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ABSTRACT

Winter in temperate zones often represents a period of greatest energetic demand for vertebrate species. Animals respond to seasonal scarcity through behavioral strategies such as migration and selecting specific habitats characteristics to maximize resource acquisition and/or minimize energy expenditures. Migration or differential habitat use in winter can complicate goals of defining and conserving core habitat for species across increasingly fragmented landscapes. Greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse") is a species of conservation concern endemic to sagebrush (*Artemisia* spp.) steppe whose populations are most threatened by anthropogenic disturbance and concomitant degradation to sagebrush communities. Conservation of sage-grouse habitat is complicated by a partially-migratory annual cycle in most populations. Seasonal ranges (spring, summer/fall, and winter) may be integrated to any degree or non-overlapping. Efforts to conserve core habitat for sage-grouse have focused primarily on breeding ranges, which may not capture the needs of sage-grouse during other seasons, with winter habitat being least protected. Greater understanding of winter habitat requirements is needed to improve conservation for sage-grouse throughout their annual cycle. My thesis focused on multi-scale winter habitat ecology of greater sage-grouse (*Centrocercus urophasianus*) in the Red Desert of southcentral Wyoming, using GPS location data from winters 2018/2019, 2019/2020, and 2020/2021. My research encompassed a 1) landscape-scale validation of management guidelines for winter concentration areas as the second phase to a state-wide analysis, 2) habitat selection and behavior within home- and population-range scales as influenced by winter weather conditions, and 3) a fine-scale evaluation of microhabitat within home- and population-range scales during

winter 2020/2021. My results support consideration of winter habitats in conservation plans for sage-grouse populations in rapidly changing landscapes.

In Chapter 1, I conducted a systematic review of literature published in the last 46 years (1977–2022) on sage-grouse winter habitat selection and survival. Out of 32 compiled publications, I found that 59.4% of sage-grouse winter habitat literature was published in the last 10 years (2013–2022) and 53.1% of articles over the last 46 years reported avoidance of anthropogenic disturbance by sage-grouse during winter. The most recent recommendations for defining year-round priority habitat for sage-grouse recommend implementation of resource selection modeling for all seasonal periods.

In Chapter 2, my research fulfilled the second phase of a larger effort to answer questions posed by the Wyoming Sage-Grouse Implementation Team, through the Winter Concentration Area Subcommittee, regarding sage-grouse winter habitat selection and response to anthropogenic disturbance. Phase 1 used existing datasets of sage-grouse GPS locations from 6 regions across Wyoming to model winter habitat selection and avoidance patterns of disturbance statewide. Results from Phase I formed the basis for developing recommendations for management of sage-grouse winter concentration areas in Wyoming. The purpose of my research in Chapter 2 was to validate results of Phase I modeling and evaluate if the statewide model accurately described sage-grouse winter habitat selection and anthropogenic avoidance in regions not considered in that modeling effort. I used 44,968 locations from 90 individual adult female grouse identified within winter habitat from winters 2018/2019, 2019/2020, and 2020/2021 in the Southern Red Desert region (my study area) for out-of-sample validation. The intent of my validations was to assess if models generated statewide or from a nearby region (Northern Red Desert) would be more effective in predicting sage-grouse habitat selection patterns in areas with little information. The statewide model better predicted sage-grouse habitat use at within-population scales and the near-region model was more predictive at within-home-range scales. I found some variation between regions and the statewide model but similar trends in environmental characteristics and avoidance of anthropogenic features even at low densities. My results from the Southern Red Desert support the recommendation from Phase 1 that anthropogenic surface disturbance should be limited to low levels (≤ 2.5%) within winter concentration areas to conserve sage-grouse winter habitat.

