0.773	0.953
Oil and gas (DD)	1600	-0.261	-0.281	-0.241	0.771	0.751	0.789
Residential develop (P)	400	-0.304	-0.353	-0.255	0.738	0.689	0.787
Residential develop (DD)	3200	0.356	0.307	0.405	1.428	1.379	1.477
All disturbances (P)	800	-1.116	-1.153	-1.079	0.328	0.290	0.365
Population							
Slope (SD)	200	-1.337	-1.364	-1.310	0.263	0.235	0.290
CTI (SD)	1600	0.188	0.170	0.206	1.207	1.189	1.224
HLI (M)	1600	-0.199	-0.217	-0.181	0.820	0.802	0.837
Sagebrush (SD)	100	-0.319	-0.344	-0.294	0.727	0.701	0.752
Shrub height (M)	1600	0.926	0.904	0.948	2.524	2.503	2.546
Shrub height-quad (M)	1600	-0.278	-0.290	-0.266	0.757	0.746	0.769
Shrub height (SD)	200	-0.450	-0.477	-0.423	0.638	0.610	0.665
Shrub height-quad (SD)	200	-0.317	-0.342	-0.292	0.728	0.703	0.754
All roads (DD)	3200	0.484	0.464	0.504	1.623	1.603	1.642
Major roads (P)	400	-0.562	-0.595	-0.529	0.570	0.537	0.603
Oil and gas (P)	800	-0.158	-0.246	-0.070	0.854	0.766	0.942
Oil and gas (DD)	1600	-0.256	-0.280	-0.232	0.774	0.751	0.798
Residential develop (P)	400	-0.305	-0.352	-0.258	0.737	0.690	0.784
Residential develop (DD)	3200	0.355	0.337	0.373	1.426	1.409	1.444
All disturbances (P)	800	-1.119	-1.156	-1.082	0.327	0.289	0.364

<sup>a</sup> Radius of circular scale for which the variable was calculated.

<sup>b</sup> Variable types were mean (M), standard deviation (SD), distance decay (DD), or proportion (P).



**Figure 1.1.** Relative probability of selection during breeding season for sage-grouse modeled using a resource selection function based on sage-grouse locations collected in Carbon County, Montana and Park County, Wyoming, USA 2018–2019. We binned probabilities of breeding habitat selection as low (0.0–0.20), moderately low (0.21–0.40), moderate (0.41–0.60), moderately high (0.061–0.80), and high (0.81–1.00).



**Figure 1.2.** Relative probability of selection for proportion of residential development during breeding, summer, and winter seasons (A) and for agricultural fields for breeding and winter seasons (B). We assessed residential development as a proportion and agricultural fields as a distance decay (DD) function. Relative probability of selection based on sage-grouse in Carbon County, Montana and Park County, Wyoming, USA 2018–2019.



**Figure 1.3.** Relative probability of selection for summer habitat for sage-grouse modeled using a resource selection function based on sage-grouse locations collected in Carbon County, Montana and Park County, Wyoming, USA 2018–2019. We binned probabilities of summer habitat selection as low (0.0–0.20), moderately low (0.21–0.40), moderate (0.41–0.60), moderately high (0.061–0.80), and high (0.81–1.00).



**Figure 1.4.** Relative probability of selection for winter habitat for sage-grouse modeled using a resource selection function based on sage-grouse locations collected in Carbon County, Montana and Park County, Wyoming, USA 2018–2019. We binned probabilities of winter habitat selection as low (0.0–0.20), moderately low (0.21–0.40), moderate (0.41–0.60), moderately high (0.061–0.80), and high (0.81–1.00).

## CHAPTER TWO: Incubation Behavior Influences Nest Survival in Greater Sage-grouse

In the format of manuscripts submitted to Ornithological Applications

# ABSTRACT

Nesting is integral to the reproductive process and incubation can be energetically costly. For Greater Sage-grouse (*Centrocercus urophasianus*), nesting is a critical stage and important vital rate that influences population dynamics. Sage-grouse exhibit low productivity that is limited, in part, by nest survival. Our objectives were to describe sage-grouse incubation behavior, examine whether sage-grouse incubation behavior influenced nest survival, and evaluate factors that influenced average recess duration, the sage-grouse incubation behavior that most influenced nest survival in our study. We used 5-min GPS locations with accelerometer data from two separate study areas: Bridger in south-central Montana, USA (2018–2019) and Red Desert in south-central Wyoming, USA (2019–2020). We used 131 nests (1557 incubation days) to describe sage-grouse incubation behavior and 118 nests (1544 incubation days) to examine nest survival and average recess duration. Bridger had lower incubation constancy, longer recess times, and greater number of recesses than Red Desert. Bridger had greater apparent nest success (44%) compared to Red Desert (29%). Adult females had higher incubation constancy but lower recess duration compared to yearling females, though number of recesses did not differ. First and renest attempts did not differ in incubation constancy, recess duration, nor number of recesses. Nest survival was best explained by weather and incubation. Average recess duration had a negative effect and average minimum temperature on the day prior to nest fate had a positive effect on risk of nest mortality. Recess duration was best explained by timing, weather, and habitat. Day of incubation and minimum temperature from the previous day had a positive effect

and sagebrush cover had a negative effect on recess duration. Understanding factors affecting nest survival is important for directing management to improve sage-grouse nest success. Knowledge of factors influencing incubation patterns helps researchers and managers understand the basics of sage-grouse nesting biology.

*Keywords: Centrocercus urophasianus*, incubation constancy, habitat, nest attentiveness, precocial, recess duration, reproduction, uniparental incubator, weather

# LAY SUMMARY

- Successful nesting is necessary to maintain Greater Sage-grouse populations and is
  influenced by factors such as incubation constancy and weather. Few sage-grouse young
  survive until breeding age, in part, due to low nest success.
- We designed our study to better understand sage-grouse nesting biology by examining the daily incubation patterns and factors that influence nest success. We used fine-scale female sage-grouse location and nest data in southern Montana and southern Wyoming.
- We found differences in incubation patterns between study areas and age groups but not nest attempts.
- Survival of nests was best explained by how much time female sage-grouse spent off nests and temperature the day before nest fate. We found the amount of time females spent off nests was best explained by ordinal day, temperature, and habitat.
- Our results refine our understanding of fundamental sage-grouse nesting biology and factors that may be important for increasing sage-grouse nest success.

### **INTRODUCTION**

For birds, reproduction is energetically costly and reproductive costs can reduce survival of parents (Martin 1987). Energetic costs during reproduction include those associated with producing eggs and raising chicks, whereas incubation and nesting are considered to be less costly (Monaghan and Nager 1997). However, nesting is integral to the reproductive process and influences population growth. Nest survival is affected by a variety of factors, including rate and duration of incubation recesses (Marasco and Spencer 2015, Shi et al. 2019), age of nest (Coates and Delehanty 2010), precipitation events, nesting attempts (Moynahan et al. 2007), predators (Ricklefs 1969, Coates and Delehanty 2010, Taylor et al. 2017), and vegetation and ground cover characteristics surrounding nests (Dinkins et al. 2016b, Holloran et al. 2005, Webb et al. 2012, but see Smith et al. 2020). Nest survival is not constant throughout incubation, but rather can decrease or increase during later stages of incubation depending on the species (Klett and Johnson 1982, Webb et al. 2012).

Birds attending nests must allocate their time between incubating and non-breeding activities, such as self-maintenance and foraging to meet their nutritional demands (Drent 1975, Marasco and Spencer 2015). Incubation itself can be energetically costly (Nord and Williams 2015, Thomson et al. 1998, Wiebe and Martin 2000) and may affect current (Monaghan and Nager 1997) and future reproductive effort (Hanssen et al. 2005). However, incubation is an important part of reproductive investment commonly overlooked in studies (Wiebe and Martin 2000). More time incubating means less time foraging and vice versa (Martin 1987), especially for uniparental incubators. Females must prioritize their own survival with that of their nest, leading to incubation strategies that represent trade-offs between predation risk and reproductive success (Lohr et al. 2020). Adult and offspring survival may be affected by efforts during nesting

(Robinson et al. 2010, Davis et al. 2014) such that mortality rates of female birds during laying and incubation may be higher than post-hatching (Angelstam 1984).

Incubation behavior includes amount of time spent on the nest but also timing, duration, and number of recesses. Incubation behavior can be affected by ambient temperature (Carroll et al. 2018, Conway and Martin 1999), precipitation (Carroll et al. 2018), clutch size (Wiebe and Martin 2000), day of incubation (Wiebe and Martin 2000), time of day (Shi et al. 2019), vegetative cover (Hoppe et al. 2019), rate of predation (Conway and Martin 2000), proximity to roads (Hoppe et al. 2019), and weight of the female going into the nesting season (Erikstad 1986). In turn, behavior can affect the length of incubation (Carter et al. 2014), nest predation (Conway and Martin 2000), and nest survival (Shi et al. 2019). For species that nest in areas with high nest predation, incubation behavior has evolved to minimize activity at the nest (Conway and Martin 2000) as incubation patterns can influence survival of adults and young (Robinson et al. 2010).

Greater Sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) is a species of conservation concern that has undergone significant population decline (Schroeder et al. 2004) and were warranted but precluded for listing in 2010 under the Endangered Species Act (U. S. Fish and Wildlife Service 2010). Sage-grouse exhibit low productivity which is limited by nest and chick survival (Taylor et al. 2012). Though nest survival is one of the three most important vital rates for sage-grouse (Taylor et al. 2012), it is variable across the species' range, estimated to be between 20–56% (see Holloran et al. 2005; Moynahan et al. 2007; Taylor et al. 2012, 2017; Webb et al. 2012, Hansen et al. 2016). Most studies on sage-grouse nesting have focused on

nesting habitat (Hagen et al. 2007, Kirol et al. 2012, Fedy et al. 2014, Dinkins et al. 2016b), habitat at successful versus unsuccessful nests (Wallestad and Pyrah 1974, Gregg et al. 1994, Sveum et al. 1998, Webb et al. 2012), and predator effects on nest survival (Coates and Delehanty 2010, Webb et al. 2012, Dinkins et al. 2016a, Taylor et al. 2017). Few studies have examined incubation behavior of sage-grouse (but see Coates and Delehanty 2010, Dudko et al. 2019) and incubation behavior effects on sage-grouse nest survival.

Sage-grouse are uniparental incubators, have low productivity, and are a species of conservation concern, making them a compelling candidate species to study incubation behavior and its effect on nest survival. Female sage-grouse must balance their own needs versus that of their eggs and nests when incubating. Sage-grouse sustain long stretches of incubation interrupted usually by two approximately 26-min crepuscular recesses from their nests per day (Coates and Delehanty 2008). Adult female sage-grouse tend to have higher incubation constancy (amount of time on the nest), are more likely to take only two recesses per day, and typically take slightly shorter recesses than yearlings (Coates and Delehanty 2008). Adult sage-grouse are also more likely to have a successful nest than yearlings (Wallestad and Pyrah 1974, Taylor et al. 2012). Differences in incubation behavior and nest success, low productivity, and sharp population declines warrant research on sage-grouse incubation behavior and how this behavior influences nest survival. The goal of our study was to better understand sage-grouse nesting biology through incubation behavior and how a female's incubation behavior may affect nest survival. Our objectives were as follows: 1) describe sage-grouse incubation behavior, including incubation constancy, number of recesses, and recess duration, 2) examine whether sage-grouse incubation behavior influences nest survival, and 3) evaluate factors that influence sage-grouse incubation behavior, specifically

the behavior that best influences nest survival. We used nesting data from two separate study areas: Bridger in south-central Montana, USA (2018–2019) and Red Desert in south-central Wyoming, USA (2019–2020). We monitored nests for survival and used GPS transmitters with accelerometer data to determine when sage-grouse were on and off their nests throughout incubation. We predicted adult sage-grouse would have higher nest survival compared to yearlings (Wallestad and Pyrah 1974, Taylor et al. 2012). We predicted successful nests would have greater cover and visual obstruction compared to unsuccessful nests (Wallestad and Pyrah 1974, Winder et al. 2016). We also predicted nest survival would decrease following precipitation events and incubation constancy would be higher on days of precipitation but lower following precipitation events (Webb et al. 2012). We expected adults to have higher incubation constancy and fewer recesses compared to yearlings (Coates and Delehanty 2008) and that incubation constancy would increase throughout incubation (Wiebe and Martin 1997, Winder et al. 2016). Lastly, we predicted greater cover or visual obstruction around the nest would increase incubation constancy (Coates and Delehanty 2008).

### **METHODS**

## **Study Areas**

The Bridger study area was located in southern Carbon County, Montana and northern Park County Wyoming, bounded by Bridger, Montana to the north and Cody, Wyoming to the south (centroid at 45.007572°N, 109.043301°W; Figure 2.1). This study area encompassed approximately 1,740 km<sup>2</sup>, with elevation ranging from 1110–1830 m above sea level. Thirtyyear averages from 1991–2020 for annual high temperature was 15.7° C, average minimum temperature –5.7° C, and average precipitation 47.1 cm (PRISM Climate Data; http://www.prism.oregonstate.edu). Much of the private land in the Montana portion of the
Bridger study area was in the process of converting from cattle grazing to anthropogenic uses, mainly consisting of houses or agricultural buildings with small areas of oil and gas field infrastructure. Federal lands consisted of 917 km<sup>2</sup> (53%), the majority of which was Bureau of Land Management administered-lands (905 km<sup>2</sup>, 52%). State lands consisted of 77 km<sup>2</sup> (4%) and private lands 741 km<sup>2</sup> (43%).

