Effects of Grazing on Songbirds, Sage-grouse, and Invertebrates in Central Montana

Final Report

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CONTRIBUTORS

Elizabeth Simpson, Ph.D.	Research Scientist, Avian Science Center University of Montana
Shea Coons	Research Associate, Avian Science Center University of Montana
Kaitlyn Reintsma, Ph.D.	Ph.D. Candidate, Wildlife Biology, Avian Science Center University of Montana
Jennifer Helm, Ph.D.	Ph.D. Candidate, Wildlife Biology, Avian Science Center University of Montana
Ethan Shafron	Field Coordinator, Data Analyst, Spatial Analysis Laboratory University of Montana
Jessica Mitchell, Ph.D.	GIS Analyst, Director of Spatial Analysis Laboratory University of Montana
Lorelle Berkeley, Ph.D.	Wildlife Research Biologist Montana Fish, Wildlife and Parks
David Messmer, Ph.D	Wildlife Research Biologist Montana Fish, Wildlife and Parks
Victoria J. Dreitz, Ph.D.	Professor, Director of Avian Science Center University of Montana

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EXECUTIVE SUMMARY

The sagebrush steppe of the western US is one of the most imperiled ecosystems in North America. Corresponding declines in sagebrush avifauna mirror their disappearing sagebrush habitat. Most notably, the greater sage-grouse (*Centrocercus urophasianus*; hereafter ‘sage-grouse’) has been extirpated from approximately half of its range since European settlement. Similarly, grassland and shrubland songbirds inhabiting sagebrush habitat are exhibiting precipitous declines, more so than any other avian guild in North America. Since livestock grazing is the dominant land management practice in sagebrush ecosystems, livestock grazing may offer a promising strategy for conserving and improving avian habitat in sagebrush rangelands. Rest-rotation grazing, in particular, may be useful for promoting habitat diversity. However, grazing effects, regardless of grazing regime, vary depending on ecological context. While rest-rotation grazing has been implemented in other ecosystems, its impacts on sagebrush habitat in central Montana are unknown. A decade of data collection (2011-2020) has allowed us to evaluate the long-term and short-term effects of rest-rotation grazing implemented through the Sage Grouse Initiative (SGI) on songbird reproduction and community metrics, sage-grouse vital rates and habitat, and arthropod biomass.

Songbird species richness, composition, diversity, and reproduction metrics in SGI pastures were largely unchanged relative to non-SGI grazing pastures. However, estimates of abundance for the five most common species suggest species-specific responses to the two grazing systems. For instance, thick-billed longspurs (*Rhynchophanes mccownii*) were most abundant on lands using SGI grazing, while observations of western meadowlarks (*Sturnella neglecta*) were higher on non-SGI plots during the early years of our study. For our three focal species, Brewer’s sparrow (*Spizella breweri*), vesper sparrow (*Pooecetes gramineus*), and thick-billed longspur, we located 40% of nests on lands using non-SGI grazing, compared to 60% of nests on lands using SGI grazing. Estimated nest density was higher on SGI grazing plots for thick-billed longspur while nest densities for both Brewer’s and vesper sparrows were higher on non-SGI plots. For all focal species, nest success showed little difference between SGI and non-SGI. Both nest density and nest success varied more annually than between SGI and non-SGI.

To better understand the reproductive performance of the three focal songbird species, we developed a novel time-to-event nest success and abundance model (TNSAM; see Reintsma et al. 2023 for detailed methods and results). The TNSAM estimated nest detection, nest success, and nest abundance within the range of past estimates for these species. Average daily nest detection was 0.46 (CRI: 0.41–0.50) for Brewer’s sparrow, 0.48 (CRI: 0.41–0.55) for thick-billed longspur, and 0.52 (CRI: 0.47–0.57) for vesper sparrow. Average nest success by species was 0.47 (CRI: 0.41–0.53), 0.31 (CRI: 0.23–0.39), and 0.41 (CRI: 0.35–0.46) for Brewer’s sparrow, thick-billed longspur, and vesper sparrow, respectively. Across all seven years of the study, Brewer’s sparrow had an estimated 692 (CRI: 630–783) total nests, thick-billed longspur an estimated 491 (CRI: 403–646) total nests, and vesper sparrow an estimated 699 (CRI: 644–776) total nests. We also assessed the influence of remotely sensed sagebrush habitat characteristics, including field-based grazing metrics, on songbird reproduction (i.e.,

nest success and nest detection). For the same three focal species assessed with the TNSAM model, we found that nest success and detection were primarily influenced by abiotic weather conditions over the course of the active nesting period. For example, we detected a negative effect of variation (SD) in minimum temperature on nest success for Brewer's and vesper sparrow and a negative effect of variation (SD) in maximum temperature on nest success for thick-billed longspur. Additional temperature, precipitation, and a random effect for year also affected nest detection and survival for these species.

To investigate how the SGI grazing program influences sage-grouse habitat, we assessed whether a variety of grazing and environmental metrics affected remotely sensed rangeland productivity metrics within the study area. We found that field-based measures of grazing (e.g., number of cow patties) had weak positive effects on perennial forb and grass productivity and that pasture-level covariates (e.g., AUMs) had slight negative effects on annual forb and grass productivity. The grazing covariate effects were significantly smaller than the effect of environmental factors on productivity. This outcome suggests that local grazing management did not have a large, short-term effect on sage-grouse habitat in this study area. These results were corroborated by vegetation measurements in field plots stratified across SGI and non-SGI grazing regimes, where we found negligible effects of SGI grazing management on vegetation.

We also assessed the annual and seasonal patterns of sage-grouse hen habitat selection using resource selection functions. We evaluated selection for pastures enrolled in SGI grazing treatments as well as ground cover and topography covariates. We found that hens selected strongly for shrub cover, flatter slopes, and less tree cover across all seasons and at the annual temporal scale. Overall, sage-grouse tended to select pastures enrolled in the SGI program (as opposed to pastures not enrolled) before, during, and after the grazing program was implemented. However, the strength and pattern of the trend of this selection varied based on season and at the annual spatial scale.

For sage-grouse vital rates, our results suggest that annual variation in climate and other factors affects sage-grouse demography. Generally, SGI grazing management did not affect sage-grouse vital rates. For both nest success and chick survival, we did not detect a difference between SGI and non-SGI grazing. The 37-day nest success for SGI pastures was 0.31 (CRI: 0.22-0.40) and for non-enrolled pastures was 0.37 (CRI: 0.29-0.45). Our estimates of chick survival at 45 days were highly variable among years (range: 0.26–0.69), but overall were relatively high compared to survival rates across the species range. Chick mortality risk was not associated with brood hen age or body condition, chick sex, weather, vegetation, or other anthropogenic variables. However, chick body mass did have a slight protective effect, conferring a hazard decrease of 2.3% for every additional gram of chick mass at capture (adjusted for age-at-capture). Annual hen survival estimates were also highly variable among years (range: 0.46–0.84), but again fairly consistent with sage-grouse hen survival rates across their range. We drew covariates from each hen's annual home range to assess the effect of weather and vegetation on hen survival and found that mean annual temperature had a positive effect on hen survival. Mean annual temperature was positively correlated with perennial forb and grass cover and negatively correlated with variation in MAT and mean and variation in monthly cumulative precipitation, shrub cover, and annual forb and grass cover.

We obtained mean annual population growth rates of 0.90 and 1.16 from a female-based matrix population model and male-based lek count data, respectively. These estimates suggest contrasting population trends; a declining trend from the matrix model and an increasing trend from the lek counts. Additionally, the lek-based estimator was more variable, interannually, than the matrix model growth rate. Using a female-based matrix population model, we also showed that sage-grouse annual population growth was expected to be most sensitive to adult hen survival, nest success, and chick survival. In light of the contrasting trends shown by these two methods, we suggest that additional analysis will be needed to determine the status of this population. Lek-based estimators provide a generalization of population trends, but the accuracy of the trend is highly variable and does not provide insight into the demographic processes driving the trend. In contrast, female-based matrix population models can be more precise because they account for life-history processes. However, matrix models can inaccurately identify changes in population due to imprecise and/or biased annual vital rates and possible sampling bias or violation of assumptions when estimating specific vital rates.

We expanded upon the vital rate and matrix model results by building a study-area scale population model to evaluate the environmental and habitat variables that affected key vital rates and whether they cumulatively influenced annual population growth. We tested grazing-related covariates, including enrollment in SGI grazing, mean animal unit months (AUMs), and mean cow dung index, and vegetation and weather covariates, including an index of above-ground biomass of perennial forbs and grasses, and various seasonal temperature and precipitation covariates. We found support for a positive effect of the percent of the study area that had been previously enrolled in the SGI grazing program, indicating a potential lagged effect of enrollment on growth rates. This could reflect gradual improvements in habitat condition caused by the SGI program. However, because percent area post-SGI grazing increased linearly each year, this result may be conflated with other concurrent processes. This result was also strongly influenced by a very high annual population growth rate estimate in the last year of the study period. We also detected a positive effect of winter (Jan. 1 – Mar. 15) mean daily minimum temperatures on annual growth rates. The latter result aligns with others' assessment in the study area, including a positive impact of mean annual temperature on annual female survival. This suggests that hen survival in milder winters has a positive impact on annual population growth.