In Chapter 3, my research focused on shifting environmental conditions that influence patterns of sage-grouse winter habitat selection. Sage-grouse are physically well adapted to winter conditions; it's a common assumption that winter weather has little effect on sage-grouse. However, research results have varied in support of this assumption, with significant die-offs correlated to periods of extreme winter weather. My research used daily winter weather conditions to explain sage-grouse winter behavior and habitat selection. I used sage-grouse GPS locations from the Southern Red Desert over winters 2018/2019 and 2019/2020 and obtained local weather conditions for each winter from SnowModel. SnowModel used available meteorological data, landscape characteristics, and snow physics to predict weather conditions at a 30-m resolution and daily scale. By comparing habitat selection and behavior across fine temporal scales, I found that sage-grouse responded to daily weather conditions by selecting refugia habitat more than altering daily activity levels. My results suggest that, in addition to landscape features, sage-grouse selected home ranges at the population scale for warmer wind chill temperatures and greater windspeed. Within home ranges, sage-grouse appeared to respond to harsher weather (lower wind chill temperature and high wind speeds) by selecting greater sagebrush cover and leeward sides of ridges. Our research underlines the importance of examining winter habitat at narrower temporal scales than the entire winter season to identify important refugia features that may only be used periodically. Additional research into quantifying weather refugia for wintering sage-grouse populations may provide greater insight to the future sustainability of winter ranges.

In Appendix A, I compared winter microhabitat characteristics at 90 sage-grouse use sites from the 2019/2020 winter with 90 available sites within the population range and 90 available sites within home ranges. I predicted habitat characteristics at grouse use locations would be more similar to paired random locations within the home range than to random locations within the population range. I also predicted that, because sage-grouse select specific habitat characteristics, there would be fewer differences when comparing random available locations between the home and population range than comparisons of used and available habitat. I found no support for my first prediction and strong support for my second prediction. Sage-grouse dung piles were 7.0- and 9.9-times higher at used locations than random locations within home and population ranges, respectively. Our results suggested that sage-grouse are highly selective for microhabitat. Sage-grouse selected areas with higher big sagebrush (*Artemisia* spp.) and overall canopy cover, big sagebrush height, and visual obstruction compared to random locations within home and population ranges. Our results indicate concealment cover is important to sage-grouse throughout their annual cycle.

VALIDATION OF WINTER CONCENTRATION AREA GUIDELINES

AND WINTER HABITAT ECOLOGY FOR GREATER SAGE-GROUSE IN THE RED DESERT, WYOMING

Caitlyn Powell Wanner

Presented in partial fulfillment

Of the requirements for the degree of Master of Science

The University of Wyoming

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DEDICATION

I dedicate this thesis to my husband Braden. I would not have made it through my degree without Brady's unconditional love, patience, and unwavering support for my dreams. I also dedicate this work to my parents, Kerry and Grethe Powell, and my sisters, Aislin, Erica, Suzanne, and Michaela, for their much encouragement and prayers on my behalf. Lastly, I dedicate this thesis to my second family: Dan, Sandie, and McKay Cheatham, who saved my life both figuratively and possibly literally on numerous occasions. Because of them, Baggs, Wyoming became more than a field site, it became home.

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TABLE OF CONTENTS

ABSTRACT 1
DEDICATION iii
ACKNOWLEDGMENTS iv
LIST OF TABLES ix
LIST OF FIGURES xi
LIST OF APPENDICES xv
CHAPTER 1: SYSTEMATIC REVIEW OF SAGE-GROUSE WINTER ECOLOGY 1
ABSTRACT 1
INTRODUCTION 1
METHODS 5
RESULTS 6
CONCLUSIONS OF SYSTEMATIC REVIEW 7
DISCUSSION 9
RESEARCH FOCUS 10
LITERATURE CITED 11
CHAPTER 2: EVALUATING RECOMMENDED SURFACE DISTURBANCE GUIDELINES WITHIN GREATER SAGE-GROUSE WINTER CONCENTRATION AREAS 26
ABSTRACT 26
INTRODUCTION 27
STUDY AREA 31
METHODS 32
Capture and GPS Locations 32
Landscape Predictor Variables 33
Data Analysis 35
Validation 37
RESULTS 38
Winter Range (Second Order or Population-Range Scale) Resource Selection 38
Within Winter Range (Third Order or within Home-Range Scale) Resource Selection 39
Validation 40
DISCUSSION 41