The Bridger study area was dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and basin big sagebrush (*A. t. tridentata*). Other common shrubs included black sagebrush (*A. nova*), broom snakeweed (*Gutierrezia sarothrae*), Gardner's saltbush (*Atriplex gardneri*), greasewood (*Sacrobatus vermiculatus*), rubber rabbitbrush (*Ericameria nauseosa*), shadscale saltbush (*A. confertifolia*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*). Isolated stands of juniper (*Juniperus spp.*) were found on steeper hillsides or at higher elevation. Dominant perennial grasses included blue grama (*Bouteloua gracilis*), Indian ricegrass (*Achnatherum hymenoides*), needle-and-thread (*Hesperostipa comata*), and Sandberg bluegrass (*Poa secunda*). The invasive annual, cheatgrass (*Bromus tectorum*), was abundant throughout the Bridger study area and invasive and annual field brome (*Bromus arvensis*) occurred less frequently but was also prevalent.

The Red Desert study area was located northwest of Baggs in southern Carbon and Sweetwater counties, Wyoming (centroid at 41.243677°N, 107.879613°W; Figure 2.1). Red Desert was approximately 6150 km<sup>2</sup> with elevation ranging from 1847–2773 m above sea level. Climate in Red Desert was similar to Bridger with an average annual maximum temperature of 15.0° C, average annual minimum temperature of -3.2° C, and average annual precipitation of 46.3 cm

(1991–2020; PRISM Climate Data; http://www.prism.oregonstate.edu). Within the Red Desert, federal land consisted of 5,089 km<sup>2</sup> (83%), state land 289 km<sup>2</sup> (5%), and private land 767 km<sup>2</sup> (12%). Bureau of Land Management public lands dominated this study area, consisting of 5,082 km<sup>2</sup> (83%). Oil and gas development was the main form of anthropogenic disturbance in the Red Desert study area.

The Red Desert study area was dominated by Wyoming and basin big sagebrush, black sagebrush, antelope bitterbrush (*Purshia tridentata*), broom snakeweed, Gardner's saltbush, greasewood, horsebrush (*Tetradymia spp.*), rubber rabbitbrush, and yellow rabbitbrush. A mixed shrub community including mountain big sagebrush (*A. t. vaseyana*) and Utah serviceberry (*Amelanchier utahensis*) were found at higher elevations. Dominant perennial grasses included bottlebrush squirreltail (*Elymus elymoides*), prairie Junegrass (*Koeleria macrantha*), Sandberg bluegrass, inland saltgrass (*Distichlis spicata*), and sandhill muhly (*Muhlenbergia pungens*).

# **Data Collection**

We captured female sage-grouse at leks in spring 2018–2019 in Bridger and 2019–2020 in Red Desert using spotlights and hoop-nets (Giesen et al. 1982). Female sage-grouse were also captured in summer 2018 in Bridger and winter 2019 in Red Desert near GPS-tagged birds. We fit sage-grouse with solar-powered, rump-mounted transmitters (15g-Bird Solar tag, e-obs GmbH, Grunwald, Germany with an attached 6g-VHF tag, Holohil, Ontario, Canada; total weight ~30g) programmed to record global positioning system (GPS) locations and accelerometer (ACC) data every 5 min from 0300–2300 MDT. This high frequency of location fixes (240 locations/day during incubation) provided a means for us to observe incubation

patterns and areas used during nest recesses. We determined female age (i.e. yearling or adult) during capture by examining the primary wing feathers (Braun and Schroeder 2015).

We examined each female's GPS locations weekly during the nesting season to locate nests. We looked specifically for a cluster of GPS points and female visits to the nest site during egg-laying to identify nest locations. Using GPS locations, enabled us to find nests during egg-laying or within days of the start of incubating. We also used GPS locations to determine exact start and fate date of nests and did not visit nests until after nests were completed (i.e. succeeded or failed) based on the female leaving the nest area and not returning. Using GPS locations assisted us in pinpointing exact initiation and fate dates while reducing human influence on nest survival (Webb et al. 2012). We determined fate by examining eggshell remains, with visible egg cap and detached membrane and incubation period of >24 days as signs of success (Wallestad and Pyrah 1974). A successful nest was defined as any nest where at least one egg hatched. We categorized failed nests as depredated if eggs had been removed or eggshell fragments were destroyed consistent with depredation (Wallestad and Pyrah 1974). We defined the start of incubation as the day each female sage-grouse visited her nest and stayed at the nest overnight after examining GPS locations. Incubation ended the day each female left her nest without returning. We did not include the start or end days of incubation in analyses because females started incubating and left the nest after concluding incubation at different times of the day and may or may not have had a recess on those days.

We quantified incubation patterns using GPS and ACC data. We collected accelerometer data once each 0.1 sec over a 10-sec sampling period every 5 min on X, Y, and Z axes. We used the

variance in acceleration measured over the 10-sec period along the Z-axis to quantify activity levels because this axis changed the most with bird movement. We used examination of known recess and incubation times determined through visual observations of grouse to confirm when a sample of females were on or off their nest to determine appropriate thresholds in the ACC data. We also examined distance to nest and ACC data for a separate sample of females who showed clear distinctions between incubation and recesses. From the data and visual observations, we concluded cut-offs of 400 ACC and 10-m GPS error were appropriate to identify when a female was moving off a nest. Though incubating females showed GPS error <10 m and ACC < 30, spikes in ACC occurred when females were moving at the nest, for example when turning eggs or repositioning themselves on the nest. We first determined recesses by GPS locations >10 m from the nest and when ACC was >400. Females were not always actively moving when off the nest. Therefore, the ACC variation had to be greater than 400 for the majority of the locations when off the nest. The only exception to this was during the night if females were flushed from their nest before 0500 MDT, roosted away from their nest, then returned to their nest in the morning. We used both distance from nest and ACC variation for recesses to ensure recesses were based on bird movement away from the nest and not on GPS error.

We only considered recesses that were at least 10 min long to ensure we were not inaccurately labeling recesses due to GPS error. Female grouse had to have moved at least 20 m from their nest to be considered for a recess (i.e. if our initial criteria designated several GPS locations as a recess but the female stayed within 20 m of her nest, this recess was omitted). We could not differentiate between recesses female grouse made and recesses females took because they were flushed from the nest. We determined the start time of a recess and therefore end of incubation

by the difference in time between when a female was on the nest and the subsequent location off the nest. We determined the end time of a recess and therefore start of incubation by the difference in time between when a female was off the nest and the subsequent location on the nest. For example, we calculated the median time between when incubation ended and the recess began to determine the start of the recess and the median time between when the recess ended and incubation began to determine the end of the recess.

We programmed the GPS transmitters to maximize data collection and minimize drop in battery levels because the transmitters were solar powered. When GPS battery levels dropped below the low battery threshold, GPS locations and ACC data were reduced to collection every 3 hours to conserve battery. When battery levels passed over the low battery threshold, the GPS locations and ACC data resorted back to collecting data every 5 min. To reduce time transmitters went into low battery mode, we programmed the transmitters to turn off from 2300 to 0300 MDT. However, days when GPS batteries dropped below the threshold at any point during the day, especially between 0500 and 0800 MDT when females were likely to have taken their morning recess, were removed from analysis to confirm no recesses were missed on any given day. We also removed from our analyses days when recess start or end times were unknown because transmitters were turned off for part of the day.

We examined variables that are biologically important for sage-grouse nest survival and incubation behavior for analyses (Table 2.1). For nest attempt, we examined first nests and renests (second and third nests combined) because of the small sample size of third nest attempts (n = 2). We sampled microhabitat-scale (30 m x 30 m) or third-order habitat selection (Johnson

1980) vegetation characteristics at each nest including shrub cover, herbaceous cover, ground cover, and visual obstruction. For each plot, we collected vegetation measurements along four, 15-m transects radiating out in cardinal directions from the center of each plot. At each plot we measured biologically relevant variables important for sage-grouse during the breeding season (Table 2.1). We used the line intercept method across all 4 transects resulting in 60 m total for each nest to estimate shrub canopy cover by species (Canfield 1941). We measured visual obstruction by averaging 26 Robel pole readings per nest, taking two readings at 5, 10, and 15 m in each cardinal direction from plot center and two readings at plot center (Robel et al. 1970). We recorded Robel pole readings in two directions opposite each other along the transect lines. We assessed herbaceous and ground cover within 17, 0.1-m<sup>2</sup> (20 x 50 cm) Daubenmire quadrats spaced 1, 3, 7.5, and 12.5 m away from the nest along all transects and one at the nest (Daubenmire 1959). We defined percent cover within each Daubenmire quadrat using cover classes 1 = 0-1%, 2 = 1.1-5%, 3 = 5.1-25%, 4 = 25.1-50%, 5 = 50.1-75%, and 6 = 75.1-100%. We tabulated forb species richness as the number of species of forbs found in each plot. More detail about methodology to collect microhabitat vegetation data information at each location are found in Kirol et al. (2012), Dinkins et al. (2016), and Gelling et al. (2022).

We obtained habitat characteristics beyond microhabitat surrounding the nest site from the National Land Cover Database (Multi-Resolution Land Characteristics Consortium 2016, Rigge et al 2019, Rigge et al 2020). We reasoned it was important to include habitat variables surrounding the nest in addition to the microhabitat at the nest site determined by vegetation sampling because females utilized a larger area than their nest site during incubation (e.g., when on recesses). We calculated mean bare ground and herbaceous, litter, sagebrush, and shrub cover,

and height of sagebrush and shrubs at 30, 50, 100, 200, 400, 600, 800, and 1000 m radii circles surrounding each nest. We chose these scales because all females traveled less than 1000 m on their recesses with mean distance of 225 m and 95% of the distances females traveled were within 437 m of the nest (Figure 2.2). Using scales within the distance females traveled from their nest on recesses assisted us in capturing the habitat within the complete area utilized by females during nesting.

We obtained weather data from two separate weather stations closest to Bridger (Bridger 2 N, MT, 45.32610° N -108.90910° W and Clark 3 NE, WY 44.93651° N -109.13736° W) and Red Desert (Baggs, WY 41.0383° N -107.6577° W and Sage Creek Basin, WY 41.40000° N - 107.26000° W) study areas (National Center for Environmental Information 2021). We matched each day of average precipitation, average maximum temperature, and average minimum temperature to incubation day for each nest. We also included the previous day's precipitation, minimum temperature, and maximum temperature because previous studies have found that precipitation events from the previous day decreased daily nest survival for sage-grouse (Moynahan et al. 2007, Webb et al. 2012).

From the start and end times of recesses, we calculated the duration of each recess, start time of each recess, total number of recesses, total recess duration, and number of trips to and from the nest for each nest and each incubation day. We also calculated incubation constancy (percent of time each female spent incubating per 24 hours) for each nest for each day (Coates and Delehanty 2008). We determined ordinal date (number of days elapsed since Jan 1to the date of

incubation used in analyses) and the day of incubation (number of days elapsed since the initiation of incubation; Coates and Delehanty 2008).

### **Statistical Analyses**

We used an information-theoretic approach using Akaike's information criterion for small samples (AIC<sub>c</sub>, Anderson and Burnham 2002) to develop predictive model hypotheses for nest survival and recess duration. We examined variables important for sage-grouse nest survival and incubation behavior including female age, nest, timing, incubation, weather, and habitat (Table 2.1).

We checked all variables used in each model for potential outliers (Hosmer and Lemeshow 2000). We removed one outlier for one day when a female displayed 76% incubation constancy at the start of incubation. We found females with successful nests exhibited unusual incubation behavior the day before leaving the nest with a successful brood. Of 30 successful nests for which we had the second-to-last day of incubation behavior, we found in 70% (n = 21) of nests that females showed higher incubation constancy (mean = 98.6%, range = 96.8–99.3%) compared to the average incubation constancy of all days from all nests (mean = 96.5%, range = 76.4–99.3%). The day before leaving a successful nest, 70% of females only took one morning recess and skipped the evening recess as the eggs were hatching. We therefore censored the last day of incubation for successful nests, or incubation day 26 for nests where the female left on day 27 (n = 16 nests) or incubation day 27 for nests where the female left on day 28 (n = 14 nests).

We checked all variables for collinearity by using a Pearson correlation matrix—any variable with a correlation coefficient greater than r = |0.6| or variance inflation factor (VIF) coefficient greater than 3 was removed (Menard 1995). We also examined each variable in a single variable model against a null model. When two variables were correlated, we retained the variable with the lower AIC<sub>c</sub> score. We evaluated quadratic forms of variables for shrub cover and visual obstruction. We considered variables to be biologically and scientifically significant when 95% confidence intervals did not overlap zero. We used AIC<sub>c</sub> to evaluate support for the top models (Burnham and Anderson 2002). We conducted all analyses using Program R (R Core Team 2020).

We described incubation behavior (i.e., incubation constancy, average recess time, and number of recesses) by study area, female age, and nest attempt using Welch tests (function *welch.test*, package *onewaytests*, Program R, Dag et al. 2018; R Core Team 2020), which is an alternative to an ANOVA for data with unequal variances. We also performed Games-Howell tests (package *rstatix*, Program R, Kassambara 2021; R Core Team 2020) to evaluate whether differences were significant. We set statistical significance at alpha = 0.05.