Finally, a related study objective to improve the predictive spatial model of invertebrate biomass has also been completed. Models were developed and tested for improving invertebrate biomass predictions across the sage-grouse and songbird study areas. A variety of climate and topographic predictor variables were introduced into the models to assess the potential for improving predictive performance within and across years. Additional grazing metrics (SGI enrollment and grazing timing, frequency, and duration) were tested for importance in previous models (Mitchell et al. 2021), but these variables failed to increase predictive power and were not retained in models detailed within this report. Covariates in the most parsimonious model included: April snowpack, precipitation coefficient of variation, max temperature standard deviation, max temperature coefficient of variation, and accumulated degree days. Despite intensive biomass sampling efforts in the field, prediction improvement was limited. Additional model testing rejected the hypothesis that advanced machine learning algorithms could compensate for the strong influence of multi-scale temporal variability on prediction performance over relatively large study areas.

Overall, the effects of SGI rest-rotation grazing were similar to non-SGI grazing regimes for most metrics examined. Compared to interannual environmental variation, rest-rotation grazing under the SGI program had minimal effects on songbird species richness, composition, diversity, and reproduction. We also found minimal effects of SGI grazing on invertebrate biomass, sage-grouse habitat, and sage-grouse vital rates. However, we found inconclusive evidence for positive effects of SGI grazing on sage-grouse habitat selection and population growth. We describe these latter effects as inconclusive because we suspect that they may be confounded with other covariate effects and, overall, these effects were small compared to the effects of weather and interannual variation. These results do not discount the potential positive impacts of rest-rotation grazing on sagebrush habitat, but they do suggest that a more systematic, experimental, long-term study design would be necessary to conclusively identify the positive impacts of the SGI program as a habitat management method to improve songbird or sage-grouse habitat and populations. The songbird, sage-grouse, and invertebrate study objectives are complete, although for some objectives peer-reviewed publications are still in progress. These publications are noted as “In prep. for submission” in the publications tables.

INTRODUCTION

The sagebrush steppe once covered over 62 million hectares in the western US and southwestern Canada but is now among the most imperiled ecosystems in North America (Noss et al. 1995). Conifer encroachment (Miller et al. 2011), exotic annual grass invasion (Chambers et al. 2014; D’Antonio and Vitousek 1992), altered fire regimes (Baker 2011), cropland conversion (Smith et al. 2016), and energy development (Walker et al. 2007; Walston et al. 2009) all contribute to the highly fragmented and disappearing sagebrush biome (Davies et al. 2011; Knick et al. 2003). Sagebrush habitat loss and degradation increase the risk of local and regional extirpations of sagebrush-dependent wildlife, the consequences of which are currently transpiring via emphatic avifaunal declines. Most notably, the greater sage-grouse (*Centrocercus urophasianus*; hereafter ‘sage-grouse’) has been extirpated from approximately half of its range since European settlement (Schroeder et al. 2004). Long-term declines in sage-grouse abundance and distribution (Connelly and Braun 1997; Schroeder et al. 2004) have warranted multiple evaluations for listing under the Endangered Species Act (U.S. Fish & Wildlife Service, 2015). Similarly, grassland and shrubland songbirds are exhibiting precipitous declines, more so than any other avian guild in North America (Rosenberg et al. 2019; Sauer et al. 2017), with many of these species associated with sagebrush habitat. Rangeland management practices that conserve and improve remnant sagebrush habitats may be a promising strategy for mitigating widespread population declines of sagebrush birds.

Affecting 70% of land in the western US, livestock grazing is the dominant land management practice in sagebrush ecosystems (Heady et al. 1974). While overgrazing has been implicated in sagebrush deterioration (Fleischner 1994; Mack 1981), range conditions have since improved due to advancements in rangeland ecology and better administration of public lands grazing (Holechek 2011). Moreover, grazing is not a novel process in this ecosystem (Perryman et al. 2021); sagebrush steppe-associated birds coevolved with variable vegetation structure created by dynamic disturbance processes, including grazing (Duchardt et al. 2018). In some systems, livestock grazing has even been promoted as a surrogate for historical ecological processes (Fuhlendorf and Engle 2001). Since changes to vegetation structure may be the primary mechanism through which grazing affects wildlife, managers may be able to manipulate grazing variables (e.g. stocking rate, timing, duration) to achieve specific habitat outcomes. However, it is difficult to predict the effects of grazing prescriptions because effects vary substantially based on the ecological setting (Davis et al. 2020).

To combat threats to the sagebrush biome, the Natural Resources Conservation Service (NRCS) - Sage Grouse Initiative (SGI) launched a rest-rotation grazing program designed to simultaneously support wildlife habitat and sustainable ranching (NRCS 2015). The SGI grazing system rotates livestock through different pastures for short periods (< 45 days) and shifts the annual timing of grazing each year. This method is intended to allow vegetation to recover from previous grazing disturbances (NRCS 2017). In contrast, other non-SGI grazing practices may entail a season-long livestock presence without annual changes in season of use (Holecheck et al. 1999). Rest-rotation grazing systems may also promote a mosaic of varying stages of disturbance where the resulting structural heterogeneity fulfills habitat requirements of numerous species (Fuhlendorf and Engle 2001; Krausman et al. 2009). However, grazing impacts are site-specific. Intensity, duration, timing, livestock type, and biophysical factors (e.g. soil, climate, topography; Briske et al. 2008; Holechek et al. 1999; Lipsey and Naugle 2017; Veblen et al. 2015) all influence vegetation response to grazing. Additionally, the effects of rest-rotation grazing systems have not been closely examined in central Montana where there is a need for understanding how grazing can meet desired stakeholder and wildlife management goals. Herein, we compare SGI and non-SGI grazing regimes to determine grazing impacts on the sagebrush community within a working landscape.

Management actions applied within the sagebrush steppe are often evaluated through the lens of sage-grouse conservation objectives. Over 50 years of sage-grouse population declines prompted unprecedented conservation efforts directed towards reversing these trends and precluding protections from the Endangered Species Act. Sage-grouse have subsequently become emblematic of sagebrush conservation and are often perceived as an umbrella species for other sagebrush-dependent species (Barlow et al. 2020; Rowland et al. 2006). While single-species approaches to conservation, like that of sage-grouse, allow managers to make the most of limited resources, this umbrella may not always be adequate for co-occurring species that require separate management actions (Carlisle et al. 2018; Carlisle et al. 2020; Dinkins and Beck 2019; Smith et al. 2021). Alternatively, a multi-species strategy can broaden the protections offered by a single umbrella species since an umbrella species may be unaffected by ecological factors that inevitably limit some co-occurring species (Roberge and Anglestam 2004; Timmer et al. 2019). Systematically selecting multiple focal species that require a range of habitat types and landscape attributes across different spatial scales can provide a holistic perspective on ecosystem integrity and management impacts.

This report uses a multi-species assemblage to examine impacts of rest-rotation grazing employed through SGI. Our focal species included songbirds, sage-grouse, and invertebrates (e.g., arthropods) because of their interrelated roles in sagebrush systems. Songbirds are integral to ecological communities because they function as predators, prey, pollinators, and seed dispersers (Whelan et al. 2008). Their sensitivity to habitat change makes songbirds effective indicators of shifting habitat conditions that may occur as a result of grazing (Canterbury et al. 2000; Coppedge et al. 2006; Milchunas et al. 1998). Sage-grouse conservation has strongly shaped land use policy and management actions that affect other sagebrush-dependent wildlife, but there remains a paucity of information regarding specific grazing effects on sage-grouse demographics and habitat in central Montana (Dettenmaier et al. 2017). Finally, arthropod communities are an important food source for sagebrush songbirds and are especially vital for sage-grouse chick development and survival (Johnson and Boyce 1990).

This final report outlines the outcomes of a decade (2011-2020) of research evaluating SGI rest-rotation grazing on songbird community and reproduction metrics, sage-grouse habitat and demographics, and invertebrate biomass within a central Montana sagebrush ecosystem. This research has the following long-term objectives:

Songbird

Objective 1: Investigate migratory songbird abundance, species richness, species diversity, and community composition responses to SGI versus non-SGI grazing.

Objective 2: Investigate migratory songbird breeding performance of three focal songbird species (Brewer's sparrow, vesper sparrow, and thick-billed longspur) responses to SGI and non-SGI grazing as a management tool.

Sage-grouse

Objective 1: Measure the vegetation response in pastures receiving different grazing and resting treatments, relative to published sage-grouse habitat needs.

Objective 2: Create habitat-based measures of fitness which can be compared among grazing treatments by measuring individual vital rates known to impact population growth in sage-grouse and relating estimated vital rates directly to habitat variables and other important drivers.

Objective 3: Identify movements by sage-grouse between grazed and rested pastures to quantify use of treatments proportional to habitat availability and other drivers of sage-grouse resource selection.