MANAGEMENT IMPLICATIONS 45
LITERATURE CITED 46
CHAPTER 3: INFLUENCE OF WINTER WEATHER ON HABITAT SELECTION AND BEHAVIOR OF GREATER SAGE-GROUSE 69
ABSTRACT 69
INTRODUCTION 70
STUDY AREA 73
METHODS 74
Capture and Monitoring 74
Landscape and Weather Variables 75
Resource Selection Function Model 77
Behavioral Model 79
RESULTS 81
Habitat Selection Model 81
Behavioral Model 83
DISCUSSION 85
ACKNOWLEDGMENTS 88
REFERENCES 89
APPENDIX A: WINTER MICROHABITAT SELECTION BY GREATER SAGE-GROUSE WITHIN HOME AND POPULATION RANGES 115
ABSTRACT 115
INTRODUCTION 116
METHODS 117
Study Area 117
Capture and Monitoring 118
Microhabitat Measurements 118
Statistical Analysis 120
RESULTS 121
DISCUSSION 122
Declaration of Competing Interest 123
Acknowledgments 123
REFERENCES 124

LIST OF TABLES

Table 1.1	Inclusion criteria for greater sage-grouse winter studies in a systemic review of known environmental and anthropogenic features associated with winter habitat selection or winter survival …………………………..	19
Table 1.2	Summary of literature on adult greater sage-grouse winter habitat selection influenced by environmental features from 1977 to 2022. Effects are signified as selection (+), avoidance (–), and differing context-dependent (+/–) for topographic, vegetation, and proximity to lek variables ..………..	20
Table 1.3	Summary of literature on adult greater sage-grouse (*Centrocercus urophasianus*) winter habitat selection influenced by anthropogenic features from 1977 to 2022. Effects are signified for anthropogenic disturbance as selection (+), avoidance (–), and differing context-dependent trends (+/–) …………………………………………………	22
Table 1.4	Summary of literature on adult greater sage-grouse (*Centrocercus urophasianus*) winter habitat selection influenced by anthropogenic features from 1977 to 2022. Effects are signified for anthropogenic disturbance as selection (+), avoidance (–), and differing context-dependent trends (+/–) …………………………………………………	23
Table 2.1	Characteristics of sagebrush and surface disturbance within the novel study area (Southern Red Desert) and each of the 6 study regions used to assess greater sage-grouse winter resource selection, Wyoming, 2008–2018 (Smith et al. 2021). Values represent mean characteristics within each study region defined by a minimum convex polygon surrounding all seasonal grouse use locations …………………………………………….	54
Table 2.2	Variables used in models evaluating greater sage-grouse winter habitat selection at the population-range (second order) and home-range (third order) scales ………………………………………………………………	55
Table 2.3	Candidate models using environmental and anthropogenic covariates to explain sage-grouse winter range selection (population-range scale selection) using data from the Southern Red Desert of Wyoming, 2018–2021 …………………………………………………………………	57
Table 2.4	Parameter estimates with 95% confidence intervals for predictor variables describing greater sage-grouse resource selection within population-range and home-range scales in the Southern Red Desert, Wyoming, 2018–2021……………………………………………………………………	58
Table 2.5	Candidate models using environmental and anthropogenic covariates to explain sage-grouse habitat selection within winter home ranges (third-	

order selection) using data from the Southern Red Desert of Wyoming, 2018–2021 …………………………………………………………………. 59

Table 2.6 Scales (radii size) and effects in parameter estimates for predictor variables describing winter greater sage-grouse resource selection from data pooled statewide (2008–2018), from the near-region Northern Red Desert (2009–2014), and from the Southern Red Desert study area (Phase II, 2018–2021), Wyoming. Parameters were derived from the most parsimonious model describing environmental and anthropogenic covariates that influenced resource selection within the population and within winter home ranges by sage-grouse. Scales and trends of all surface disturbance predictors were included for comparison ………………………………… 60

Table 3.1 Variables used in models evaluating greater sage-grouse winter habitat selection and daily activity, with sources are sited for variables that have been predictive of sage-grouse winter habitat selection or survival in other literature ……………………………………………………………….... 103

Table 3.2 Parameter estimates for predictor variables from conditional logistic regression models that describe daily winter resource selection by greater sage-grouse within home ranges (third-order selection) and within population range (second-order selection) in the Southern Red Desert, Wyoming, winters 2018/2019 and 2019/2020 ……………………………... 105