We modeled nest survival by examining the risk of nest mortality using Cox's proportional hazards regression (Cox 1972) using function *coxph* (package *survival*, Program R, Therneau 2020; R Core Team 2020). We only used nests with >1 day of incubation data in nest survival models. We first examined random effects to be included in a base model, including female age, nest attempt, study area, and year by comparing single variable models and models with combinations of these variables. The top model served as our base model. We next examined

incubation, weather, and habitat hypotheses individually and combinations of each that had potential to influence nest survival (Table 2.1). We included variables previously found in the literature to influence sage-grouse and similar species nest survival, including weather (Moynahan et al. 2007, Webb et al. 2012, Dinkins et al. 2016), habitat (Wallestad and Pyrah 1974, Gregg et al. 1994, Webb et al. 2012, Winder et al. 2016), and incubation patterns (Winder et al. 2016, Hoppe et al. 2019, Shi et al. 2019). For each hypothesis, we included variables from the base model. We started by comparing single-variable models for each predictor and dropped any variables that did not outcompete the base model. Finally, we used forward stepwise selection (package *MASS*, Program R, Venables and Ripley 2002; R Core Team 2020) to determine the top model for each hypothesis if more than one variable remained after initial variable screening.

Our third objective was to evaluate the factors that influenced incubation behavior that most affected nest survival. We found average recess duration to be the top incubation variable for nest survival, though average recess duration was negatively correlated with incubation constancy for nest survival (r = -0.8). We modelled daily average recess duration (i.e. the average amount of time a female spent on her recesses per day and was therefore not incubating) using a generalized linear mixed effects model with gamma distribution (package *lme4*, Program R, Bates et al. 2015; R Core Team 2020). We only used nests with >1 day of incubation data in recess duration models. We examined timing, weather, and habitat hypotheses individually and combinations of each that had potential to influence average recess duration (Table 2.1). We first examined variables and random effects to be included in a base model for average recess durations

of these variables and determining the base model based on the model with the lowest  $AIC_c$ score. We next compared single-variable models for each predictor for each hypothesis and dropped any variables that did not outcompete the base model. We used forward stepwise selection to determine final models for each hypothesis for average recess duration if more than one variable remained after initial variable screening. Finally, we compared all top models in each hypothesis set.

# RESULTS

We collected data at 162 nests (Bridger, n = 86; Red Desert, n = 76), however, we monitored and completed vegetation surveys at 157 nests (Bridger, n = 81, Red Desert, n = 76; 5 nests were not surveyed due to logistical constraints). At Bridger, 38 nests were successful (44%) and 48 failed (56%) and at Red Desert, 22 nests were successful (29%) and 54 failed (71%). There were 69 first nest attempts (80%) and 17 second attempts (20%) at Bridger. At Red Desert there were 58 first attempts (76%), 16 second attempts (21%), and 2 third attempts (3%). At Bridger, 30/69 first nesting attempts were successful (44%) while 39 failed (57%) and 8/17 second attempts (47%) were successful while 9 failed (53%). At Red Desert, 16/58 first nesting attempts were successful (28%) and 42 failed (72%), whereas 4/16 second attempts (25%) were successful and 12 failed (75%). Both third attempts in Red Desert were successful (100%). We removed from our analyses nests where microhabitat data were not collected, nests that failed during egglaying, and nests that failed the day incubation started, resulting in 131 nests used for analyses.

We used 131 nests and 1557 days of incubation data to examine our first objective of describing sage-grouse incubation behavior. Recesses followed a relatively bimodal pattern with the majority of recesses occurring in the morning and evening (Figure 2.3). Incubation constancy

 $(F_{1,1513.5} = 20.22, n = 1557, P < 0.001)$  was lower in Bridger compared to Red Desert. Average recess time  $(F_{1,1458.9} = 7.76, n = 1557, P = 0.005)$  and number of recesses  $(F_{1,1450.9} = 12.83, n = 1557, P < 0.001)$  were greater in Bridger compared to Red Desert. Females in Bridger had a mean incubation constancy of 96.1% (range = 76–99%) and females in Red Desert had a mean incubation constancy of 96.4% (range = 76–99%). Bridger females had an average recess time of 27.7 min (range = 10–165 min) while females in Red Desert had an average recess time of 26.2 min (range = 10–165 min). Bridger females also had on average 2.1 recesses (range = 1–4) per day, which was more than Red Desert females who had on average 1.9 recesses (range = 1–7) per day. Though Bridger females had lower incubation constancy and greater recess duration and number of recesses, nest survival was greater in Bridger (44% of nests were successful) than Red Desert (29% of nests were successful).

Incubation constancy ( $F_{1,332.4} = 11.45$ , n = 1557, P < 0.001) and average recess time ( $F_{1,329.9} = 17.23$ , n = 1557, P < 0.001) differed between adult and yearling females. Incubation constancy was 96% (range = 76–99%) for adult females and 96% (range = 82–99%) for yearlings (Figure 2.4). Adult females had an average recess time of 26.6 min (range = 10–170 min) and recesses for yearling females were 3.2 min longer (mean = 29.8 min; range = 15–130 min). Average number of recesses did not differ between adult females with 2.0 recesses (range = 1–4) per day ( $F_{1,343.8} = 0.14$ , n = 1557, P = 0.71). Incubation constancy was 96% (range = 76–99%) for first attempts and did not differ from incubation constancy for renest attempts at 96% (range = 77–99%;  $F_{1,686.9} = 2.32$ , n = 1557, P = 0.13; Figure 2.4). Average recess time was 27.0 min (range = 10.0–170.0 min) for first attempts and 27.4 min (range = 15.0–112.0 min) for renest attempts; recess times for first and renest

attempts did not differ ( $F_{1,862.7} = 0.50$ , n = 1557, P = 0.48). Average number of recesses did not differ between first (mean = 2.0, range = 1–4 recesses) and renest attempts (mean = 2.1; range = 1–5;  $F_{1,602.6} = 2.65$ , n = 1557, P = 0.10).

#### **Nest Survival**

We examined nest survival for 118 nests (1,544 incubation days); we only examined nests with >1 day of incubation data. Overall nest success was 57% for adults and 50% for yearlings but varied by study area (Figure 2.5). In Bridger, 52% of nests initiated by adults (n = 47) were successful and 64% of nests initiated by yearlings (n = 14) were successful compared to 35% of nests initiated by adults (n = 49) and 25% of nests initiated by yearlings (n = 8) in Red Desert. We examined study area, year, female age, and nest attempt as variables and combinations of these variables for the base model. The model with the lowest AIC<sub>c</sub> score included only study area, therefore the final base model for nest survival included study area as a variable. We examined ordinal day and its quadratic effect but found neither of these variables outcompeted the base model and were therefore not brought forward in analysis.

Average total recess duration was correlated to average recess duration and average incubation constancy (r = 0.8). Average incubation constancy was negatively correlated with average recess duration (r = -0.8). We chose average recess duration to move forward in analysis because when comparing all three variables in single-variable models, average recess duration had the lowest AIC<sub>c</sub>. After initial variable and correlation screening, average recess duration was the only variable that remained. The top model for incubation effects on nest survival when combined with the base model included average recess duration (Table 2.2). No other models were within 2

 $\Delta AIC_c$  of the top model for incubation. Average recess duration was significant and had a positive coefficient, indicating nest failure increased with longer recesses (Table 2.2).

We found no precipitation variables outcompeted the base model, therefore none were brought forward in analysis. Average maximum temperature from the previous 7 days and average minimum temperature from the day prior to nest fate were the top temperature variables that were brought forward. However, the two temperature variables were highly correlated (r = 0.8). Average minimum temperature from the day prior to nest fate had the lowest AIC<sub>c</sub> when comparing these two variables in single-variable models and was therefore brought forward. There was only one top model for weather effects on nest survival that included average minimum temperature from the day prior to nest fate (Table 2.2). Average minimum temperature from the day prior to nest fate had a significant negative effect on risk of nest mortality, indicating nest survival increased with higher minimum temperatures (Table 2.2).

Forb cover and forb species richness were the only habitat variables that outcompeted the base model and were brought forward in nest survival modeling. The resulting final model for habitat effects on nest survival included forb cover (Table 2.2). Forb cover had a negative coefficient, however, this variable was not considered informative for nest survival (P > 0.05; Table 2.2). The lack of support for habitat variables including forb cover in the top model suggest habitat was not informative for sage-grouse nest survival.

All hypothesis models (i.e. top models for incubation, habitat, and weather and combinations of the top models) outperformed the base model for nest survival. When examining all the models

for each hypothesis on nest survival, the model that best explained nest survival included weather and incubation (Table 2.3). The next best model included incubation, weather, and habitat, and had an AIC<sub>c</sub> score that was 0.55 away from the top model. The top model included average minimum temperature from the day prior to nest fate, average recess duration, and study area. Average minimum temperature had a negative effect on the risk of nest mortality while average recess duration had a positive effect on the risk of nest mortality (Figure 2.6). Sagegrouse nests were more likely to fail when the females spent more time off their nests on recesses. Nest survival was higher when minimum temperature increased. The second-best model contained the same variables in addition to forb cover, however, habitat did not influence sage-grouse nest survival.

# **Average Recess Duration**

We examined average recess duration for 118 nests (1,544 incubation days); we only examined nests with >1 day of incubation data. The final base model for average recess duration included female age and study area as variables and nest ID as a random effect. All temperature variables were positively correlated with each other (r > 0.7), therefore we compared all temperature variables in single-variable models to determine that average minimum temperature from the previous day would move forward in analysis. Using forward stepwise selection, we found the top weather model only included average minimum temperature from the previous day (Table 2.4). The next variable added to the model, average precipitation, did not improve model fit (i.e.  $\Delta AIC_c < 2$ ). Sage-grouse spent less time on recesses when average minimum temperature from the previous day increased.

The top model for timing effects on average recess duration included day of incubation (Table 2.5). The next closest model that included ordinal date was more than 2  $\Delta$ AIC<sub>c</sub> from the top model. Day of incubation had a negative effect on average recess duration (Table 2.4). The farther into incubation for a given nest, the less time females spent on recesses and more time incubating.

For habitat effects on average recess duration, we examined microhabitat surrounding the nest and habitat surrounding the nest area. Shrub cover and sagebrush cover were positively correlated (r = 0.7), but shrub cover outperformed sagebrush cover with the lowest AIC<sub>c</sub> score. Litter was negatively correlated to bare ground (r = -0.8) and positively with visual obstruction (r = 0.6), but visual obstruction had the lowest AIC<sub>c</sub> score of the three variables. After initial screening, we brought shrub cover, perennial grass cover, and visual obstruction forward in analyses. Of the habitat variables considered at different scales, herbaceous cover at 200 m, bare ground cover at 30 m, litter cover at 30 m, sagebrush cover at 30 m, sagebrush height at 50 m, shrub cover at 30 m, shrub height at 30 m, shrub cover (microhabitat), perennial grass cover (microhabitat), and visual obstruction outcompeted all other scales and the base model. Most of the sagebrush and shrub variables were correlated, so we compared all the shrub and sagebrush variables in single-variable models and brought forward the one with the lowest  $AIC_c$  score (i.e. sagebrush cover at 30 m). After reducing variables that were correlated or non-informative, shrub cover, perennial grass, herbaceous cover at 200 m, and sagebrush cover at 30 m were considered in the final habitat model. The top habitat model only included sagebrush cover at 30 m; no other variables improved model fit. Sagebrush cover at 30 m was positively associated

with average daily recess duration, indicating that females spent more time on their recesses with increased sagebrush cover within 30 m of the nest (Table 2.4).

When comparing every hypothesis model (i.e. timing, weather, habitat, and combinations thereof) for effects on average daily recess duration, the model that had the most support ( $w_i = 0.50$ ) included timing, weather, and habitat variables (Table 2.5). One other model was within 2  $\Delta$ AIC<sub>c</sub> of the top model, which included timing and habitat and also had good support ( $w_i = 0.48$ ). In the top model, sagebrush cover at 30 m had a positive association, whereas day of incubation and average minimum temperature from the previous day had a negative association with average daily recess duration (Figure 2.7). Recess duration increased with an increase in minimum temperature from the previous day, though minimum temperature from the previous day was not informative (P > 0.05). Recess duration decreased as incubation progressed indicating that females spent more time on their nests as hatching drew closer. However, recess duration increased with sagebrush cover within 30 m of the nest, indicating cover at the nest influenced sage-grouse incubation behavior.

# DISCUSSION

Nesting is integral to the reproductive process for sage-grouse and success is affected by a variety of factors. We described nest survival and incubation patterns, examined factors that influence nest survival and factors that influence recess duration for sage-grouse using data from study areas in southcentral Montana and southcentral Wyoming. The nesting process is a critical stage in reproduction for sage-grouse and an important vital rate that influences population dynamics (Taylor et al. 2012). We found that weather and incubation patterns were the driving predictors of nest survival, specifically, average minimum temperature the day prior to nest fate

and average recess duration. When we examined the factors that influence average recess duration, we found weather, timing, and habitat were the driving predictors, specifically, day of incubation and sagebrush cover within 30 m of the nest. Examining nest survival and incubation patterns provides a comprehensive view of sage-grouse nesting and factors that influence this important stage for sage-grouse.