Objective 4: Create a habitat-linked population model to:

a. Evaluate and forecast the benefits of treatments within a rotational grazing system on sage-grouse populations in the context of other drivers of sage-grouse vital rates, so as to put the influence of grazing management on population dynamics in context, and
b. Identify current areas that are most important to sage-grouse to prioritize locations where habitat management will have the most benefit to populations.

Objective 5: Quantify the population-level response of grazing treatments by indexing lek counts to our population modeling results, then by comparing lek counts within the Roundup study area to surrounding populations. To the extent that lek counts represent population changes reflected in population models, bird response to grazing might be forecasted in other areas where only lek count data are available.

Objective 6: Generate spatially explicit maps for areas with high quality seasonal habitat. Specifically, we will produce maps that delineate areas with habitat attributes that define relative probability of use and that have a positive influence on vital rates during the nesting, brood-rearing, and winter periods, and extrapolate to similar landscapes to the extent that these models validate well.

Invertebrates

Objective 1: Create a spatial layer that predicts invertebrate biomass for the sage-grouse and songbird grazing project study areas.

Objective 2: Link information from the invertebrate spatial layer to sage-grouse and songbird populations.

We have completed ~10 years of data collection towards these objectives. Previous years' work is detailed in prior annual reports (see Coons et al. 2023; Dreitz et al. 2021; Berkeley et al. 2021; Mitchell et al. 2021). However, data collection in the 10th year (2020) was minimal because we were not able to hire seasonal technicians and expend our usual effort to collect data due to the coronavirus (COVID-19) pandemic. Songbird, sage-grouse, and invertebrate objectives have been completed. Final updates about objectives, deliverables, and publications are aggregated by project (songbird, sage-grouse, invertebrates) within this report.

STUDY AREA

The study area was in central Montana in rolling topography that ranged from 975-1,250m in elevation (Smith et al. 2018b) and covered approximately 150,000 hectares in Musselshell and Golden Valley counties (Figure 1). The vegetation was consistent with big sagebrush steppe, the most widely distributed sagebrush system in Montana. Wyoming big sagebrush (*Artemisia tridentata ssp. wyomingensis*) and silver sagebrush

(*A. cana*) were both common and co-dominant, with a mix of perennial bunchgrasses, perennial rhizomatous grasses, and forbs composing up to 25% of cover (Montana Natural Heritage Program 2021).

This region has cooler soil temperature and higher soil moisture than other parts of the sage-grouse range (Pyke et al. 2015). The average monthly temperature in Roundup (2009-2020) ranged from a low of -3.8º Celsius (25.1º Fahrenheit) in January to a high of 21.8º Celsius (71.2º Fahrenheit) in July (National Centers for Environmental Information 2021). Average monthly precipitation in Roundup (2009-2020) ranged from a low of 9.40 millimeters (0.37 inches) in January to a high of 73.41 millimeters (2.89 inches) in June (National Centers for Environmental Information 2021). The climate is cold, semi-arid (Pyke et al. 2015), with distinct seasons that include cool and wet springs, hot and dry summers, cool and wet autumns, and cold, snowy winters. The study area is a mosaic of public (federal, state, and county) and private ownership dominated by cattle rangeland, with some sheep rangeland and some dryland farming (Smith et al. 2018a, Smith et al. 2018b).

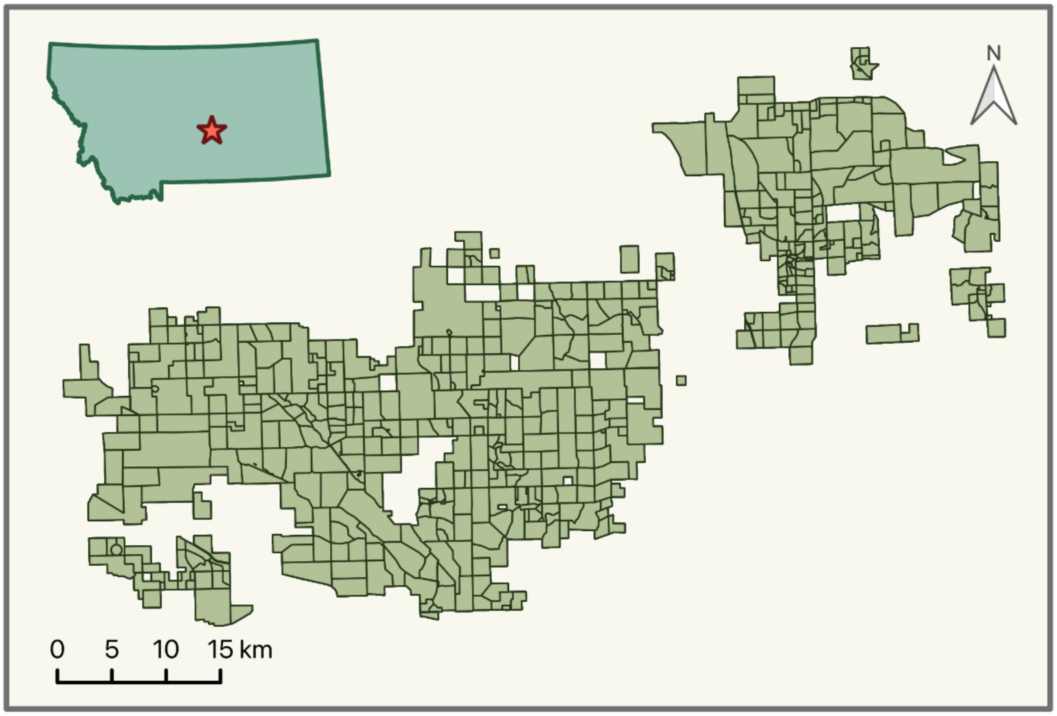

Figure 1. Livestock pasture boundaries within the study area in Golden Valley and Musselshell Counties, Montana, USA during 2011-2020.

THE SAGE GROUSE INITIATIVE (SGI) GRAZING PROGRAM

The SGI grazing program in central Montana focused on improving livestock production and rangeland health while simultaneously alleviating threats to and improving habitat for greater sage-grouse (NRCS 2015). The SGI program was implemented on private ranches containing potential sage-grouse habitat as defined by topography and sagebrush canopy cover ≥5% (NRCS pers. comm.) within sage-grouse core areas. FWP has designated core areas in Montana as locations of highest conservation value for sage-grouse based on habitat and number of breeding males. FWP has estimated that the core areas included ~76% of the displaying males in Montana as of 2013.

Livestock producers enrolled in the SGI program implemented an approximately three-year grazing regime developed with NRCS range management specialists. SGI grazing regimes were rotational and used a combination of rest and deferment to increase vegetation cover for nesting hens (Doherty et al. 2014, Smith et al. 2018b), in addition to other strategies. Range management specialists suggested pasture rest, pasture deferment, changing the number of animal units, or installing fences or water sources to adjust pasture size or livestock distribution. SGI grazing regimes were tailored to each ranch and varied by the needs of the producer or pasture condition while following the NRCS Conservation Practice Standard for Prescribed Grazing (Natural Resources Conservation Service 2017, Smith et al. 2018b). Additionally, plans align with four minimum criteria intended to support sage-grouse habitat:

1. Grazing utilization rates of ≤50% of the current year's key forage species growth,
2. ≥ 20-day shift annually in the timing of grazing,
3. a plan to address unexpected circumstances like drought or fire, and
4. ≤ 45-day continuous grazing within any one pasture (Smith et al. 2018b).

Our work evaluated the effects of these recommendations to determine if this program yields biologically relevant benefits to songbirds, sage-grouse, and their invertebrate food sources. We categorized enrolled pastures into before, during, and after implementation of SGI grazing to disentangle direct and indirect effects of SGI grazing. Non-SGI grazing involved multiple types of grazing systems with less intensively managed and slower rotations, usually lacking annual changes in use.

SONGBIRD COMMUNITY AND REPRODUCTION

From 2013-2019 we collected field data to evaluate the relationships between grazing and sagebrush steppe songbird community composition and demographic parameters related to SGI's rotational grazing regime. Detailed methods and results can be found in the Migratory Songbird Grazing Study Final Report (P-R grant W-165-R-1 to FWP; Dreitz et al. 2021). This study had two objectives, which are detailed below.

Objective 1: Investigate migratory songbird abundance, species richness, species diversity, and community composition responses to SGI versus non-SGI grazing.

We conducted avian count transect surveys using the dependent double-observer method. During 2013–2019, the total number of individuals we observed in the study area, regardless of grazing regime, ranged from 5,954–14,097, and the total number of species ranged from 72–88. We observed low variation in avian community composition amongst years, suggesting a relatively stable species richness in our study area over time. The migratory songbird species observed most often since 2013 were: thick-billed longspur (*Rhynchophanes mccownii;* previously named McCown's longspur), vesper sparrow (*Pooecetes gramineus*), Brewer's sparrow (*Spizella breweri*), horned lark (*Eremophila alpestris*), and western meadowlark (*Sturnella neglecta*). Estimates of abundance for the five most common species suggest species-specific responses to grazing (see Dreitz et al. 2021 for specific categorizations of SGI and non-SGI pastures used in songbird community analyses). For instance, thick-billed longspurs were most abundant on lands using SGI grazing, while observations of western meadowlarks were higher on non-SGI plots during the early years of our study.