Table 3.3 Parameter estimates with 95% confidence intervals for predictor variables describing greater sage-grouse daily activity index (ln[DSA]) in the Southern Red Desert, Wyoming, during winters 2018/2019 and 2019/2020 …………………………………………………………...……...…….. 107

Table A.1 Mean (± SE) of winter microhabitat characteristics at locations used by sage-grouse, random locations within home ranges, and random locations within the population range. Vegetation characteristics and dung counts (piles/400 m^2) at winter 2019/2020 plots were recorded in summer 2020, northwest Colorado and southcentral, Wyoming, USA …………………… 128

Table A.2 Paired *t*-tests for microhabitat characteristics and dung counts (piles/400m^2) between grouse-use locations and paired home range randomly available plots. Student's *t*-tests comparisons between population range available plots and the home range available and use plots. We recorded vegetation characteristics and dung counts (piles/400 m^2) at winter 2019/2020 habitat plots in summer 2020, northwest Colorado and southcentral, Wyoming, USA ……………………………………………… 129

LIST OF FIGURES

Figure 1.1	Locations of study areas conducting research on greater sage-grouse winter habitat selection and winter survival published between 1977 and 2022 …..	24
Figure 1.2	Number of published studies on greater sage-grouse winter habitat selection, grouped in 6-year bins (1977–2022) …………………………….	25
Figure 2.1	Greater sage-grouse locations from GPS datasets in 7 regions in Wyoming, USA, 2008–2018. 6 regions, including the Northern Red Desert, were used in Resource Selection Function analyses for sage-grouse winter habitat (Phase I). Locations from the Southern Red Desert were used as out-of-sample data to test the effectiveness of the statewide model to predict sage-grouse winter habitat selection in regions outside the dataset (Phase II) …..	61
Figure 2.2	Comparison of greater sage-grouse resource selection coefficients used to evaluate selection of winter ranges **(population-range scale selection**) for all surface disturbance (A), press disturbance (B), all oil and gas surface disturbance (C), active oil and gas surface disturbance (D), and oil and gas well pad density © in the Southern Red Desert (2018–2021), Northern Red Desert (near-region; 2009–2014) and within 6 study regions across Wyoming (statewide; 2008–2018 …………………………………………..	62
Figure 2.3	Potential disturbance thresholds for greater sage-grouse from 6 study regions, Wyoming, 2008–2018 (Statewide; A), the Northern Red Desert study region, 2009–2014 (Near-Region; B) and the Southern Red Desert study region, 2018–2021 (C). The red line represents the percent of available habitat in a 100% minimum convex polygon around all winter grouse use locations (**population scale analysis**; Y-axis) with the indicated amount of disturbance or greater (X-axis) for all surface disturbance within 10.0 km. The black line represents the percent of grouse-use locations across differing levels of disturbance within the same region sizes ………..	63
Figure 2.4	Potential disturbance thresholds for greater sage-grouse within 6 study regions, 2008–2018 (Statewide), the Northern Red Desert, 2009–2014 (Near-region) and in the Southern Red Desert, Wyoming study region, 2018–2021. The red line represents the percent of available habitat in a 100% minimum convex polygon around all year-round grouse use locations (**population-range scale analysis**; Y-axis) with the indicated amount of disturbance or greater (X-axis) for press disturbance within 3.2 km (A), all disturbance within 0.8 km (B), all oil and gas disturbance within 0.8 km (C), and active oil and gas disturbance within 0.8 km (D). The black line represents the percent of grouse-use locations across differing levels of disturbance within the same region sizes ……………….	64

Figure 2.5 Comparison of greater sage-grouse resource selection coefficients used to evaluate selection of habitat within winter home ranges for all surface disturbance (A), press disturbance (B), all oil and gas surface disturbance (C), active oil and gas surface disturbance (D), and oil and gas well pad density (E) in the Southern Red Desert (2018–2021), Northern Red Desert (near-region; 2009–2014) and within 6 study regions across Wyoming (statewide; 2008–2018) ………………………………………………….. 65