Nest survival can vary depending on population and female characteristics. Adult sage-grouse nest earlier than yearlings (Schroeder 1997) and have a season of nesting experience under them that may make them more likely to be successful. Adult sage-grouse have greater nest success than yearlings (Wallestad and Pyrah 1974, Taylor et al. 2012), but this may change depending on the population as nest success in a population in Washington state did not differ by female age (Schroeder 1997). Our data shows that nest success for adults was higher than for yearlings in Bridger but not Red Desert and Bridger had higher nest success overall than Red Desert. Therefore, nest success by age group may vary by population.

Weather events like rainfall can have effects on sage-grouse nest survival. Research has shown daily sage-grouse nest survival decreases the day after precipitation (Moynahan et al. 2007, Webb et al. 2012) but increases on days with precipitation (Moynahan et al. 2007). Moynahan et al. (2007) hypothesized that nest survival is better on days with precipitation because predators are less likely to be out, and nest survival decreases after precipitation because predators are more likely to be active and sage-grouse are more likely to be off their nests. However, we did not find precipitation to have an effect on nest survival. Sage-grouse prefer to locate their nest in

areas that provide concealment from predators but these locations may not be suitable for concealing their nests from olfactory-oriented predators (Conover et al. 2010). It may be that populations or geographic areas differ in how precipitation effects nest survival or that other factors like abundance and type of predators affects nest survival more than precipitation. Some bird species reduce the time they are off their nests during heavy rain events (Afton 1980) while others increase the number of recesses as daily precipitation increases (Carroll et al. 2018). Our results differ from these findings in that we found precipitation did not have an effect on recess duration though minimum temperature did. Temperature also has an effect on nest survival. Sage-grouse nests exposed to cooler temperatures prior to the nesting season and higher temperatures the week before nest fate had greater survival (Dinkins et al. 2016a). We found minimum temperature the day prior to nest fate to have a positive effect on nest survival in that as the minimum temperature increased, risk of mortality decreased. Minimum temperature from the previous day affected recess duration such that recess duration was reduced as temperatures from the previous day increased, though this was not significant. As the breeding season progresses, minimum daily temperatures will steadily increase, meaning nest survival could be a factor of increasing temperatures as the season progresses because successful nests are likely to continue past the date that other nests fail. However, minimum temperatures as a proxy for time of season is unlikely because ordinal date of nest initiation did not improve model fit. More research on temperature effects on sage-grouse nest survival is warranted as overall temperatures increase in the future due to climate change.

Incubation patterns change over the course of incubation and may be related to female age. Number of recesses increased but recess duration decreased in White-tailed Ptarmigan (*Lagopus*  *leucura*) over the course of incubation (Wiebe and Martin 1997). Yearling sage-grouse in northeastern Nevada took shorter recesses in mid-incubation (days 15–31) and longer recesses earlier and later in incubation, compared to adults whose recess duration did not significantly change during incubation (Coates and Delehanty 2008). We found that as incubation progressed, females spent less time on recesses and more time incubating, highlighting a shift in incubation patterns during nesting. Spending more time on the nest as incubation progresses could be an indication that females are more devoted to their nests' success, especially after the possibility of renesting has passed. Our results also indicated recess duration had a positive effect on nest survival in that longer recesses improved nest survival. Female grouse in Bridger had longer recess times and more recesses compared to females in the Red Desert and nest survival was greater in Bridger than Red Desert. However, the effect of incubation patterns for grouse and similar species varies. Nest survival has been shown to be higher for female Greater Prairie-Chickens (Tympanuchus cupido) who took fewer recesses per day (Winder et al. 2016) but a separate study showed that recess duration and frequency did not differ between successful and unsuccessful nests (Hoppe et al. 2019). For Chinese Grouse (Tetrastes sewerzowi), recess duration was longer and number of recesses greater for successful nests compared to unsuccessful nests (Shi et al. 2019). Our results suggested incubation patterns for sage-grouse may vary by population and factors affecting nest survival.

Incubating sage-grouse females show incubation patterns that are trade-offs between their own and their nest's survival (Lohr et al. 2020). Morning recesses are shorter than evening recesses in some species, including sage-grouse (Naylor et al. 1988, Coates and Delehanty 2008, Dudko et al. 2019, Shi et al. 2019) and recesses taken earlier in the year are shorter than during later dates (Coates and Delehanty 2008). Recess patterns and duration also differ between adult and yearlings, yearlings often supplementing the bimodal recess pattern typical of sage-grouse with irregular daytime recesses and longer recess times (Coates and Delehanty 2008). We found adults had shorter recess times and greater incubation constancy than yearlings. However, we also found that adults and yearlings did not differ in the number of recesses they took, contrary to a previous study showing sage-grouse yearlings took more recesses than adults (Coates and Delehanty 2008). Differences between adult and yearling sage-grouse incubation patterns may be related to experience, female weight, and the need for females to acquire enough food and energy before and during the nesting season. Adults typically go into the nesting season with higher weights and a season of nesting experience and therefore can have higher incubation constancy and spend less time on recesses compared to yearlings.

Habitat modeling suggests mixed results for sage-grouse nest survival and incubation patterns. Vegetation surrounding sage-grouse nest sites has been shown to influence nest survival in some studies (Holloran et al. 2005, Webb et al. 2012, Dinkins et al. 2016b) but not others (Smith et al. 2020). As Smith et al. (2020) suggests, sage-grouse select nest sites in areas that are slightly shrubbier but otherwise not particularly different from available habitat. However vegetation did not influence sage-grouse nest survival in our study. Other species, like Northern Bobwhite (*Colinus virginianus*), also show similar vegetative characteristics between successful and unsuccessful nests (Carroll et al. 2015) or no effect of habitat on nest success (Carroll et al. 2018). Our results agree with the finding that habitat does not play a role in sage-grouse nest survival; however, our results indicated weather and incubation patterns as the factors influencing nest survival. Habitat did, however, influence recess duration in our study,

specifically sagebrush cover within 30 m surrounding a nest. Greater sagebrush cover surrounding a nest resulted in incubating female sage-grouse spending more time on their recesses. Coates and Delehanty (2008) found sage-grouse spent less time away from their nest as visual obstruction at the nest increased, however we did not find any influence of visual obstruction on recess duration. Habitat may, therefore, influence sage-grouse incubation patterns in different ways throughout their range and other factors like predators may be more influential in sage-grouse nest success than habitat.

Predation is the greatest mortality factor for game species (Ricklefs 1969) and is the most significant factor causing sage-grouse nest mortality (Webb et al. 2012). Sage-grouse nest predators include Common Raven (Corvus corax; Coates and Delehanty 2008, Dinkins et al. 2016a), coyote (Canis latrans; Taylor et al. 2017), and American badger (Taxidea taxus) among other animals (Coates and Delehanty 2008). Sage-grouse nest in areas with lower densities of avian predators (Dinkins et al. 2012) and in areas that are obscured from visual predators (Conover et al. 2010). Still, incubation patterns may be influenced by the predators around sagegrouse nests. For instance, raven abundance affects sage-grouse recess duration by reducing recess duration in areas with greater raven abundance (Coates and Delehanty 2008). Raven predation occurs diurnally (Coates and Delehanty 2008), so sage-grouse may limit the time they spend away from their nest when ravens are more likely to be active. The majority of sagegrouse fly when leaving their nest for a recess but may walk or fly back to their nest at the end of a recess (Dudko et al. 2019). Flying may alert predators to the location of sage-grouse nests, such that females in populations that differ in types and abundance of predators may also differ in their incubation patterns. The presence of predators, such as ravens, may explain why Red Desert

females experienced shorter recess duration and number of recesses compared to females in Bridger. However, we did not examine predator influences on nest survival or recess duration. Predator influences on sage-grouse nesting behavior should be further examined, especially for populations where predators are abundant.

We examined factors affecting nest survival and incubation patterns in Greater Sage-grouse, a ground-nesting bird of conservation concern. Understanding factors affecting nest survival is important for directing management to improve sage-grouse nest success, especially in areas where nest success may be lower. We found that weather and incubation patterns influenced sage-grouse nest survival and not habitat. Nest predators may also influence nest success but their effects were not considered in our study. Knowledge about incubation patterns and the factors influencing these patterns helps researchers and managers understand the basics of sagegrouse and similar species nesting biology. Our results indicate sage-grouse incubation patterns were influenced by weather, timing, and habitat. Managers can alter sagebrush cover, for instance, but not weather patterns that influence recess duration for sage-grouse. Wildlife biologists should identify the important parameters influencing sage-grouse nest survival in their area to guide management and conservation actions. Discrepancies between studies on the importance of habitat variables and few studies focused on the influence of predators warrant further research on sage-grouse nest survival and incubation patterns in relation to habitat and predators.

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### **Ethics statement**

All capture, handling, and post-release monitoring of sage-grouse for the Bridger Study Area followed protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (protocols No. 20180102JB00289, -01 and -02) and Montana Fish, Wildlife & Parks Scientific Collector's Permit (No. 2018-072-W and No. 2019-039-W). Capture, handling, and post-release monitoring of sage-grouse in the Red Desert Study Area followed protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (protocols No. 20170324AP00266 -01, -02, -03, and -04) and Wyoming Game and Fish Department Chapter 33-1160 permit.

### **Author contributions**

Erin L. Gelling, ELG; Aaron C. Pratt, ACP; Jeffrey L. Beck, JLB; Caitlyn P. Wanner, CPW. ACP and JLB conceived research ideas and study design, and supervised research. ELG and CPW collected data. ELG, ACP, and JLB developed or designed methods. ELG analyzed the data. ELG wrote the paper. JLB and ACP edited the manuscript. JLB contributed substantial material, resources, or funding.

# Data availability

Data available upon request from the authors.

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# **TABLES & FIGURES**

Table 2.1. Variables considered in recess duration (R) and nest survival (N) modeling. Variables

were screened for correlation and variance inflation factors before building initial models.

Incubation constancy and daily nest survival were examined at Greater Sage-grouse nests in

Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020.

Variable	Model	Description
Female age	R, N	Yearling or adult
Nest		
Attempt	R, N	First nest or renest
Timing		
Day of incubation	R	Day since the start of incubation
Ordinal day <sup>a</sup>	R, N	Day since 1 January of that year
Incubation		
Incubation constancy	Ν	Percentage of time the female was on the nest per day
Average recess duration (mins)	Ν	Minutes per day
Total recess duration (mins)	Ν	Minutes per day
Number of recesses (no.)	Ν	Total number of recesses per day
Weather <sup>b</sup>		
Average precipitation (cm) <sup>c</sup>	R	Average daily precipitation
Average max temp (°C) <sup>c</sup>	R	Average maximum daily temperature
Average min temp (°C) <sup>c</sup>	R	Average minimum daily temperature
Habitat		
Bare ground (%) <sup>d</sup>	R, N	Mean bare ground cover from Daubenmire quadrats and NLCD
Sagebrush cover (%) <sup>d</sup>	R, N	Sagebrush cover from line intercept and NLCD
Shrub cover (%) <sup>d</sup>	R, N	Shrub cover from line intercept and NLCD
Visual obstruction (dm)	R, N	Visual obstruction estimated from Robel pole
Annual grass (%) <sup>e</sup>	R, N	Mean annual grass cover from Daubenmire quadrats
Perennial grass (%)	R, N	Mean perennial grass cover from Daubenmire quadrats
Residual grass (%) <sup>f</sup>	R, N	Mean residual grass cover from Daubenmire quadrats
Litter (%) <sup>d</sup>	R, N	Mean litter cover from Daubenmire quadrats and NLCD
Cactus (%)	RΝ	Mean cactus cover from Daubenmire quadrats
Biocrust (%)	R N	Mean biological soil crust from Daubenmire quadrats
Forb (%)	R N	Mean forb cover from Daubenmire quadrats
Forb species richness (spp. no.)	R. N	Forb species richness from Daubenmire quadrats
Herbaceous cover (%) <sup>d</sup>	R. N	Mean herbaceous cover from NLCD
Sagebrush height $(dm)^d$	R. N	Mean sagebrush height from NLCD
Shrub height (dm) <sup>d</sup>	R. N	Mean shrub height from NLCD

<sup>a</sup> For nest survival models, ordinal day was the day of nest initiation.

<sup>b</sup> Climate data from two nearby weather stations to each study area from National Center of Environmental Information (National Center for Environmental Information 2021).

<sup>c</sup> Weather variables were calculated for the day of nest fate, previous day prior to nest fate, mean for 2 days prior to and including nest fate, mean for 7 days prior to and including nest fate, and the month of April of the year the nest was initiated.

<sup>d</sup> Habitat data for 30, 50, 100, 200, 400, 600, 800, and 1000 m radii circles surrounding each nest calculated using National Land Cover Database data.

<sup>e</sup> Annual grass consisted of mostly cheatgrass with some (<5%) field brome (*B. arvensis*).

<sup>f</sup>Residual grass was defined as the standing, dead perennial grass leaves from the previous year.

Table 2.2. Top models for weather, incubation, habitat, and combinations on risk of nest mortality for sage-grouse survival models. Every model included study area as a variable.
Variables within each model, coefficients, standard errors (SE) and *P*-values are shown. Models based on data from sage-grouse nests in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020.