Objective 2: Investigate migratory songbird breeding performance of three focal songbird species responses to SGI and non-SGI grazing as a management tool.

We identified three focal species, each associated with one of the three most common vegetation characteristics in sagebrush steppe. We conducted nest searches and monitored nesting activity of Brewer's sparrow (sagebrush nester), vesper sparrow (generalist ground nester), and thick-billed longspur (grassland ground nester). For our three focal species, we located 40% of nests on lands using non-SGI grazing, compared to 60% of nests on lands using SGI grazing. Estimated time-to-event nest density was higher on SGI grazing plots for thick-billed longspur while time-to-event nest densities for both Brewer's and vesper sparrows were higher on non-SGI plots. For all focal species, time-to-event nest success showed little difference between SGI and non-SGI (see Dreitz et al. 2021 for specific categorizations of SGI and non-SGI pastures used in songbird reproduction analyses). Both time-to-event nest density and nest success varied annually.

To better understand the reproductive performance of the three focal species, we developed a novel time-to-event nest success and abundance model (TNSAM; see Reintsma et al. 2023 for detailed methods and results). This model can use nest data collected with any nest survey method (i.e., opportunistic or structured surveys) given the nest age is recorded and the nest is monitored until success or failure. We assessed the model performance using simulations and validated the model using nest data collected from the three focal species during 2013-2019. The nest data consisted of a total of 1,148 nests from the three species where approximately half of the nests were found opportunistically. The TNSAM performed well for these species, with little bias under the range of detection, survival, and abundance conditions we observed. We estimate nest detection, nest success, and nest abundance that were within the range of past estimates. From 2013–2020, average daily nest detection was 0.46 (CRI: 0.41–0.5) for Brewer's sparrow, 0.48 (CRI: 0.41–0.55) for thick-billed longspur, and 0.52 (CRI: 0.47–0.57) for vesper sparrow. Daily next detection values represent the daily probability that a nest was detected, given that it was available for detection. Average nest success was 0.47 (CRI: 0.41–0.53), 0.31 (CRI: 0.23–0.39), and 0.41 (CRI: 0.35–0.46) for Brewer's sparrow, thick-billed longspur, and vesper sparrow, respectively. Across the seven years of the study, Brewer's sparrow had an estimated 692 (CRI: 630–783) total nests, thick-billed longspur an estimated 491 (CRI: 403–646) total nests, and vesper sparrow an estimated 699 (CRI: 644–776) total nests. These findings suggest that the TNSAM can estimate nest success, detection, and abundance using data commonly collected for time-to-event nest success and is easily extended to other nesting species or study interests. Thus, the TNSAM provides a tool for improving understanding of reproduction, which is a vital rate influential to the growth or decline of many populations.

We also assessed the influence of remotely sensed sagebrush habitat characteristics and field-based grazing metrics on songbird reproduction (i.e., nest success and nest detection). We looked at the same three focal songbird species as in the TNSAM model. Despite the distinct habitat associations of the focal species, we found that nest success and detection were primarily influenced by abiotic weather conditions over the course of the active nesting period. For example, we detected a negative effect of variation (SD) in minimum temperature on nest success for Brewer's and vesper sparrow and a negative effect of variation (SD) in maximum temperature on nest success for thick-billed longspur (Figure 2). Additional temperature, precipitation, and a random effect for year also affected nest success and detection for these species. Relative to similar studies, this study provides a unique perspective because it uses a large number of nests over a long period of time. It also adds to the limited information about the relationship between songbird reproduction vital rates and sagebrush steppe habitat (Gilbert and Chalfoun 2011). Notably, weather and random effects had a more substantial impact on songbird reproduction than vegetation or other habitat covariates. This work shows broader landscape patterns may be more appropriate for assessing songbird biodiversity (Gregory and Strien 2010) but may differ from finer-scale covariate effects (Johnson 2007). Despite these differences, the major effects we detected align with previous habitat assessments for these species.

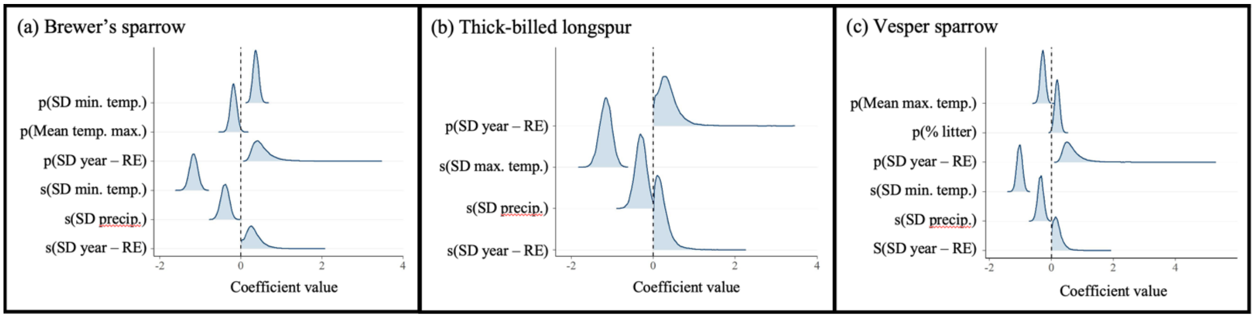

Figure 2. The covariate effects included in the final models for estimating nest detection (p), success (s), and abundance for (a) Brewer's sparrow, (b) thick-billed longspur, and (c) vesper sparrow.

Final Status:

We have completed the songbird community and reproduction study objectives. Two more peer-reviewed publications detailing the development of the time-to-event nest success and nest abundance model and its use in determining factors that influence sagebrush songbird reproduction are in preparation.

Deliverables:

Objectives	Description	Status

Objective 1	Investigate migratory songbird abundance, species richness, species diversity, and community composition responses to SGI versus non-SGI grazing.	**Complete**
Objective 2	Investigate migratory songbird breeding performance of three focal songbird species responses to SGI and non-SGI grazing as a management tool.	**Complete**

Student	Description	Status
MS Student	Individual officially enrolled at the University of Montana in August 2016 (year 1). Student participated in 2016, 2017, and 2018 field seasons, year 1, 2, and 3 respectively. Degree awarded May 2019.	**Complete**
PhD Student	Selected PhD candidate in spring 2017 (year 2). Individual officially enrolled at the University of Montana in August 2017. Degree awarded May 2023.	**Complete**

Publications	Status
Reintsma, K. M., D. P. Walsh, V. J. Dreitz. Time-to-event nest success and nest abundance model: a novel integrated Bayesian framework for estimating reproductive metrics with one data source.	**In prep. for submission**
Reintsma, K. M., L. I. Berkeley, V. J. Dreitz. Identifying high-quality habitat to support biodiversity in the sagebrush steppe of Montana using songbird reproductive metrics.	**In prep. for submission**
Coons, S.P., K.M. Reintsma, V.J. Dreitz. 2024. Co-occurance and nest success of thick-billed and chentnut-collared longspurs in a central Montana rangeland. Western North American Naturalist.	**Complete**
Ruth, K. A., L. I. Berkeley, K. M. Strickfaden, and V. J. Dreitz. 2023. Density dependence of songbird demographics in grazed sagebrush steppe. PLoS ONE. 18(12): e0289605.	**Complete**
Reintsma, K.M., A.H. Harrington, V.J. Dreitz. 2019. Validation of a novel time-to-event nest density estimator on passerines: An example using Brewer’s sparrows (Spizella breweri). PLoS ONE 12: e0227092	**Complete**
Reintsma, K.M., V.J. Dreitz, L.I. Berkeley. 2022. Thick-billed Longspur (Rhynchophanes mccownii) reproduction shows minimal short-term response to conservation-based program. Wilson Journal of Ornithology 134 (2): 365–372	**Complete**
Golding, J.D., J.J. Nowak, and V.J. Dreitz. 2017. A multispecies dependent double-observer model: A new method for estimating multispecies abundance. Ecology and Evolution 7: 3425–3435.	**Complete**
Golding, J.D. and V.J. Dreitz. 2017. Songbird response to rest-rotation and season-long cattle grazing in a grassland sagebrush ecosystem. Journal of Environmental Management 204: 605-612.	**Complete**

Golding, J.D. and V.J. Dreitz. 2016. Comparison of removal-based methods for estimating abundance of five species of prairie songbirds. Journal of Field Ornithology 87: 417–426.	**Complete**

GREATER SAGE-GROUSE DEMOGRAPHICS AND HABITAT

We evaluated the effectiveness of SGI rotational grazing systems in managing sage-grouse habitat in central Montana. To do so, we measured sage-grouse vital rates (including nest success, chick survival, and hen survival) within these grazing systems and compared them with vital rates in non-SGI grazing systems. We included factors describing vegetation structure and composition to evaluate the effects of grazing on sage-grouse habitat. Data collection occurred during 2011-2020. Detailed methods and results can be found in the "The Effects of Grazing on Greater Sage-Grouse Population Dynamics and Habitat in Central Montana" final report (PR grant W-158-R to FWP; Berkeley et al. 2021).