Figure 2.6 Potential disturbance thresholds for greater sage-grouse from 6 study regions, Wyoming, 2008–2018 (Statewide; A), the Northern Red Desert study region, 2009–2014 (B) and the Southern Red Desert study region, 2018–2021 (C). The red line represents the percent of available habitat in a 100% minimum convex polygon around all winter grouse use locations (**home-range scale analysis**; Y-axis) with the indicated amount of disturbance or greater (X-axis) for all surface disturbance within 10.0 km. The black line represents the percent of grouse-use locations across differing levels of disturbance within the same region sizes ………………. 66

Figure 2.7 Potential disturbance thresholds for greater sage-grouse within 6 study regions, 2008–2018 (Statewide), the Northern Red Desert, 2009–2014 (Near-region) and in the Southern Red Desert, Wyoming study region, 2018–2021. The red line represents the proportion of available habitat in a 100% minimum convex polygon around all year-round grouse use locations (**home range scale analysis**; Y-axis) with the indicated amount of disturbance or greater (X-axis) for press disturbance within 3.2 km (A), all disturbance within 0.8 km (B), all oil and gas disturbance within 0.8 km (C), and active oil and gas disturbance within 0.8 km (D). The black line represents the proportion of the grouse-use locations across differing levels of disturbance within the same region sizes ……………………………….. 67

Figure 2.8 Probability of sage-grouse winter habitat occurrence as predicted by a statewide and near-region model at sage-grouse locations in the Southern Red Desert, Wyoming, 2018–2021. Resource Selection Function models at the population-range and home-range scales were binned into 5 quantiles using percentile breaks at 20% intervals. Predicted relative probability of occurrence (X-axis) and mapped across the Southern Red Desert study area. The Y-axis represents the proportion of sage-grouse locations that fell within each predicted probability bin.……………………………………… 68

Figure 3.1 Comparison of model coefficients from the home range (third order) conditional logistic model to confirm coefficient convergence in greater sage-grouse resource selection modeling, Southern Red Desert, Wyoming, winters 2018/2019 and 2019/2020 …………………………………………. 108

Figure 3.2 Predicted sage-grouse winter resource selection response to the interaction between the proportion of area with vegetation protruding above snow (0/1; Bnry) within 0.1 km and other vegetation and other landscape characteristics from the 2018/2019 and 2019/2020 winters in the Red Desert of southcentral Wyoming. Landscape characteristics included terrain roughness index (TRI) within 0.1 km, terrain position index (TPI) within 0.8 km, and percent sagebrush canopy cover (Sage) within 0.1 km. Predicted selection response was calculated on a new dataset using 20 groups of 1:15 use versus available locations. Bnry variables in the new dataset set to minimum, median, and max values. Terrain and vegetation values in the new data set were randomly sampled equally from the 1st, 2nd, 3rd, and 4th quantiles of observations from the original dataset ……………. 109

Figure 3.3 Predicted sage-grouse winter resource selection response to the interaction between weather and landscape variables on a daily temporal during the 2018/2019 and 2019/2020 winters in Red Desert of southcentral Wyoming. Predicted selection response was calculated on a new dataset using 20 groups of 1:15 use versus available locations. The weather variables of wind speed (m/s; Wspd) within 0.1 km, wind chill (°C; Chil) within 0.1 km, and blizzard conditions (kg/m/s snow; Bliz) were set to their respective minimum, median, and maximum values from the original observation dataset. Landscape parameter values in the new data set were randomly sampled equally from the 1st, 2nd, 3rd, and 4th quantiles of observations from the original dataset. Landscape characteristics included terrain roughness index (TRI) within 0.1 km, terrain position index (TPI) within 0.8 km, and percent sagebrush canopy cover (Sage) within 0.1 km. All variables not included in each interaction were set to their respective mean values ……………………………………………………………… 111

Figure 3.4 Biplot of principal components analysis of sage-grouse daily winter movement metrics in the South Red Desert, Wyoming, 2018-2020 ………. 113