Model	Variables	Coefficient	Hazard Ratio	SE	P-value
Incubation					
	Average recess duration	0.051	1.053	0.019	0.005
Weather					
	Average minimum temperature	-0.279	0.756	0.043	0.000
	(previous)				
Habitat					
	Forb cover	-0.032	0.968	0.018	0.080
Weather + Incubation					
	Average minimum temperature	-0 279	0.756	0.043	0.000
	(previous)	0.279	0.750	0.045	0.000
	Average recess duration	0.053	1.054	0.018	0.003
Incubation + Habitat					
	Average recess duration	0.048	1.049	0.019	0.010
	Forb cover	-0.026	0.974	0.018	0.143
Weather + Habitat					
	Average minimum temperature	-0.273	0.761	0.043	0.000
	Forb cover	-0.025	0.976	0.017	0.152
Incubation + Weather + Habitat					
	Average recess duration	0.049	1.051	0.018	0.005
	Average minimum temperature	-0.275	0.759	0.043	0.000
	Forb cover	-0.019	0.981	0.016	0.239

 Table 2.3. Top and competing models that best explained Greater Sage-grouse risk of nest

 mortality for survival models in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming)

 from 2010, 2020, Dasa model in sluded study area as a variable

Model	K	AICc	Δ AIC <sub>c</sub>	Wi
Weather + Incubation + Base	3	529.35	0.00	0.53
Incubation + Weather + Habitat + Base	4	529.90	0.55	0.40
Weather + Habitat + Base	3	534.63	5.28	0.04
Weather + Base	2	534.91	5.56	0.03
Incubation + Habitat + Base	3	575.39	46.04	0.00
Incubation + Base	2	575.72	46.37	0.00
Habitat + Base	2	578.94	49.59	0.00
Base	1	580.37	51.02	0.00

from 2019–2020. Base model included study area as a variable.
**Table 2.4.** Top models for weather, timing, habitat, and combinations for recess duration models for Greater Sage-grouse in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020. Variables within each model, coefficients, standard errors (SE) and *P*-values are shown.

Model	Variables	Estimate	SE	<i>P</i> -value	
Weather					
	Average minimum temperature (previous)	-0.127	0.030	0.000	
Timing					
	Day of incubation	-0.209	0.025	0.000	
Habitat					
	Sagebrush cover (30m)	0.231	0.079	0.003	
Weather + Timing					
	Average minimum temperature (previous)	-0.045	0.032	0.000	
	Day of incubation	-0.196	0.026	0.000	
Timing + Habitat					
-	Day of incubation	-0.211	0.025	0.000	
	Sagebrush cover (30m)	0.241	0.076	0.002	
Weather + Habitat					
	Average minimum temperature (previous)	-0.129	0.030	0.000	
	Sagebrush cover (30m)	0.247	0.081	0.002	
Weather + Timing + Habitat					
	Average minimum temperature (previous)	-0.046	0.032	0.146	
	Day of incubation	-0.198	0.026	0.000	
	Sagebrush cover (30m)	0.246	0.077	0.000	

**Table 2.5.** Top and competing models that best explained Greater Sage-grouse average recessduration in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020.

Model	K	AICc	Δ AIC <sub>c</sub>	Wi
Timing + Weather + Habitat + Base	8	10376.71	0.00	0.50
Timing + Habitat + Base	7	10376.80	0.09	0.48
Timing + Base	6	10384.17	7.46	0.00
Timing + Weather + Base	7	10384.22	7.51	0.00
Habitat + Weather + Base	7	10429.30	52.59	0.00
Weather + Base	6	10436.07	59.36	0.00
Habitat + Base	6	10445.37	68.65	0.00
Base	5	10451.49	74.78	0.00

Base model included female age and study area as variables and nest ID as a random effect.



**Figure 2.1.** Bridger study area in Montana, USA (blue polygon) and Red Desert study area in Wyoming, USA (red polygon) shown in the inset map. Locations of nests used in analysis are shown for Red Desert (red circles, bottom map) and Bridger (blue circles, top map). Incubation constancy and nest survival were examined at Greater Sage-grouse nests in Bridger from 2018–2019 and Red Desert from 2019–2020.



**Figure 2.2.** Distances of GPS-tagged female Greater Sage-grouse from their nests during recesses in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020. The 25% quartile was at 245 m, 50% quartile (median) was at 217 m, and 75% quartile was at 291 m. Ninety-five percent of the distances from nests during recesses were 437 m or closer to the nest. The largest distance from the nest on a recess was 978 m.



**Figure 2.3.** Number of recesses initiated for adult (n = 2633) and yearling (n = 510) Greater Sagegrouse by time of day based on incubation days. Recess time was examined for each incubation day for adult (n = 1303) and yearling (n = 254) nests in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020.



Day of Incubation

Figure 2.4. Incubation constancy (percent of each day a female incubates her nest) for each day of incubation separated by age group (adults and yearlings; A) and nest attempt (first and renest; B). Incubation constancy was examined at Greater Sage-grouse nests in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020.



**Figure 2.5.** Number of Greater Sage-grouse nests that failed or succeeded for each day of incubation by female age. Nests whose fates occurred on days 26, 27, or 28 were successful (n = 53), whereas any nest whose fate was before day 26 failed (n = 78). Nests tended to fail early on and as incubation progressed, the rate of nest failure decreased. Nest survival was examined at nests in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020.



**Figure 2.6.** Relative mortality risk of Greater Sage-grouse nests for average minimum temperature on the day before nest fate (A) and for average recess duration (B). Nest mortality risk was examined at nests in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020.



**Figure 2.7.** Average recess duration (min) for day of incubation (A) and sagebrush cover at 30 m (B). Points represent the mean values for each variable. Day of incubation had a negative effect on recess duration while sagebrush cover had a positive effect. Recess duration was examined at Greater Sage-grouse nests in Bridger (Montana) from 2018–2019 and Red Desert (Wyoming) from 2019–2020.

# **CHAPTER THREE:** Linking microhabitat selection, range size, reproductive state, and behavioral state in greater sage-grouse

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## ABSTRACT

A female's reproductive status influences her behavior which affects habitat selection and range size; however, reproduction and behavior are generally unaccounted for in habitat selection studies. Range size, daily activity, and habitat selection between reproductive states have rarely been investigated in a connected manner. We focused on brood-rearing and broodless (i.e., females without young) greater sage-grouse (*Centrocercus urophasianus*). Our objectives were as follows: 1) identify differences between reproductive state (females with broods 0-2 weeks, broods 3-5 weeks, and broodless females) and behavioral state (foraging, day roosting, and night roosting) in microhabitat selection, 2) evaluate daily activity for brood-rearing and broodless females, and 3) contrast daily and seasonal range sizes for each reproductive state. We collected Global Positioning System location and accelerometer data every 5 min from female sage-grouse in Carbon County, Montana, and Park County, Wyoming, USA, in 2018–2019. We sampled microhabitat for 36 females at 276 bird-use and random plots, estimated ranges for 38 females, and measured activity for 43 females. Females with broods 0-2 weeks selected against visual obstruction and for perennial grasses at night roosts, females with broods 3–5 weeks selected for visual obstruction when foraging and against visual obstruction and annual grasses but for sagebrush cover at night roosts; however, broodless females showed no selection. Patterns of daily activity differed between females with broods 0-2 weeks and broodless females; females with broods 3-5 weeks showed an intermediate pattern. Females with broods 0-2 weeks had the smallest daily (0.027 km<sup>2</sup>) and seasonal (0.21 km<sup>2</sup>) ranges compared with females with broods

3-5 weeks (daily = 0.038 km<sup>2</sup>, seasonal = 0.36 km<sup>2</sup>) and broodless females (daily = 0.035 km<sup>2</sup>, seasonal = 0.44 km<sup>2</sup>). Our results indicated the importance of considering reproductive and behavioral state and accounting for habitats and space required by all individuals in conservation and management decisions.

## **INTRODUCTION**

Understanding how reproductive state influences behavior, which in turn influences habitat selection and range size has important implications for effective management by improving our understanding of how animals use landscapes. During the breeding season, reproductive state (i.e., caring for young or not; Mackie and Racey 2007, Smith et al. 2018, Viejou et al. 2018) affects behavior (e.g., resting or foraging; Roever et al. 2014). Behavior then influences habitat selection, range size (van Beest et al. 2011), and an animal's activity patterns (e.g., time when active; Walker et al. 2006) throughout the day. Females with young have a greater need to avoid risky habitat and prioritize their offspring's safety by more strongly avoiding predation risk than females without young (Viejou et al. 2018), therefore increasing the amount of time using safe habitats (Brown 1999). Moreover, reproductive state influences habitat selection in numerous species, for example, noctule bats (Nyctalus noctule; Mackie and Racey 2007), blue crabs (*Callinectes ornatus*; Segura de Andrade et al. 2014), and greater sage-grouse (*Centrocercus*) *urophasianus*; Smith et al. 2018). Nonreproductive females may use a greater variety of habitat (Rayment et al. 2015, Smith et al. 2018), use the same habitat but for a different amount of time (Mackie and Racey 2007), or use different size ranges (Dahle and Swenson 2003, Henry et al. 2005, van Beest et al. 2011) than their counterparts with young. Differences in range sizes may be due in part because nonreproductive females are more mobile than females with young (Thiebot et al. 2011) and can thus access a greater area and greater diversity of habitat.

Reproductive state may also influence a female's activity levels throughout the day. For example, females without young can spend more time in reduced activity than their reproductive counterparts who must remain vigilant to reduce predation risk for themselves and their young or remain active to increase time spent foraging.

A female's behavioral state changes throughout the day and is influenced by her reproductive state. Females may change their behavior to become more vigilant, for foraging, for resting, or for moving from one habitat patch to another depending on the time of day. Different behavioral states influence a female's activity levels and time spent in each activity. Females expressing different behavior may show differences in habitat selection throughout the day (Roever et al. 2014) as suggested by previous research showing differences in sage-grouse habitat selection during different times of the day (Dunn and Braun 1986, Sveum et al. 1998), at night (Dzialak et al. 2011), and within and between patches (Dzialak et al. 2015). Aside from changing behavioral state, the time spent therein may change throughout the day (Walker et al. 2006). Additionally, different behavioral states or time spent therein may influence range size; for example, resting animals with low activity may utilize smaller ranges than when animals are actively foraging (Christiansen et al. 2017).

Assessing how behavioral state affects habitat selection can provide important insight and better understanding into species-habitat relationships compared to studies that do not account for various behaviors (Beyer et al. 2010, Roever et al. 2014). Selection for or against specific habitat components may differ depending upon the animal's behavior, sometimes resulting in identifying different selection patterns depending on whether behavior is accounted for in models (Roever et al. 2014). Even between reproductive states, behaviors can impact habitat use and the amount of time spent within certain habitat features (Walker et al. 2006). Incorporating daily

behavior into habitat selection analyses can elucidate habitat selection by highlighting different habitats used during different behaviors or different selection patterns that other studies that do not account for behavior are unable to do. However, though accounting for behavior is important, it has received relatively little attention because much of the location data used by many telemetry studies with few locations lacks a behavioral component (Beyer et al. 2010). Advanced Global Positioning System (GPS) technology, tri-axial accelerometer data, and high frequency rates of location fixes can help distinguish between animal behaviors that were once only possible through direct observation (Wilmers et al. 2015). Behaviors such as walking, resting, foraging, swimming, and grooming have been revealed using GPS and accelerometer data in a variety of species (e.g., Yoda et al. 2001, Graf et al. 2015, Wang et al. 2015), including birds (Nathan et al. 2012).

Greater sage-grouse (hereafter, sage-grouse) is a species of conservation concern that has undergone substantial range contraction and population decline (Schroeder et al. 2004, Nielson et al. 2015). Greater sage-grouse were considered "warranted, but precluded" for listing in 2010 under the Endangered Species Act due to habitat loss, fragmentation, and lack of regulatory mechanisms (U. S. Fish and Wildlife Service 2010). Declines in populations and concern about habitat loss and degradation have prompted a considerable number of studies on sage-grouse, such that habitat selection during the breeding season by brood-rearing females has been well studied (Drut et al. 1994, Dinkins et al. 2012, Kirol et al. 2012, Mabray and Conover 2015). Both female and chick survival are important vital rates for sage-grouse population growth (Taylor et al. 2012) even though sage-grouse are a relatively long-lived galliform with low reproductive output (Connelly et al. 2011). Due to variation in sage-grouse productivity across years from environmental stochasticity (Taylor et al. 2012), survival of broodless females (i.e., females without a brood) may become even more important during years of low reproductive success. Different sage-grouse reproductive states can influence habitat selection (Gregg et al. 1993, Kirol et al. 2015, Smith et al. 2018) but little is known about how sage-grouse behavior influences habitat selection (but see Dzialak et al. 2015).

The concern for sage-grouse populations and need for conservation of their habitat make sage-grouse an ideal candidate for studying the links between reproductive and behavioral state effects on habitat selection, range size, and daily activity. Although previous studies have examined breeding season habitat selection (Drut et al. 1994, Thompson et al. 2006, Mabray and Conover 2015, Smith et al. 2018) and range size (Drut et al. 1994) separately, or reproductive state influence on habitat selection (Mabray and Conover 2015, Smith et al. 2018) these studies did not account for behavioral state nor examined reproductive state influence on daily activity and range. We chose to examine 3 reproductive states based on differences in habitat selection between females with broods 0–2 weeks and 3–5 weeks (Thompson et al. 2006, Kirol et al. 2012, Kirol et al. 2015, Smith et al. 2018) and between brood-rearing and broodless female sagegrouse (Smith et al. 2018). The goal of our study was to understand the links between reproductive state, behavioral state, habitat selection, range, and daily activity to help elucidate how behavioral and reproductive state influence how sage-grouse utilize their landscape. Our objectives were as follows: 1) identify differences between reproductive states (females with broods 0-2 weeks, broods 3-5 weeks, and broodless females) and behavioral states (foraging, day roosting, and night roosting) in third-order habitat selection (i.e., microhabitat; Johnson 1980); 2) examine the effect of reproductive state on daily activity; and 3) examine the influence of reproductive state on daily and seasonal range sizes. We predicted sage-grouse would select for less cover when night roosting and greater forb cover when foraging (Table 3.1; Drut et al.