Objective 1: Measure the vegetation response in pastures receiving different grazing and resting treatments, relative to published sage-grouse habitat needs.

During 2012-2019, we measured herbaceous vegetation in potential sage-grouse habitat using the line-intercept technique at a set of random field plots stratified by grazing system (SGI and non-SGI) to test for differences in vegetation metrics across the project area. While effects were not statistically significant, we observed tendencies for SGI pastures to contain more herbaceous vegetation, taller live grasses, and less forb and shrub cover. However, for most metrics the variation among years and pastures was greater than differences observed in these metrics. Our results are consistent with analyses from Smith et al. (2018a) which found negligible effects of SGI grazing management on vegetation in sage-grouse habitat.

Since the completion of the 2021 sage-grouse PR report (Berkeley et al. 2021), we have done additional analyses of vegetation in the study area (Reintsma et al. 2024). We used mixed-effect generalized linear models to test for the effects of grazing management on rangeland biomass and productivity metrics while accounting for environmental factors. In these models, remotely sensed productivity measures were response variables, while the explanatory variables consisted of both field-based grazing data and remotely sensed environmental factors. We found point-level field measures of grazing (e.g., cow patties, percentage of dung in Daubenmire plots, and number of plants grazed) showed positive effects, especially on perennial plant rangeland responses (Figure 3). Grazing measures at the pasture-level showed a small negative effect on annual plant rangeland responses. Grazing metrics tend to have smaller covariate effects on rangeland biomass and productivity compared to environmental factors, indicating a greater importance of environmental factors in influencing rangeland productivity and biomass in this study area. The effect of grazing metrics may be small because sampling was opportunistic and landowners in this area already practice moderate grazing and adapt annually based on pasture conditions (Budd and Thorpe 2009; Davies et al. 2014). Additionally, the time span of this study was relatively small given that vegetation can take decades to over a century to respond to changes in grazing practices (Fuhlendorf and Smeins 1997).

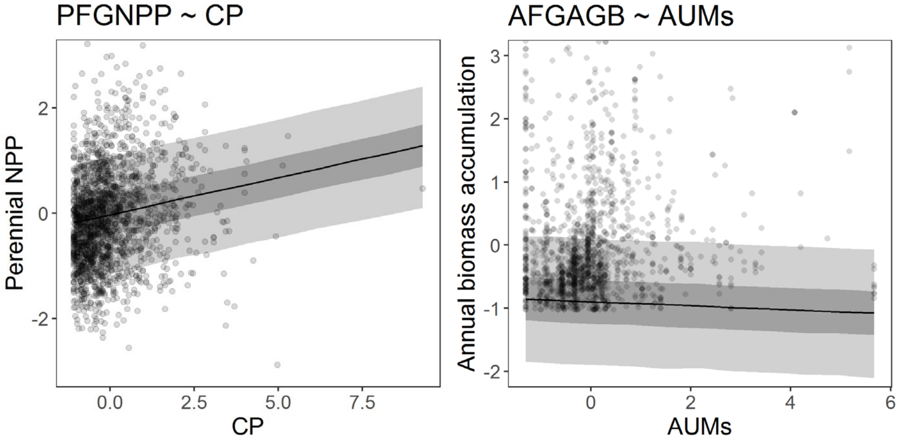

Figure 3. These plots show examples of the partial effects of grazing predictor coefficient values [number of cow patties (CP) and animal units per month (AUMs); centered and scaled] on rangeland response variables: perennial forbs and grasses net primary productivity (PFGNPP) and annual forb and grass above ground biomass (AFGAGB) based on final GLMMs for each rangeland productivity response and grazing metric. The most positive grazing coefficient is shown on the left and the lowest on the right. The predicted rangeland response is shown by the black line, the 50% credible intervals shown by the dark gray shading, and the 95% credible intervals shown in the light gray shading. The data values of the grazing predictor and associated rangeland response values are shown using transparent points.

Objective 2: Create habitat-based measures of fitness which can be compared among grazing treatments by measuring individual vital rates known to impact population growth in sage-grouse and relating estimated vital rates directly to habitat variables and other important drivers.

We collected nest data from 2011-2019 on sage-grouse hens, including yearling (second-year) females and adult (after-second-year) females. Sage-grouse nests were located by monitoring pre-nesting females using radio telemetry ≥2 times per week at the onset of the nesting season. Nests were classified as either failed (eggs were either destroyed or missing) or successful (≥1 hatched egg had a detached membrane, Wallestad and Pyrah 1974). We monitored 736 nests, 391 of which failed. Across all years, 37% of nests were located in SGI pastures, and 63% were located in non-SGI pastures. We estimated sage-grouse nest daily survival rate (DSR) accounting for exposure days (e.g., days between field observations) and derived an estimate of nest success. The SGI status and grazing treatment of each nest location were used to investigate livestock grazing effects on estimated DSR. We used a logistic exposure nest survival model in a Bayesian framework (e.g. Schmidt et al. 2010, Smith et al. 2018b**,** Specht et al. 2020) to estimate the effects of SGI grazing program and grazing-related covariates on sage-grouse nest success. Nest success across the 37-day nesting period averaged 0.36 (CRI: 0.36-0.45) from 2011-2019. We found weak to no evidence for an effect of SGI grazing systems, distance to nearest fence, number of cow patties, proportion of vegetation grazed, or senesced grass height on sage-grouse nest success. Overall, interannual variation, and the unknown or unmeasured factors it represents, explained the most variance in sage-grouse nest success.

Chicks were monitored using VHF radio transmitters that were attached to four randomly selected chicks per brood from 2011-2019. We estimated chick survival to 45 days post-hatch using separate analyses for missing chicks (i.e., individuals whose signals were lost or had unknown fates) treated as 1) right-censored at the last date a signal was obtained and 2) treated as mortalities in a sensitivity analysis. We estimated an overall chick survival rate and survival as a function of female age and sex of chicks using a staggered entry Kaplan-Meier model. We used univariate Cox proportional hazards models to test for differences in mortality risk between female age, chick sex, female body condition index, and chick mass adjusted for age. Finally, we used the Andersen-Gill formation of the Cox proportional hazards model to explore the effects of spatially dependent covariates including SGI program enrollment status, weather, vegetation, terrain, and anthropogenic disturbance. For all years combined, the Kaplan-Meier median survival rate at 45 days was 0.51 (95% CRI: 0.46-0.56). In the sensitivity analysis treating chicks with unknown fates as mortalities, the Kaplan-Meier survival rate estimate was 0.29 (95% CRI: 0.25-0.33). Survival rate estimates for the 510 chicks included in the analysis were highly variable among years (range: 0.26–0.69; Figure 4), but overall were relatively high compared to survival rates across the species range. Chick mortality risk was relatively unassociated with brood hen age or body condition, chick sex, weather, vegetation, and other anthropogenic variables. However, chick body mass did have a slight protective effect, conferring a hazard decrease of 2.3% for every additional gram of chick mass at capture (adjusted for age-at-capture).

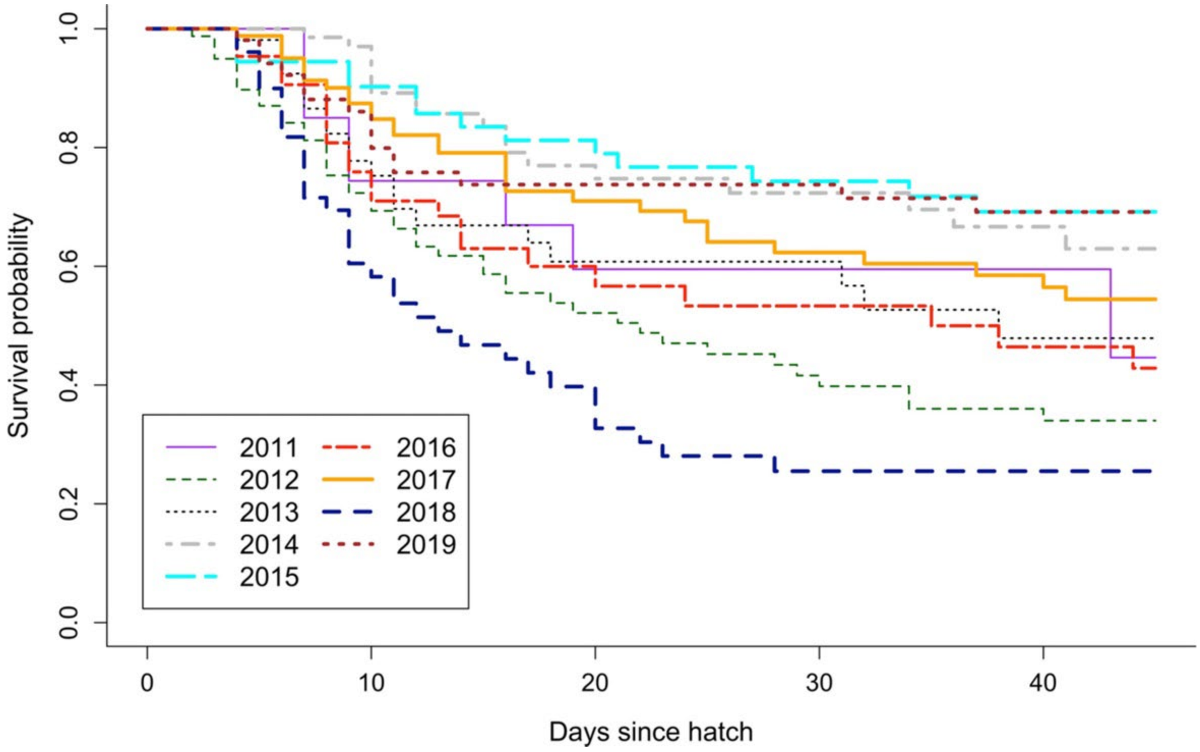

Figure 4. Kaplan-Meier survival curves by year (2011-2019) for marked greater sage-grouse chicks in Golden Valley and Musselshell Counties, MT.