Figure 3.5 Interaction trends in predicted daily sage-grouse activity response to snow variables and landscape characteristics in the Southern Red Desert, Wyoming, winters 2018/2019 and 2019/2020. Snow variables included month-long trends in blizzard conditions (kg/m/s; Blizzard) and proportion daily home range with vegetation protruding above snow depth (0-1; Binary vegetation). The weather variable was the rate of change in wind chill temperature over 3-day periods (Chil.trend3). Landscape variables included shrub height (cm) and terrain position index (TPI) within each daily home range. Predicted selection response was calculated on a new dataset (n=320) with all non-interacting variables set to mean values. For each interaction, we set the snow and weather variables to minimum, median, and maximum values. Terrain and vegetation values in the new data set were randomly sampled equally from the 1st, 2nd, 3rd, and 4th quantiles of observations from the original dataset ………………………... 114

Figure A.1 Study area location map depicting locations of used grouse and random locations within home ranges and at the population scale, southwestern Wyoming and northwestern Colorado, winter 2019/2020 ………………..... 130

LIST OF APPENDICES

Appendix A Winter Microhabitat Selection by Greater Sage-Grouse within Home and Population Ranges ………………………………………………………….. 115

CHAPTER 1: SYSTEMATIC REVIEW OF SAGE-GROUSE WINTER ECOLOGY

ABSTRACT

Logistical difficulty in tracking animals during winter has resulted in limited information concerning the ecology of wintering greater sage-grouse (*Centrocercus urophasianus* ‘sage-grouse’). In addition, sage-grouse winter survival is typically higher than other seasons, leading to greater research and conservation devoted to breeding habitat. Advances in technology have increased understanding the importance of sage-grouse winter habitat to influence annual vital rates. Conservation priority areas for sage-grouse are delineated by breeding habitat, yet research has identified they are often insufficient in conserving all seasonal habitats, particularly during winter. I conducted a systematic review of literature published between 1977 and 2022 on sage-grouse winter habitat selection and survival. Out of 32 compiled publications, I found that 59.4% of articles on sage-grouse winter habitat were published in the last 10 years (2013–2022) and 53.1% of habitat selection articles reported avoidance of anthropogenic disturbance by sage-grouse during winter. The most recent recommendations for defining year-round priority habitat for sage-grouse recommend implementation of resource selection function (RSF) modeling for all seasonal periods.

INTRODUCTION

Winter in temperate zones often represents a period of greatest energetic demand for vertebrate species (Gray and Prince 1988, Andreev 1991). Animals use innate and learned behaviors such as migration and habitat selection to maximize resource acquisition and/or minimize energy expenditures in response to seasonal scarcity (Alerstam et al. 2003, Shaw and Couzin 2013). Migration or differential habitat use in winter can complicate goals of defining and conserving core habitat for species across increasingly fragmented landscapes. Protected areas must sufficiently capture habitat needs of a species throughout their annual life cycle to sustain declining populations (Johnson et al. 2004, Holdo et al. 2010, Allen and Singh 2016).

Greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse") is a species of critical concern in the western United States and Canada that has undergone significant population declines and range contractions since the early 1900s (Hornaday 1916, Coates et al. 2021*a*). Sage-grouse are listed as Endangered in Canada by the Committee on the Status of Endangered Wildlife (Government of Canada 2021). The United States Fish and Wildlife Service ruled in 2015 that sage-grouse were not warranted for protection under the Endangered Species Act based on the unprecedented collaboration of federal and state agencies over the preceding 5 years to create management plans that addressed and decreased threats to sage-grouse populations (USFWS 2015). Concern over this declining and iconic species continues to heavily influence land management policy in the western United States. Changes in traditional land use and energy development will be an enduring challenge to land management and sage-grouse conservation in the 21st century (Newbold et al. 2015, Trainer et al. 2016).