1994, Fedy et al. 2014), differentiating their selection based on behavior. Similarly, we predicted brood-rearing females would choose areas with less cover and more forbs compared with broodless females who would select a variety of habitats (Smith et al. 2018). We predicted activity levels would differ during the day between reproductive states, such that brood-rearing females would take longer to become active in the morning and be more active during the day to satisfy nutrient requirements of the chicks whereas broodless females would show more variable activity levels throughout the day (Maxson 1974). We also predicted brood-rearing females would have smaller ranges than broodless females due to mobility constraints of having chicks.

## **STUDY AREA**

Our study area was approximately 487 km<sup>2</sup> located in southern Carbon County, Montana and northern Park County, Wyoming (from 109°3'57.6" W 45°10'33.6" N to 109°4'55.2" W 44°57'28.8" N). Elevation ranged from 1158–2080 m above sea level. Annual mean high temperature was 13.5° C and 12.3° C (30-year average was 12.6° C from 1981–2010), mean minimum temperature was –0.9° C and –1.5° C (30-year average was –0.6° C from 1981–2010), and mean precipitation was 35.5 cm and 40.5 cm (30-year average was 42.0 cm from 1981– 2010) in 2018 and 2019, respectively (PRISM Climate Data; http://www.prism.oregonstate.edu). Exurban residential development, cattle grazing, and recreational use all occurred within the study area. Anthropogenic development was primarily houses or agricultural fields and associated buildings with some small areas of oil and gas infrastructure. Within the study area, 61% was public land (54% Bureau of Land Management, 3% U.S. Forest Service, and 4% State Trust) and 39% was private land. The landscape was dominated by basin big sagebrush (*Artemisia tridentata tridentata*) and Wyoming big sagebrush (*A. t. wyomingensis*). Other common shrubs in the study area included black sagebrush (*A. nova*), broom snakeweed (*Gutierrezia sarothrae*), Gardner's saltbush (*Atriplex gardneri*), greasewood (*Sacrobatus vermiculatus*), rubber rabbitbrush (*Ericameria nauseosa*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), and shadscale saltbush (*A. confertifolia*). Isolated stands of juniper (*Juniperus spp*.) were found on steeper hillsides or at higher elevation. Dominant perennial grasses included blue grama (*Bouteloua gracilis*), Indian ricegrass (*Achnatherum hymenoides*), needle-and-thread (*Hesperostipa comata*), and Sandberg bluegrass (*Poa secunda*). Cheatgrass (*Bromus tectorum*) was abundant throughout a majority of the study area.

## **METHODS**

We captured female sage-grouse from the Montana portion of our study area in spring and summer of 2018 and 2019 across 7 leks during spring or near GPS-tagged birds in the summer. We captured sage-grouse at night using spotlighting and hoop-netting techniques (Giesen et al. 1982). We fitted sage-grouse with solar-powered, rump-mounted transmitters (15g-Bird Solar tag, e-obs GmbH, Grunwald, Germany, with attached 6g-VHF tag, Holohil, Ontario, Canada; total weight ~30g including harness material) collecting location and accelerometer data every 5 minutes during daylight and some nighttime hours (0330–2300 MDT). We collected data from the remote-download transmitters weekly to monitor the status of each female by examining their locations and movement patterns. We examined GPS locations to monitor the time and day each female grouse completed nesting, with brood-rearing beginning when the female moved from a successful nest without returning. We monitored nests for success or failure, with a successful nest hatching at least one egg, as determined by examining the eggshell for a detached membrane (Wallestad and Pyrah 1974). We monitored broods until 5 weeks posthatch by examining movement data to ensure females still had chicks. We searched specifically for evidence a female flew long distances or flew off a night roost (without quickly returning), with

a large flight (>100 m when chicks were <2 weeks old) indicative of a broodless female (Dzialak et al. 2011). We used 35 d posthatch as the conclusion of brood-rearing success because the majority of chick mortality occurs before 35 d (Gregg et al. 2007). In addition, we checked all broods 2 weeks posthatch by going to the previous night's roost based on the female's locations and examining the roost for chick droppings (presence of chick droppings indicating the female had a brood) while eliminating any disturbance to the brood. If a female was suspected to have lost her brood within the 5-week window, we immediately verified by locating and flushing the female at night. We determined the success of each brood-rearing female at 35 d posthatch by checking the female at night, with the presence of at least one chick with the female signifying brood success (Kirol et al. 2015). If either of the physical checks on brood status contradicted our estimated status based on movement data, we checked the female grouse again the following night to confirm brood status. After physical brood checks, the status of every brood matched our estimated status based on movement data. If a female was confirmed to have lost her chicks or her nest failed with no subsequent renest, we censored this female for one week before she was considered a broodless female to ensure she completely transitioned behavior, movement, and habitat selection. Females that never nested were considered broodless starting on 15 May of each year. We monitored broodless females until they either moved to summer range (usually irrigated hayfields or pastures) or the last brood reached 5-weeks posthatch, whichever occurred first.

#### **Microhabitat Selection**

We separated brood-rearing females into 2 categories, 0–2 weeks (d 1–14) and 3–5 weeks (d 15– 35) posthatch, due to differences in habitat use shown for these 2 brood periods (Thompson et al. 2006, Kirol et al. 2012, Kirol et al. 2015, Smith et al. 2018). We focused on 3 reproductive states for analyses: females with broods 0–2 weeks, broods 3–5 weeks, and broodless females. To

examine behavioral state influence on microhabitat selection of brood-rearing and broodless females, we sampled vegetation at locations associated with foraging and roosting. We separated out the activities to include one foraging, one day roost, and one night roost location, basing each of the locations on the behavior of a unique sage-grouse for one day. We determined each used point for vegetation sampling based on GPS locations and accelerometer data collected by the transmitters. We collected accelerometer data once each 0.1 sec over a 10-sec sampling period every 5 min on X, Y, and Z axes. We used the variance in acceleration measured over the 10-sec period along the Z-axis to quantify activity levels because this axis changed the most with bird movement. We calculated location-specific nautical dawn/dusk and sunrise/sunset to aid in defining foraging and day roosting points (suncalc R package, Hieurmel and Elmarhraoui 2019; R Core Team 2020). For the foraging points, we were attempting to identify foraging behavior by selecting the locations when the birds were most active for an extended time (minimum 10) min) without moving the farthest distances. For day roost points, we were attempting to identify day roosting behavior by selecting locations when the birds were inactive for an extended time (minimum 10 min) and not moving. We defined foraging points for sampling as locations where the variance in measured acceleration was within the highest 25<sup>th</sup> guartile measured that day and the average of the previous and subsequent locations within 10 min (median over a 20-min window) was also within the highest 25<sup>th</sup> quartile. Foraging locations had to be between nautical dawn (~0400–0430 MDT) and dusk (~2200–2230 MDT). Besides having a high variance in acceleration, foraging points also needed a step length (i.e., distance between previous and subsequent locations) that was not an outlier (i.e., less than the  $75^{\text{th}}$  quartile + 1.5 times the interquartile range) of all the distances recorded for that bird-day. Using these criteria, we were attempting to identify locations when grouse were active but not flying or walking/running

quickly in a straight line. We identified day roost points by distance moved and acceleration variance in the lowest 25<sup>th</sup> quartile for the location and the average of locations within the 20min window. Day roost locations could occur at any time during the day within one hour after sunrise and one hour before sunset. We identified night roosts by randomly selecting between the first (0330 MDT) and last (2300 MDT) GPS locations recorded that day, which were before nautical dawn or after nautical dusk. For night roosts, we ensured the female had not been flushed earlier in the night by checking the female's locations. We ensured each bird-use location was based on behavior of the grouse, foraging or roosting, so time of day of each location varied.

We paired each of the individual bird-use locations (foraging, day roost, and night roost) with one random location, therefore we considered these 3 sets to be paired microhabitat plots. We created a minimum convex polygon (MCP) based on all the female's locations for that day and selected a random location within that MCP to use as the paired-random plot to compare microhabitat to each of the used locations. In this way the female could have selected the paired-random plot as it was available within her daily home range (Jones 2001). We set all plots a minimum of 40 m apart, hence, no plots could overlap, and the random plot could not overlap any of the bird's locations and was therefore unused on that day. We completed no more than 2 paired microhabitat plots per each reproductive state-bird-year (Smith et al. 2018). We sampled all vegetation for bird use and paired random plots within 7 d of use by the female to accurately capture microhabitat characteristics due to logistical constraints, the female died before having a brood, or the female died before we were able to sample vegetation used by the female.

We sampled microhabitat-scale (30 m x 30 m) or third-order habitat selection (Johnson 1980) vegetation characteristics at each bird-use and random plot including shrub cover, herbaceous cover, ground cover, and visual obstruction. For each plot, we collected vegetation measurements along 4, 15-m transects radiating out in cardinal directions from the center of each plot. At each plot we measured biologically relevant variables important for sage-grouse during the brood-rearing season (Table 3.1). We used the line intercept method across all 4 transects resulting in 60 m total for each plot to estimate shrub canopy cover by species (Canfield 1941). We measured visual obstruction by averaging 26 Robel pole readings per plot, taking 2 readings at 5, 10, and 15 m in each cardinal direction from plot center and 2 readings at plot center (Robel et al. 1970). Each Robel pole reading was taken in the opposite direction along the transect lines. We assessed herbaceous and ground cover within 17, 0.1-m<sup>2</sup> (20 x 50 cm) Daubenmire quadrats equally spaced at 3.75-m increments from the center along all transects and one at the center of each plot (Daubenmire 1959). We defined percent cover within each Daubenmire quadrat using the following cover classes: 1 = 0 - 1%, 2 = 1.1 - 5%, 3 = 5.1 - 25%, 4 = 25.1 - 50%, 5 = 50.1 - 75%, and 6 = 75.1 - 100%. We grouped forbs considered to be eaten by sage-grouse together as food forbs (see Kirol et al. 2012), whereas all other forbs we considered non-food. We tabulated forb species richness as the number of species of forbs (both food and non-food) found in each plot. More details about methodology to collect microhabitat vegetation data information at each location are found in Kirol et al. (2012) and Dinkins et al. (2016).

We employed a modified Design IV from Erickson et al. (2001) to analyze microhabitat characteristics at both use and available locations for individual grouse, resulting in paired useavailable data. We paired each bird-use location (foraging, day roost, night roost) with one random location for analyses. Due to logistical constraints, we used the same available location per behavioral state, for example, for one female we sampled 4 microhabitat plots per day including one day roost, night roost, foraging, and available plot. We modeled microhabitat selection using a binomial conditional logistic regression model with a use-available design (survival R package, Therneau 2020; R Core Team 2020), where we considered bird-use plots as used and paired-random plots as available. We modeled each behavioral state (foraging, day roost, night roost) and reproductive state (females with broods 0–2 weeks, broods 3–5 weeks, and broodless) separately. We evaluated quadratic expressions for cover variables but found they did not improve model fit. We also did not include interactions due to small sample size. We accounted for repeated sampling of the same individual by using Bird ID as a random effect. We checked for collinearity by using a Pearson correlation matrix—any variable with a correlation coefficient greater than 0.6 or variance inflation factor (VIF, Menard 1995) coefficient greater than 3 was removed. When 2 variables were correlated, we retained the variable that we considered more biologically relevant. We checked all variables for each model for potential outliers (Hosmer and Lemeshow 2000). We conducted model selection using quasi-likelihood under the independence model criterion that accounts for repeated sampling of the same individuals (QIC; Pan 2001, Craiu et al. 2008). We limited models to less or equal to 3 variables to prevent overfitting of our data due to sample sizes. We then model averaged using models with  $\Delta QIC < 4$  from the top model. We validated top models by checking residual plots for normality and outlier influence on data. We considered variables to be biologically and scientifically significant when 95% confidence intervals did not overlap zero.

## Activity

We evaluated times of activity (i.e., times when females were active) throughout the day between females with broods 0–2 weeks (d 0–14), females with broods 3–5 weeks (d 15–35),

and broodless females. We were not limited by logistical constraints in obtaining activity data as we were with sampling microhabitat, therefore our sample size for activity was larger than for the microhabitat analysis. We reduced locations of broodless females to a random, consecutive 3-week timeframe to be comparable with females with broods 0–2 weeks and 3–5 weeks because these females may be broodless for a few days up to numerous weeks. We only included broodless females in analyses 7 d after losing a nest with no subsequent renest, 7 d after losing a brood, or 15 May of each year for females that never nested. We stopped using locations for activity analyses once a broodless female moved from her breeding area towards summer range or 31 July, the latest date all broods would have reached 5 weeks, whichever occurred first to ensure brood-rearing and broodless female locations and timeframes were comparable. Brood-rearing females may have lost their brood during weeks 0–2 or weeks 3–5, hence the actual number of days in each reproductive state may have been less than 2 weeks for females with broods 0–2 weeks or 3 weeks for females with broods 3–5 weeks.