Of the chicks that survived, we recaptured and monitored 45 as juveniles during the late summer/early fall. Seventeen of these juveniles survived to become yearlings (first breeding season), and 13 of these nested. Eleven nested during their first breeding season, 2 waited until their second breeding season, and 2 nested during both their first and second breeding seasons. Five of the 13 nests were successful, with one individual nesting successfully in years 1 and 2. The longest-lived of these individuals was 2.5 years.

Hens were marked with VHF transmitters at the beginning of the breeding season (March and April) from 2011-2020 to monitor hen location and survival. After the first year, additional hens were captured to maintain about 100 hens in our sample per year. To achieve consistency in terms of how mortality was determined and the number of locations per hen, and to avoid the potential negative effects of GPS transmitters on survival, we focused the hen survival analysis on hens marked with VHF transmitters that also met the criteria for known fate models (N = 408 hens). We used known-fate models to estimate annual survival with each year starting when the initial cohort of hens was captured in March and April and ending in February of the following year. Across the entire study (2011-2020) we estimated a hen survival of 0.57 (95% CRI: 0.54–0.61). Like other demographic rates for this species, annual survival estimates varied, with the highest annual survival in 2015 (0.82, 95% CRI: 0.71–0.89) and the lowest annual survival in 2020 (0.21, 95% CRI: 0.09–0.41).

To assess the effects of weather and vegetation-related habitat characteristics on hen survival, we calculated individual, annual home ranges for using utilization distributions for all hens with at least five locations within a sage-grouse year (March 1–end of February of the following year, *n* = 341 hens). We used these distributions to draw covariates from DAYMET (Thornton et al. 2022) and the Rangeland Analysis Platform (Allred et al. 2021; Jones et al. 2018) using Google Earth Engine (Gorelick et al. 2017) including mean and variation in mean annual temperature (MAT), mean monthly cumulative precipitation, and percent cover for shrub, perennial forbs and grasses, annual forbs and grasses, and bare ground. We built a suite of models that accounted for multicollinearity and represented hypothesized predictions about how these covariates may affect hen survival. We hypothesized that vegetation structure, particularly shrub and perennial forb and grass cover, would positively influence survival, due to its role in providing visual obstruction from predators, thermoregulation, and food resources throughout the sage-grouse life cycle (Dinkins et al. 2014; Webb et al. 2012; Davis et al. 2014; Anthony et al. 2021; Moynahan et al. 2006). Additionally, we examined variation in vegetation cover which sage-grouse are hypothesized to select for its resource diversity and potential reduction in predation risk (Aldridge and Boyce 2007; Popham and Gutíerrez 2003; Beers and Frey 2022; Davis et al. 2014).

We found evidence for a positive effect of MAT on hen survival. Mean annual temperature was positively correlated with perennial forb and grass cover and negatively correlated with variation in MAT and mean and variation in monthly cumulative precipitation, shrub cover, and annual forb and grass cover. Interestingly, years with warmer MAT also had less variation in MAT (MAT_{SD}). This indicates that higher MAT could represent years with warmer winters; harsh winters are known to negatively impact sage-grouse in similar parts of their range (Moynahan et al. 2006). Warmer years may also be associated with higher productivity in a sage-brush ecosystem that is less limited by water than some. Higher perennial forb and grass cover associated with higher MAT may provide this sage-grouse population with greater visual obstruction from predators and more foraging opportunities during key parts of their life cycle.

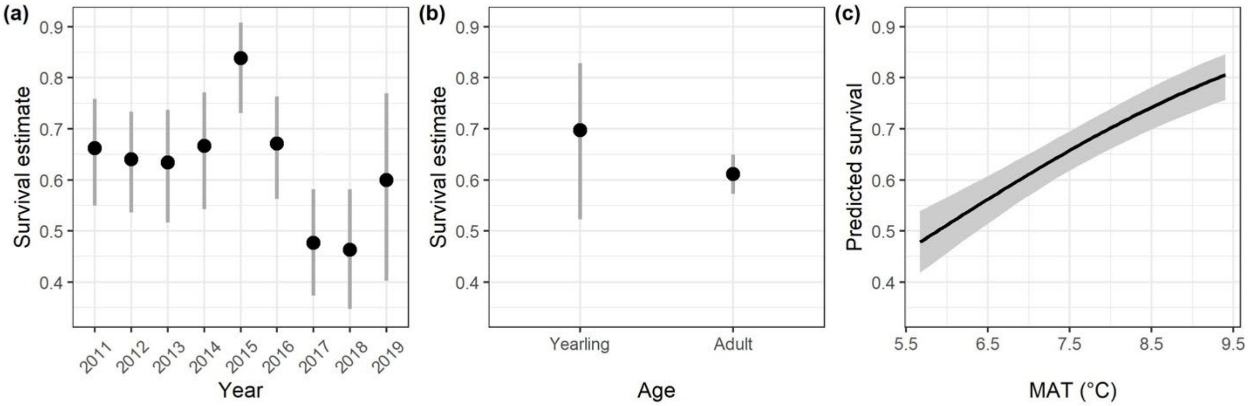

Figure 5. Sage-grouse hen survival varied across (a) years but not between (b) age classes within a central Montana population (*n* = *341*). (c) Higher annual hen survival was best predicted by higher mean annual temperature (MAT, ºC). Variation in estimates plotted as 95% confidence intervals on all plots. While variation in survival was fairly consistent across years (until 2019), there was more variation in yearling survival (*n* = 160) than adult survival (*n* = 181) survival.

Objectives 3 & 6: Identify movements by sage-grouse between grazed and rested pastures to quantify use of treatments proportional to habitat availability and other drivers of sage-grouse resource selection, and generate spatially explicit maps for areas with high quality seasonal habitat.

We assessed the drivers of hen habitat selection in the context of the SGI grazing program. This allowed us to identify the relative influence of broad-scale seasonal habitat characteristics on sage-grouse habitat selection, which can provide direction for management guidelines (Smith et al. 2020). We used location data collected from all VHF- and GPS-monitored hens to assess how female sage-grouse habitat selection varied at two temporal scales: (a) the seasonal scale (divided into four biologically relevant seasons), and the sage-grouse annual cycle (Helm 2023). We defined the seasonal boundaries based on sage-grouse life history—nesting (April 1–May 31), brood-rearing (June 1–July 15), summer-fall (July 16–November 30), and winter (December 1–March 31). We used resource selection functions (RSFs) to assess sage-grouse selection for plant functional type, topography, and pastures enrolled in SGI grazing. Across all four seasons and at the annual scale, sage-grouse hens selected most strongly for shrub cover, flatter slopes, and less tree cover. Overall, sage-grouse tended to select pastures enrolled in the SGI program (as opposed to pastures not enrolled) before, during, and after the grazing program was implemented. However, the strength and pattern of the trend of this selection varied based on season and at the annual spatial scale.

Objective 4: Create a habitat-linked population model to: a) evaluate and forecast the benefits of treatments within a rotational grazing system on sage-grouse populations in the context of other drivers of sage grouse vital rates, so as to put the influence of grazing management on population dynamics in context, and b) identify current areas that are most important to sage grouse to prioritize locations where habitat management will have the most benefit to populations.

We evaluated the environmental and habitat-based variables that may affect key vital rates—adult hen survival, next success, and chick survival—at the study area population scale. We assessed several grazing-related covariates—enrollment in SGI grazing, mean animal unit months (AUMs), and mean cow dung index—as well as vegetation and weather covariates—a remotely sensed index of above-ground biomass of perennial forbs and grasses, various seasonal temperature and precipitation covariates, and drought severity indices—hypothesized to affect annual population growth rate. We predicted that sage-grouse populations would respond positively to relative reductions in grazing intensity because this could result in more residual forb and grass cover during the nesting season and better escape and foraging cover during the brooding rearing season. This hypothesis stemmed from the rationale for implementing the SGI grazing program. We also predicted that favorable weather resulting in more productive rangeland conditions (ample precipitation combined with relatively warm growing season temperatures) would benefit grouse during the brood-rearing period and that warmer winter temperatures would benefit grouse survival. We also made additional predictions related to interacting weather and vegetation conditions, focused on the seasonal effect of conditions on sage-grouse vital rates that contribute to annual population growth rate.

We found support for a positive effect of the annual percent of the study area previously enrolled in SGI grazing program, which indicates a potential lagged effect of enrollment on growth rates. This could reflect gradual improvements in habitat condition caused by the SGI program. However, because percent area post-SGI increased linearly each year, this result may be conflated with other concurrent processes. This result was also strongly influenced by a very high annual growth rate estimate in the last year of the study period. We detected a positive effect of winter (Jan. 1 – Mar. 15) mean daily minimum temperatures on annual growth rates. This temperature effect interacted with an index of snow depth whereby negative effects of cold temperatures were higher in years with increased snow depth. The latter result aligns with vital rate analyses described above, including a positive impact of mean annual temperature on annual female survival and the high importance of annual survival to growth rates in the matrix model sensitivity analysis. This suggests that hen survival in milder winters has a positive impact on annual population growth. Notably, we did not detect effects of other indices of habitat conditions such as the index of above ground biomass drought severity indices, or weather effects during nesting or early brood-rearing periods.

Objective 5: Quantify the population-level response of grazing treatments by indexing lek counts to our population modeling results, then by comparing lek counts within the Roundup study area to surrounding populations.

Comparing data collection techniques and analyses used to monitor managed species provides a better understanding of sources of uncertainty and variation in different methods (Dahlgren et al. 2016). Across the 10 years of this study, we compared estimates of annual population growth rates derived from matrix populations models based on demographic rates from sage-grouse chicks and female sage-grouse to estimates derived from male-based lek count data. Sage-grouse chicks and hens were monitored from 2011-2019 as described above and by Berkeley et al. (2024) and Helm (2023). The matrix population model included nest initiation probability, clutch size, nest success, chick survival, juvenile survival, and hen survival (all described in Helm 2023). Lek count data from 1959 -2022 was obtained from Montana Fish, Wildlife, and Parks, and abundance estimates were derived from these counts as described by Helm (2023).

The geometric mean of the ten-year annual population growth rate derived from the female-based matrix population model was 0.90, which indicates a 10% annual decline in the sage-grouse population. The geometric mean of the annual population growth rate estimated from the male-based lek count data for the same timeframe was 1.16, which indicates an overall increase in the population. While the population growth rates calculated from these two methods track each other in terms of interannual increases and decreases from 2011-2019 (Figure 6), the geometric means suggest opposite trends. In light of the contrasting trends that the geometric mean from these two methods show, we suggest that additional analysis will be needed to determine the status of this population. Higher variability in growth rate estimates from the lek count estimator could make it challenging for managers to use this method to detect population declines over short time periods. In contrast, female-based matrix population models can be more precise, because they account for more life-history processes, but can inaccurately identify changes in population due to imprecise annual vital rates and possible sampling bias or violating assumptions when estimating vital rates.

Final Status:

We have completed the sage-grouse demography and habitat study objectives. Four more peer-reviewed publications detailing sage-grouse nest success, adult hen survival, population growth rate, and an integrated population model are in preparation.

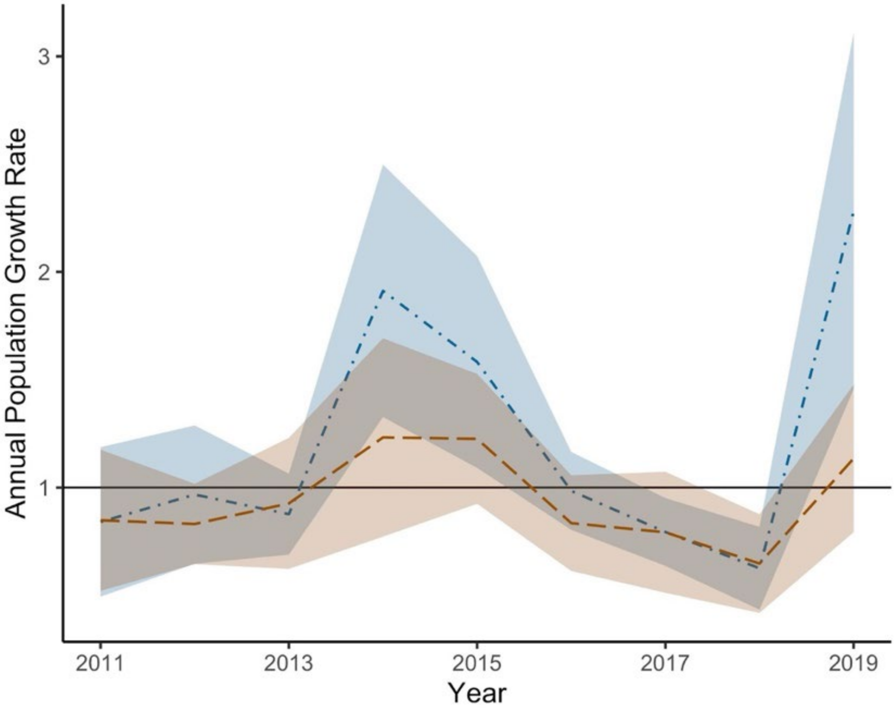

Figure 6. Comparison of the annual population growth rates (2011-2019) from the female-based single-stage population model (brown dashed line) and the male-based lek counts (blue dot dashed line). Error ribbons represent 95% confidence intervals around each annual estimate of population growth rate. A stable population growth rate (λ=1) is shown as a solid, black horizontal line.

Deliverables:

Objective	Description	Status
Objective 1	Measure the vegetation response in pastures receiving different grazing and resting treatments, relative to published sage-grouse habitat needs.	**Complete**
Objective 2	Create habitat-based measures of fitness which can be compared among grazing treatments by measuring individual vital rates known to impact population growth in sage-grouse and relating estimated vital rates directly to habitat variables and other important drivers.	**Complete**
Objective 3	Identify movements by sage-grouse between grazed and rested pastures to quantify use of treatments proportional to habitat availability and other drivers of sage-grouse resource selection.	**Complete**

Objective 4	Create a habitat-linked population model to: a) evaluate and forecast the benefits of treatments within a rotational grazing system on sage-grouse populations in the context of other drivers of sage grouse vital rates, so as to put the influence of grazing management on population dynamics in context, and b) identify current areas that are most important to sage grouse to prioritize locations where habitat management will have the most benefit to populations.	**Complete**
Objective 5	Quantify the population-level response of grazing treatments by indexing lek counts to our population modeling results, then by comparing lek counts within the Roundup study area to surrounding populations. To the extent that lek counts represent population changes reflected in population models, bird response to grazing might be forecasted in other areas where only lek count data are available.	**Complete**
Objective 6	Generate spatially explicit maps for areas with high quality seasonal habitat. Specifically we will produce maps that delineate areas with habitat attributes that define relative probability of use and that have a positive influence on vital rates during the nesting, brood-rearing, and winter periods, and extrapolate to similar landscapes to the extent that these models validate well.	**Complete**

Student	Description	Status
PhD Student	Selected PhD candidate in fall 2018. Individual officially enrolled at the University of Montana in August 2018. Degree awarded May 2023.	**Complete**

Publications	Status
Simpson, E.G., S.P. Coons, D. Messmer, V.J. Drietz. Inter-annual variation in greater sage-grouse (*Centrocercus urophasianus*) hen survival driven by interaction between temperature and vegetation heterogeneity.	**In prep. for submission**
Helm, J.E., E.G. Simpson, L.I. Berkeley, S.P. Coons, M. Szczypinski, V.J. Dreitz. *In review.* The influence of a conservation-based grazing program on greater sage-grouse habitat selection across temporal scales.	**Complete**
Helm, J.E., L.I. Berkeley, S.P. Coons, M. Szczypinski, V.J. Dreitz. Using livestock to manage greater sage-grouse (*Centrocercus urophasianus*) nest success on sagebrush rangelands.	**In prep. for submission**
Berkeley, L.I., M. Szcyzpinksi, S.P. Coons, V.J. Dreitz, J.A. Gude. 2024. Greater sage-grouse chick mortality risk relative to livestock grazing management, environmental factors, and morphometric measurements. The Journal of Wildlife Management: e22596.	**Complete**