We defined active behavior (which also included both flying and walking besides foraging behavior as described earlier) as when the variance in acceleration measured along the Z-axis was within the highest 25<sup>th</sup> quartile measured every 5 min and averaged over a 20-min moving window (from 0330 MDT to 2300 MDT). We wanted to compare the pattern of activity between reproductive states, therefore, we calculated the proportion of bird-days that met this criterion at each of the 5-min sampling periods.

## **Daily and Seasonal Ranges**

We assessed both daily and seasonal range size (km<sup>2</sup>) by reproductive state using a dynamic Brownian Bridge Movement Model (BBMM; Kranstauber et al. 2012). Dynamic BBMMs do not have assumptions of independence of points as do some home range models and recognizes

behavioral change along animal tracks to more accurately describe space use compared with regular BBMMs (Kranstauber et al. 2012). We used a window size of 9 locations and a margin of 3 locations to create the dynamic BBMM (Pratt et al. 2017). We calculated a daily range size for each individual as the mean of daily ranges measured over 2 weeks for females with broods 0–2 weeks old, 3 weeks for females with broods 3–5 weeks old, and 3 weeks for broodless females. We calculated individual seasonal ranges from all locations observed over the same time periods. We used the same dataset and criteria for including brood-rearing and broodless females in analyzing range sizes as for the activity analysis. However, females in any reproductive state with fewer than 8 d of locations were excluded from analyses to ensure an adequate number of days of locations to measure seasonal home ranges.

We estimated daily and seasonal range size based on a 95% utilization distribution calculated from a dynamic BBMM (move R package, Kranstauber et al. 2020; R Core Team 2020). We used a Welch Test (onewaytests R package, Dag et al. 2018; R Core Team 2020), which is an alternative to an ANOVA for data that does not have equal variances (Levene's Test, daily range sizes P = 0.207 and seasonal range sizes P = 0.006, Kohr and Games 1974; car R package, Fox and Weisberg 2019; R Core Team 2020), to determine whether a difference in daily and seasonal range size existed between reproductive states. To understand which reproductive states differed in range size, we used a Games-Howell test (userfriendlyscience R package, Peters 2018; R Core Team 2020). We set statistical significance at alpha = 0.05.

## RESULTS

We monitored 39 female sage-grouse including 17 with broods and 22 broodless females in 2018 and 43 females including 19 with broods and 24 broodless females in 2019. At 5-weeks posthatch, there were 10 (58.8%) successful broods (minimum of one chick remaining at 5

weeks) in 2018 and 11 (57.9%) successful broods in 2019. By the end of the breeding season, broodless females accounted for 60.7% and 60.6% of all living females in 2018 and 2019, respectfully.

#### **Microhabitat Selection**

We sampled microhabitat vegetation characteristics from 36 unique females at 276 plots, of which 207 were bird-use and 69 were paired-random plots (Table 3.2). Microhabitat surveys for bird-use and paired-random plots were completed from 20 May to 30 June for females with broods 0–2 weeks, 4 June to 17 July for females with broods 3–5 weeks, and 10 June to 24 July for broodless females. Median brood age at the time plots were identified for microhabitat sampling was 7 d posthatch (range = 2–14 d) for broods 0–2 weeks and 28 d posthatch (range = 18–34 d) for broods 3–5 weeks. We found several competing models for each reproductive state and behavior, therefore, we model averaged the competing models within 4  $\Delta$ QIC for each behavior and reproductive state (Table 3.3).

Females with broods 0–2 weeks and 3–5 weeks selected microhabitat characteristics at night roosts, but only females with broods 3–5 weeks selected for or against specific characteristics when foraging (Table 3.3, Figure 3.1). We documented no significant selection across all reproductive states when day roosting. Females with broods 0–2 weeks selected against visual obstruction and for perennial grasses when night roosting but showed no selection when day roosting or foraging (Figure 3.2). Females with broods 3–5 weeks selected against visual obstruction and annual grass but for sagebrush cover when night roosting. Females with broods 3–5 weeks selected for visual obstruction and forbs when foraging but showed no selection when day roosting (Figure 3.1). Broodless females showed no selection of any habitat characteristics during any behavioral state.

#### Activity

We examined daily activity from 43 unique females spanning 1,317 bird-days across reproductive states, resulting in 424 bird-days from 29 females with broods 0–2 weeks, 418 birddays from 22 females with broods 3–5 weeks, and 475 bird-days from 25 broodless females. Females with broods 0–2 weeks had the largest proportion of bird-days active at 0905 MDT, females with broods 3–5 weeks at 2110 MDT, and broodless females at 2105 MDT (Figure 3.3). A greater proportion of females with broods 0–2 weeks became active later in the morning, maintained higher activity during the middle of the day, and a smaller proportion were active in the evening compared with broodless females. A smaller proportion of broodless females were active during the day and a greater proportion were active in the morning and evening. Females with broods 3–5 weeks showed a pattern that was intermediate between that of females with broods 0–2 weeks and broodless females.

## **Daily and Seasonal Ranges**

We analyzed daily and seasonal range size from 27 females with broods 0–2 weeks, 22 females with broods 3–5 weeks, and 23 broodless females spanning 2018–2019 from 39 unique individuals. There were 24 individual grouse that appeared in more than one reproductive state. Mean daily range sizes were 0.027 km<sup>2</sup> for females with broods 0–2 weeks, 0.038 km<sup>2</sup> for females with broods 3–5 weeks, and 0.035 km<sup>2</sup> for broodless females ( $F_{2,42} = 8.27$ , n = 69,  $P \le$ 0.001; Table 3.4, Figure 3.4). Mean seasonal range size was 0.21 km<sup>2</sup> for females with broods 0– 2 weeks, 0.36 km<sup>2</sup> for females with broods 3–5 weeks, and 0.44 km<sup>2</sup> for broodless females ( $F_{2,37}$ = 19.76, n = 69,  $P \le 0.001$ ). Broodless females had mean daily ranges that were 1.3-times larger than that of females with broods 0–2 weeks ( $t_{df = 39.83} = 2.79$ , P = 0.021) and mean seasonal ranges that were 2.1-times the size of females with broods 0–2 weeks ( $t_{df = 29.62} = 5.42, P \le 0.001$ ). Females with broods 3–5 weeks had a daily range size that was 1.4-times larger ( $t_{df = 36.98} = 3.71, P = 0.002$ ) and seasonal range size that was 1.7-times larger ( $t_{df = 30.65} = 4.15, P = 0.001$ ) than females with broods 0–2 weeks. We found females with broods 3–5 weeks did not differ in daily ( $t_{df = 42.76} = 0.88, P$ -value = 0.658) or seasonal ( $t_{df = 42.37} = 1.43, P$ -value = 0.335) range sizes compared with broodless females.

#### DISCUSSION

The goal of our study was to more comprehensively understand the habitat and space requirements of female sage-grouse during the breeding season by linking reproductive state, behavioral state, microhabitat selection, daily and seasonal range, and daily activity. We analyzed behavioral and reproductive state influence on microhabitat selection and reproductive state influence on range size and daily activity. We found differences in microhabitat selection based on behavioral state and reproductive state for female sage-grouse. Brood-rearing females selected against visual obstruction at night roosts, while females with broods 3–5 weeks selected for visual obstruction and forbs when foraging, and broodless females showed no selection regardless of behavioral state. Our results confirm previous studies showing differences in habitat selection between brood-rearing and broodless sage-grouse (Gregg et al. 1993, Kirol et al. 2015, Smith et al. 2018). For sage-grouse, incorporating behavioral state aided in understanding differences in daily habitat selection (Roever et al. 2014). Daily and seasonal range size, like in other species, differed by reproductive state with females with young broods having smaller ranges than their counterparts without young (Henry et al. 2005, van Beest et al. 2011, Edwards et al. 2013). Activity levels also differed between reproductive states and changed throughout the course of the day, with a greater proportion of broodless females and females with broods 3-5

weeks being most active in the morning and evening contrasting with a smaller proportion of females with broods 0–2 weeks being active in the morning and evening.

For females with broods 0-2 weeks, we found no significant selection of cover variables when foraging or day roosting, contrary to other studies that have found brood-rearing females selecting for visual obstruction (Mabray and Conover 2015, Schreiber et al. 2015, Smith et al. 2018). Broods 0–2 weeks also showed no selection for forbs, indicating forbs are not significant drivers of habitat selection at the microhabitat scale for younger broods but do become more important for older broods (Smith et al. 2019). Previous research has suggested that when broods are young, female sage-grouse generally select for greater grass cover (Thompson et al. 2006, Hagen et al. 2007), shrub cover (Thompson et al. 2006, Mabray and Conover 2015), and dense sagebrush (Thompson et al. 2006), allowing for protective cover when chicks have limited flight capability. In general, predation has been shown to be the most common cause of yearling/adult sage-grouse mortality (Connelly et al. 2000) and survival of chicks is low during the first week (Gibson et al. 2017). Hence, it has been suggested that brood-rearing females select habitat to maximize both food resources and concealment (Smith et al. 2018), which are positively correlated with chick survival (Gregg and Crawford 2009). Females with broods have also been observed avoiding areas with higher densities of avian predators (Dinkins et al. 2012, Dinkins et al. 2014). However, our results indicated females with broods 0–2 weeks showed no selection for visual obstruction during the day and their probability of selection decreased as visual obstruction increased when night roosting. Our results suggested that females with broods 0-2weeks have different selection patterns depending on behavior and time of day, and females with broods 0–2 weeks may seek out less cover when night roosting than during the day. We accounted for behavior of brood-rearing sage-grouse in our habitat selection models and

compared used sage-grouse locations with random locations that were available to those females (i.e., within an MCP of used locations from the same day) at a smaller scale than most habitat selection studies. Our methods for sampling microhabitat and accounting for behavior may explain discrepancies between our study and others that measure habitat selection on a larger scale that showed females with young broods selected for visual obstruction compared to randomly available habitat (Mabray and Conover 2015, Smith et al. 2018).

Females with broods 0–2 weeks showed different patterns of activity and daily and seasonal range sizes than females with broods 3–5 weeks and broodless sage-grouse. Females with broods 0-2 weeks exhibited smaller daily and seasonal ranges than females with broods 3-5weeks or broodless females. Smaller daily ranges for younger broods may be due to chicks being brooded by females for about half the day (Schroeder et al. 1999). Sage-grouse broods 0-2 weeks are constrained by the mobility of chicks, and, as chicks age, females are able to increase the size of their ranges (Drut et al. 1994), similar to brood-rearing female dusky grouse (Dendragapus obscurus) whose range sizes increased steadily throughout brood-rearing (Sopuck and Zwickel 1992). Females with broods 0-2 weeks were slower to become active in the morning and quicker to lessen activity in the evening compared with females with broods 3-5weeks and broodless females, similar to activity levels seen in ruffed grouse (Bonasa umbellus) broods (Maxson 1974). Less activity in the morning and evening is likely due to females needing to brood their chicks more during cooler temperatures when chicks are still unable to thermoregulate. Females with broods 0-2 weeks then may need to compensate for inactivity by being relatively more active during the day to meet the food requirements of chicks. Predation was related to one-third of sage-grouse chick mortality in Utah (Dahlgren et al. 2010) and the

activity pattern of females with broods 0–2 weeks may cause them to be more susceptible to predation.

As chicks became more mobile, females with broods 3–5 weeks showed stronger microhabitat selection than broods 0-2 weeks, possibly in part due to larger daily and seasonal ranges and changes in chick diet. Previous research found that compared with younger broods, selection by older broods for sagebrush cover decreased but forb cover increased, highlighting a shift in habitat selection throughout brood-rearing (Hagen et al. 2007, Smith et al. 2019). Females with broods 3–5 weeks selected for visual obstruction and forb cover when foraging but not when day roosting. Females with broods 3-5 weeks showed variability in selection for shrub cover (Smith et al. 2018), having selected for sagebrush cover when night roosting but made no selection for sagebrush cover while foraging. As broods become older, their rate of survival also increases, and shifts in habitat use might be one reason why chick survival increases as chicks age (Gibson et al. 2017). Females with broods 3–5 weeks selected for forb cover when foraging, but not when day roosting, suggesting females with broods 3–5 weeks were selecting microhabitat relative to behavioral state and their selection changed throughout the day. Forbs are important for brood-rearing sage-grouse (Sveum et al. 1998) and forb cover is selected by broods as they become older (Hagen et al. 2007, Smith et al. 2018, Smith et al. 2019). However, Kirol et al. (2012) found forb cover was not informative for microhabitat selection by broods 3-5 weeks. Differences in microhabitat selection by behavioral state in females with broods 3-5 weeks suggest the need to incorporate behavior in habitat selection studies (Roever et al. 2014). More specifically, habitat studies should focus on times when brood-rearing sage-grouse are exhibiting specific behaviors.

Broodless females were similar to those with broods 3–5 weeks in daily and seasonal range size and activity patterns but differed from females with broods 3–5 weeks in microhabitat selection. Our results indicated broodless females were not strongly selecting for microhabitat features when foraging, day roosting, or night roosting, possibly in part due to broodless females utilizing a greater diversity of cover types (Gregg et al. 1993). Similar to 3–5-week-old brood females, broodless females had larger daily and seasonal ranges than females with broods 0-2 weeks resulting in a greater amount of habitat from which to select. Sveum et al. (1998) and Dunn and Braun (1986) found sage-grouse selected for different habitats in the morning, midday, and afternoon. Activity patterns during the day indicated a greater proportion of broodless females were more active in the morning and evening compared with midday. Broodless females form small, loose flocks and are most active when avian and mammalian predators are also active, which may contribute to their higher survival rate compared with brood-rearing females (Smith et al. 2018). After incorporating behavior, our results suggested broodless sage-grouse utilized a variety of habitats and their selection was not dependent on behavior, even though their activity changed throughout the day.