Messmer, D. *and others.* Habitat-linked Population Model.	**In prep. for submission**
Helm, J.E., L.I. Berkeley, S.P. Coons, M. Szczypinski, D. Messmer, V.J. Dreitz. Estimating greater sage-grouse population growth rate in central Montana: A comparison of methods with implications for future monitoring.	**In prep. for submission**
Reintsma, K.M., M. Szczypinski, S.W. Running, S.P. Coons, V.J. Dreitz. 2024. Sagebrush Steppe Productivity, Environmental Complexity, and Grazing: Insights From Remote Sensing and Mixed-effect Modeling. Rangeland Ecology & Management, 95: 20-29.	**Complete**
Smith, J.T., J.D. Tack, L.I. Berkeley, M. Szczypinski, and D E. Naugle. 2018a. Effects of Rotational Grazing Management on Nesting Sage-Grouse. Journal of Wildlife Management, 82: 103-112.	**Complete**
Smith, J.T., J.D. Tack, L.I. Berkeley, M. Szczypinski, and D.E. Naugle. 2018b. Effects of Livestock Grazing on Nesting Sage-Grouse in Central Montana. Journal of Wildlife Management, 82: 1503-1515.	**Complete**
Smith, J.T., J.D. Tack, K.E. Doherty, B.W. Allred, J.D. Maestas, L.I. Berkeley, S. Dettenmaier, T.A. Messmer, D.E. Naugle. 2017. Phenology largely explains taller grass at successful nests in greater sage-grouse. Ecology and Evolution, 8: 356-364.	**Complete**

INVERTEBRATE BIOMASS PREDICTIVE SPATIAL LAYER

The objective of this project was to create a predictive spatial layer of invertebrate biomass across the sage-grouse (PR grant #F15AF00490 “MT Sage-Grouse Grazing Evaluation”) and songbird (PR grant #F16AF00294 “Migratory Songbird Grazing Study”) grazing project study areas in central Montana to provide invertebrate food availability data for sage-grouse grazing project vital rate, habitat use, and population models, and songbird grazing project reproduction, community, and abundance models. We completed data collection during spring/summer 2020 and generated a predictive invertebrate biomass spatial layer in 2021 for the sage-grouse and songbird study areas (Mitchell et al. 2021). Results reported herein represent further analysis and fine-tuning of the invertebrate biomass spatial layer for PR grant #F21AF01330. Detailed methods and results can be found in “Predictive Spatial Layer of Invertebrate Biomass for Sage-Grouse and Songbird Grazing Studies in Central Montana” report (PR grant W-164-R-1 to FWP; Mitchell et al. 2021).

Objective 1: Create a spatial layer that predicts invertebrate biomass for the sage-grouse and songbird grazing project study areas.

Building on previous work (see Mitchell et al. 2021), we focused on identifying meaningful predictors of arthropod biomass that fit the sampling strategy employed during the 2019 and 2020 field seasons. While arthropod biomass data were collected for 2012-2020, we constrained observations to 2019 and 2020 because these years had identical sampling frameworks. Previous years used both pitfall and sweep-net samples, whereas 2019 and 2020 used only sweep nets. We represented each sampling location as a point feature and extracted variables related to cumulative growing degree-days, soil moisture, extreme weather, and late spring snow since these are important drivers of arthropod growth (Shaftel et al. 2021; Telfer and Hassall 1999; Wu et al. 2021). These variables were used to compare the predictive power of temporally-static versus dynamic variables. For the biomass data, we aggregated individual survey events by location and date/time to get total biomass for each site. Biomass was then log-transformed. To standardize interpretation of effect sizes, the log-transformed biomass plus all other numeric variables were scaled to have a mean and standard deviation values of 0 and 1, respectively. We used these data to predict log biomass using spatiotemporal variables in ordinary-least-squares (OLS) and linear mixed effects models.

We produced four models to explain the variance of arthropod biomass and used Akaike Information Criterion (AIC; Akaike 1991) to measure bias and select the most parsimonious model. The first model was a linear mixed effects model containing 20 predictors (Table 1; Table 2) and fixed effects for each year. The conditional R^2 was 0.66, Intra-class Correlation was 0.54, and the AIC value was 996.33. While this model had decent predictive power and reasonable within-year correlation, it had a high degree of bias, and many of the predictors were insignificant. The second model was a mixed effects model with annual fixed effects. This model contained topographic variables (slope; Topographic Wetness Index (TWI); elevation) and the most significant predictors from the first mixed effects model, including the coefficient of variation of precipitation[1], standard deviation of daily max temperature[1], coefficient of variation of daily max temperature[1], total precipitation[1], and cumulative degree days[2] (with a 17.8 degree C threshold) (Brust, 2009). A conditional R^2 of 0.63, Intra-class Correlation of 0.47, and lower AIC of 955.9 indicates a more parsimonious model, but there is still a high degree of bias. To reduce bias, we fit two OLS models. To compensate for the observed intra-class correlation in the mixed models that could not be replicated in an OLS model, we incorporated total April snowfall[3] as a predictor. This approach theoretically provided some of the information lost in the annual effects since April snowfall differed significantly between 2019 and 2020 ($p < 0.0001$). The first OLS model had the same predictors as the previous mixed effects model and produced an adjusted R^2 of 0.64, and a lower AIC of 940.9. For the second OLS model, we removed redundant topographic predictors. This final model yielded an adjusted R^2 of 0.65 and the lowest AIC value of 928, indicating the most parsimonious model yet using only weather-related covariates (Table 2).

Given the large spatial extent and lack of repeat site visits, we were unable to disentangle individual observations from the temporal window in which they were taken. This is due to mechanistic relationships between weather and arthropod life stages,

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[1] Variable was calculated for the 60 days prior to the sample date, roughly equal to the average lifespan of the most abundant arthropods (Orthoptera).

[2] Variable was calculated from the start of the calendar year.

[3] Variable was extracted for a single month in the year of sampling.

coupled with a sample size of 1 for each unique site (Brust et al. 2009; Shaftel et al. 2021). Previous studies that have attempted to predict arthropod biomass with remote sensing have used drones, as the timing of imagery acquisition must be nearly identical to that of the field sampling for reliable results (Traba et al. 2022). Results from this study indicate that future sampling efforts should include static plots with repeat sampling at regular intervals to reduce temporal confounding of spatial covariates.

Final Status:

We have completed exploring the ability to make a predictive spatial layer for invertebrate biomass. Since we did not have the sampling effort needed to generate a predictive layer of invertebrate biomass, we were unable to link this spatial layer to sage-grouse and songbird populations to complete Objective 2.

Deliverables:

Objectives	Description	Status
Objective 1	Create a spatial layer that predicts invertebrate biomass for the sage-grouse and songbird grazing project study areas.	**Complete**

Publications	Status
Goosey, H. B., J. T. Smith, K. M. O'Neill, and D. E. Naugle. 2019. Ground-Dwelling Arthropod Community Response to Livestock Grazing: Implications for Avian Conservation. Environmental Entomology 48:856-866.	**Complete**

Table 1: Climate, topographic, and field data predictor variables used in invertebrate model development.

Climate Predictors	Source	Spatial Resolution	Temporal Resolution
Average maximum June temperature between 2011 and 2020	Daymet (Thornton et al. 2020)	1 km	1 day
Average maximum July temperature between 2011 and 2020	Daymet	1 km	1 day
Average maximum August temperature between 2011 and 2020	Daymet	1 km	1 day
Average maximum June precipitation (water equivalent) between 2011 and 2020	Daymet	1 km	1 day
Average maximum July precipitation (water equivalent) between 2011 and 2020	Daymet	1 km	1 day
Average maximum August precipitation (water equivalent) between 2011 and 2020	Daymet	1 km	1 day

Total precipitation in water equivalency during 60 days prior to sampling	Daymet	1 km	1 day
Cumulative degree days: sum of differences between temperature threshold (17 C) and daily average temperature	Daymet	1 km	1 day
Daily max temperature coefficient of variation 60 days prior to sampling	Daymet	1 km	1 day
Daily precipitation coefficient of variation 60 days prior to sampling	Daymet	1 km	1 day
Number of days within 60 days before the survey where the temperature dropped one standard deviation below the mean temperature	Daymet	1 km	1 day
Number of days within 60 days before the survey where the max daily temperature increased one standard deviation above the mean temperature	Daymet	1 km	1 day
Daily max temperature standard deviation 60 days prior to sampling	Daymet	1 km	1 day
Daily precipitation standard deviation 60 days prior to sampling	Daymet	1 km	1 day
Average total snow water equivalent (SWE) between 2011 and 2020	SNODAS (NOHRSC 2004)	1 km	1 day
April SWE of the sample year	SNODAS	1 km	1 day
Topographic Predictors	Source	Spatial Resolution	Temporal Resolution
Topographic Wetness Index	NED (USGS 2012)	10 m	NA
Slope	NED	10 m	NA
Elevation	NED	10 m	NA
Other Predictors	Source	Spatial Resolution	Temporal Resolution
Year	NA	NA	NA

Table 2: Model coefficients and their estimates for the final ordinary-least-squares model predicting invertebrate biomass.

Predictors	Estimates	Confidence Intervals	*p*-value
Intercept	0	-0.05 – 0.05	1
April Snow Water Equivalent	0.3	0.24 – 0.37	**<0.001**
Precipitation Coefficient of Variation	0.07	0.00 – 0.14	**0.036**
Max Temperature Standard Deviation	0.23	0.14 – 0.32	**<0.001**

Max Temperature Coefficient of Variation	-0.44	-0.56 – -0.32	**<0.001**
Cumulative Degree-Days	0.35	0.25 – 0.45	**<0.001**
Observations	512		
R2 / R2 adjusted	0.644 /0.640		

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