Foraging animals may allocate time and amount of vigilance differently between different habitat patches to manage predation risk (Brown 1999). Females with young may avoid predation risk more strongly than females without young (Viejou et al. 2018), for example, brood-rearing female black grouse (*Tetrao tetrix*) traded-off food biomass for habitat cover, most likely to reduce predation risk (Signorell et al. 2010). Brood-rearing sage-grouse utilize areas with fewer avian predators, therefore they also select brood-rearing habitat to avoid predators, not necessarily only for microhabitat characteristics (Dinkins et al. 2012, Mabray and Conover 2015). The same habitat may be used between reproductive states but for a different duration of time (Walker et al. 2006, Mackie and Racey 2007). Though we did not directly measure the amount of time sage-grouse spent in different habitat patches when foraging and roosting, we identified that females with broods 0–2 weeks showed different activity patterns than females with broods 3–5 weeks and broodless females.

Combining accelerometer and GPS locations assists researchers in answering questions at the interface of animal behavior and habitat selection (Nathan et al. 2012). Linking habitat selection, range size, and daily activity provides a comprehensive understanding of habitat and space use by female sage-grouse during the breeding season. Habitat selection, daily and seasonal range size, and daily activity differed across reproductive states, and understanding how these differ will help wildlife managers better accommodate for all individuals in a population. Our results indicated brood-rearing sage-grouse differed in habitat selection by behavior, suggesting broods need a heterogeneous landscape with both forb cover and visual obstruction within their home range to satisfy their daily needs. In addition, a greater proportion of broodless females were active in early morning and late evening compared with brood-rearing females, and therefore many previous habitat selection studies may not have adequately sampled all habitat requirements, especially when broodless females were most likely to be foraging. Quantifying more behaviors and expanding on daily activity (e.g., duration of time spent foraging) should be further examined for sage-grouse and similar species.

#### MANAGEMENT IMPLICATIONS

Our results highlighted differences in microhabitat selection, daily and seasonal range size, and daily activity between reproductive states, therefore wildlife managers need to account for the variety of habitats and space required by both brood-rearing and broodless sage-grouse composing populations. Microhabitat selection in female sage-grouse differed between day and night, indicating a diversity of habitats is needed to satisfy the requirements for all behavioral states for brood-rearing females. Specifically, our study suggests areas with more sagebrush cover ( $\bar{x} = 18.3\%$ , SE = 1.7) is needed for night roosts for females with broods 3–5 weeks, a range of visual obstruction ( $\bar{x} = 0.9$  dm, SE = 0.1) for day and night roosting for brood-rearing females, and areas with greater forb cover ( $\bar{x} = 13.7\%$ , SE = 2.4) for females with broods 3–5 weeks. Broodless females and females with broods 3–5 weeks utilized larger ranges than females with broods 0–2 weeks, therefore conserving large sagebrush landscapes with a diameter between a minimum 0.25–0.50 km, suitable for both reproductive states during brood-rearing is essential to conserving habitat for all female sage-grouse during the breeding season.

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## **ETHICS STATEMENT**

All capture, handling, and post-release monitoring of sage-grouse followed protocols approved by the University of Wyoming Institutional Animal Care and Use Committee (protocols No. 20180102JB00289-01 and No. 20180102JB00289-02) and Montana Fish, Wildlife & Parks Scientific Collector's Permit (No. 2018-072-W and No. 2019-039-W).

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## **TABLES & FIGURES**

**Table 3.1.** Variables considered in habitat selection models and predicted response with citations

for each variable for greater sage-grouse in Carbon County, Montana, and Park County,

Wyoming, USA, 2018 and 2019. Variables were screened for correlation and variance inflation

factors before building initial models.

Variable	Description	Predicted response	Citation
Sagebrush	Sagebrush cover from line	Select against when night and	Kirol et al. 2012
	intercept (%)	day roosting for brood-rearing	
		females; select for when	
		foraging	
Shrub <sup>a</sup>	Shrub cover from line intercept	Select against when night and	Smith et al. 2018
	(%)	day roosting for brood-rearing	
		females, select for females	
		with broods 3–5 weeks	
Annual grass <sup>b</sup>	Mean annual grass cover from	Select against by all behavioral	Kirol et al. 2012
	Daubenmire quadrats (%)	and reproductive states	(documented
			selection against
			for nests)
Perennial grass	Mean perennial grass cover	Select for by all behavioral and	Kirol et al. 2012
	from Daubenmire quadrats (%)	reproductive states	
Residual grass <sup>c</sup>	Mean residual grass cover	Select against by females with	Smith et al. 2018
	from Daubenmire quadrats (%)	broods 0–2 weeks	
Forb	Mean forb cover from	Select for when foraging	Drut et al. 1994
	Daubenmire quadrats (%)		
Food forb <sup>a</sup>	Mean sage-grouse food forb	Select for when foraging for all	Drut et al. 1994,
	cover from Daubenmire	reproductive states	Kirol et al. 2012,
	quadrats (%)		Smith et al. 2018
Forb species	Forb species richness from	Select for when foraging for all	Smith et al. 2018
richness	Daubenmire quadrats (no.)	reproductive states	
Litter <sup>a</sup>	Mean litter cover from	Select for by broodless	Smith et al. 2018
	Daubenmire quadrats (%)	females, no selection by brood-	
		rearing females	
Visual	Visual obstruction estimated	Different selection depending	Schreiber et al.
obstruction	from Robel pole (dm)	on behavior, select by females	2015, Smith et
		with broods 0–2 weeks and	al. 2018
		broodless females	

<sup>a</sup> Dropped from analyses after initial screening based on correlation and VIF coefficients.

<sup>b</sup> Annual grass consisted of mostly cheatgrass with some (<5%) field brome (*B. arvensis*).

<sup>c</sup> Residual grass was defined as the standing, dead perennial grass leaves from the previous year.

Table 3.2. Number (n) of 30 x 30-m microhabitat plots completed for each behavioral state (foraging, day roost, night roost) and reproductive state (females with broods 0–2 weeks, broods 3–5 weeks, broodless) for greater sage-grouse in Carbon County, Montana, and Park County, Wyoming, USA, 2018 and 2019.

		Microhabitat plots					
Daproductive state	Females	Foraging	Day roost	Night roost	Paired-	Total(n)	
Reproductive state	$(n)^{\mathrm{a}}$	<i>(n)</i>	<i>(n)</i>	<i>(n)</i>	random ( <i>n</i> )	10tar(n)	
Broods 0–2 wks	14	22	22	22	22	88	
Broods 3–5 wks	18	22	22	22	22	88	
Broodless	19	25	25	25	25	100	

<sup>a</sup> Samples represent unique females in each reproductive state (both for 2018 and 2019 combined); however, individual females could have been sampled in more than one reproductive state.

**Table 3.3.** Model-averaged estimates and 95% confidence intervals (CI) for variables in the top models for each behavioral state (foraging, day roost, night roost) and reproductive state (females with broods 0–2 weeks, broods 3–5 weeks, and broodless). Estimates with no values indicate that variable did not appear in the final model. Based on microhabitat characteristics at greater sage-grouse bird-use and paired random locations in Carbon County, Montana, and Park County, Wyoming, USA, 2018 and 2019.

Broods 0–2 Weeks							
	F	oraging	Da	Day Roost		Night Roost	
Variable	Estimate	95% CI	Estimate	95% CI	Estimate	95 % CI	
Sagebrush	-0.03	-0.13 to 0.08	0.04	-0.12 to 0.19	0.03	-0.08 to 0.15	
Visual obstruction	-0.76	-2.23 to 0.71	-1.67	-4.16 to 0.83	$-2.02^{a}$	-3.92 to -0.13	
Annual grass	0.01	-0.14 to 0.15	-0.16	-0.42 to 0.09	-0.22	-0.51 to 0.07	
Perennial grass	0.12	-0.06 to 0.29	0.13	-0.03 to 0.28	0.19 <sup>a</sup>	0.00 to 0.37	
Residual grass	0.01	-0.15 to 0.17	0.04	-0.15 to 0.23	-0.18	-0.53 to 0.17	
Forb species	0.12	-0.12 to 0.36	0.09	-0.17 to 0.35			
richness							
Forb	0.04	-0.11 to 0.18	-0.12	-0.36 to 0.13			

Broods 3–5 weeks							
	Foraging Day Ro		ay Roost	Night Roost			
Variable	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI	
Sagebrush	-0.02	-0.17 to 0.14	0.01	-0.07 to 0.09	$0.28^{a}$	0.07 to 0.49	
Visual obstruction	1.19 <sup>a</sup>	0.09 to 2.29	1.09	-0.51 to 2.71	-1.15 <sup>a</sup>	-2.07 to -0.23	
Annual grass	0.09	-0.01 to 0.21	0.03	-0.06 to 0.11	$-0.43^{a}$	-0.77 to -0.09	
Perennial grass	-0.12	-0.27 to 0.03	-0.14	-0.33 to 0.05	-0.09	-0.28 to 0.11	
Residual grass	0.07	-0.29 to 0.44	-0.02	-0.23 to 0.19			
Forb species	-0.18	-0.45 to 0.09	-0.04	-0.24 to 0.16			
richness							
Forb	0.13 <sup>a</sup>	0.02 to 0.24	-0.06	-0.18 to 0.05			

			Broodless			
	F	Foraging Da		ay Roost	Night Roost	
Variable	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
Sagebrush	-0.08	-0.24 to 0.08	0.03	-0.05 to 0.11	0.04	-0.06 to 0.13
Visual obstruction	1.21	-0.42 to 2.84	0.54	-0.62 to 1.71	-0.25	-1.72 to 1.21
Annual grass	0.01	-0.07 to 0.09	-0.07	-0.14 to 0.01	-0.06	-0.13 to 0.01

Perennial grass	-0.03	-0.14 to 0.08	-0.01	-0.14 to 0.13	0.05	-0.12 to 0.21
Residual grass	0.45	-0.20 to 1.09	0.08	-0.17 to 0.33	0.01	-0.31 to 0.33
Forb species	0.09	-0.13 to 0.31	0.00	-0.19 to 0.20		
richness						
Forb	-0.00	-0.11 to 0.12	-0.08	-0.17 to 0.02	-0.04	-0.14 to 0.06

<sup>a</sup>95% confidence interval does not include zero.

**Table 3.4.** Mean difference, lower and upper confidence intervals (CI), and *P*-values (*P*) from Games-Howell test of mean daily and seasonal range sizes  $(km^2)$  for female greater sage-grouse (n = 66) compared between females with broods 0–2 weeks, broods 3–5 weeks, and broodless females. Data based on mean daily and seasonal range sizes computed as a 95% utilization distribution from a dynamic Brownian Bridge Movement Model for sage-grouse in Carbon County, Montana, and Park County, Wyoming, USA, 2018–2019.

		Daily			Seasonal	
Reproductive	Difference	95% CI	Р	Difference	95% CI	Р
state	(km <sup>2</sup> )			(km <sup>2</sup> )		
Broods 3–5 wks–	0.011	0.003 to 0.018	0.002	0.152	0.062 to 0.243	0.001
Broods 0-2 wks						
Broods 0–2 wks– Broodless	-0.007	-0.015 to 0.001	0.021	-0.225	-0.327 to -0.122	0.001
Broods 3–5 wks– Broodless	0.003	-0.005 to 0.011	0.658	-0.072	-0.195 to 0.051	0.335



**Figure 3.1.** Relative probability of selecting visual obstruction (A) and forb cover (B) by greater sage-grouse females with broods 3–5 weeks while foraging. Relative probability of selection was plotted with 95% confidence intervals (shaded areas). Available habitat limits for microhabitat characteristics defines the x-axis limits. Data collected during 2018 and 2019 in Carbon County, Montana, and Park County, Wyoming, USA.



**Figure 3.2.** Relative probability of selecting visual obstruction by greater sage-grouse females with broods 0–2 weeks and 3–5 weeks while night roosting. Relative probability of selection was plotted with 95% confidence intervals (shaded areas). Available habitat limits for visual obstruction defines the x-axis limit. Data collected during 2018 and 2019 in Carbon County, Montana, and Park County, Wyoming, USA.



**Figure 3.3.** Proportion of greater sage-grouse females active during the day for females with broods 0–2 weeks, 3–5 weeks, and broodless females. Activity was defined as the upper 25<sup>th</sup> quartile of the variance in acceleration (measured every 0.1 sec for 10 sec) along the Z-axis collected at 5-min intervals averaged over a 20-min moving window. Data collected during 2018 and 2019 breeding seasons in Carbon County, Montana and Park County, Wyoming, USA.



**Figure 3.4.** Distribution of daily (A) and seasonal (B) range sizes (km<sup>2</sup>) for females with broods 0-2 weeks (n = 27), broods 3-5 weeks (n = 22), and broodless females (n = 23) computed as a 95% utilization distribution from a dynamic Brownian Bridge Movement Model of greater sagegrouse during 2018 and 2019 breeding seasons in Carbon County, Montana, and Park County, Wyoming, USA. Boxes report the interquartile range ( $25^{th}-75^{th}$  percentile) in range size by reproductive state, horizontal lines inside boxes are the median, lower and upper whiskers are 1.5-times the interquartile range, and points above and below whiskers are outliers.