Sage-grouse populations are threatened by anthropogenic disturbance and concomitant degradation to the sagebrush (*Artemisia* spp.) communities they depend on for resources for population persistence (Knick et al. 2003, Aldridge et al. 2008, Walker et al. 2010). Anthropogenic disturbance to sage-grouse habitat includes cropland conversion (Aldridge et al. 2008, Smith et al 2016*a*), rural development (Leu and Hanser 2011), wind energy infrastructure (LeBeau et al. 2014, 2017), mineral extraction (Pratt and Beck 2019), oil and gas development (Walker et al. 2010, Gregory and Beck 2014, Hovick et al. 2014, Green et al. 2017), and all associated transmission lines, roads, and human traffic (Dinkins et al. 2014, Hansen et al. 2016, Kohl et al. 2019, LeBeau et al. 2019, Kirol et al. 2020). Habitat degradation results from invasion of annual grasses (Billings 1994, Miller et al. 2011), concomitant increased frequency of fires (Whisenant 1990, Balch et al. 2013, Pilliod et al. 2021), long-term overgrazing by non-native ungulates (Hemstrom et al. 2002, Beever and Aldridge 2011, Coates et al. 2021b), encroachment of pinyon pine (*Pinus edulis* and *monophylla*)-juniper (*Juniperus* spp.; Miller et al. 2000, Coates et al. 2017), and increased aridity due to climate change (Miller et al. 2011, Palmquist et al. 2016). Habitat effectiveness, or the actual use of habitat by animals, is also lost through avoidance of human activity and infrastructure (Holloran et al. 2015). Sage-grouse avoid disturbance associated with energy development year-round, with multiple studies reporting lower winter selection (Doherty et al. 2008, Smith et al. 2014), lek attendance (Green et al. 2017), nest success (LeBeau et al. 2014), and survival (Holloran et al. 2010) with proximity to energy infrastructure.

Sage-grouse are best described as an intermediate K-selected species (Taylor et al. 2012), with longer lifespans and lower annual reproductive effort compared to most Galliformes (Connelly et al. 2011, Taylor et al. 2012, Schroeder et al. 2020). Asymptotic population growth for K-selected species is theorized to be more susceptible to changes in adult annual survival than changes in fecundity or offspring survival (Saether and Bakke 2000). This prediction has been confirmed by demographic analysis of sage-grouse (Johnson and Braun 1999, Dahlgren et al. 2016) and other avian species with similar life histories (e.g., lesser snow goose [*Chen caerulescens caerulescens*], Rockwell et al. 1997; and common eider [*Somateria mollissima*], Allen et al. 2019). Adult female survival has the greatest effect on sage-grouse population growth, followed by juvenile survival, then nest survival (Johnson and Braun 1999, Taylor et al. 2012, Dahlgren et al. 2016). Adult female survival has been shown to be a primary population driver even in Galliformes with higher reproductive effort (e.g., greater prairie chickens [*Tympancuchus* *cupido*], McNew et al. 2012; and white-tailed ptarmigan [*Lagopus leucurus*], Sandercock et al. 2005). Thus, management of sage-grouse populations should include plans to conserve habitat that increases probability of adult female survival throughout their annual cycle.

The partially migratory behavior of sage-grouse complicates efforts to identify core habitats that meet all seasonal requirements. Sage-grouse have distinct seasonal ranges, but seasonal ranges may be integrated (e.g., winter and breeding habitat overlap) or separate (10 to greater than 200 km apart; Fedy et al. 2012, Cardinal and Messmer 2016, Newton et al. 2017, Pratt et al. 2017, 2019). Even though sage-grouse spend a greater portion of the year on winter range (5 months or more between October and the end of March; Pratt et al. 2017), greater conservation emphasis has been placed on breeding habitat (Doherty et al. 2010). Conservation priority areas are typically delineated by core breeding habitat surrounded by a buffer area (Doherty et al. 2010, 2011), a strategy that risks insufficiently protecting migratory populations that overwinter outside core conservation areas (Fedy et al. 2012).

Logistical difficulty in tracking animals in winter conditions has resulted in historically few robust studies quantifying sage-grouse habitat requirements during winter compared to other seasons (Connelly et al. 2000). In the last 2 decades, advancements in GPS transmitters and other technology have facilitated insights into sage-grouse behavior and habitat selection at unprecedented fine scales (e.g., Gelling et al. 2022), including during winter. With the growing body of research and understanding has come increased concern over the ability of current conservation areas delineated by sage-grouse breeding habitat to adequately conserve other important seasonal ranges from increasing development (Fedy et al. 2012, Dinkins et al. 2014, Hovick et al. 2014, Smith et al. 2016*b*). To better understand range-wide trends in sage-grouse winter habitat selection and the threat of energy development to sage-grouse, I conducted a systematic review of literature reporting results on sage-grouse winter habitat selection. The goal of my review was to identify range-wide patterns of selection for environmental characteristics and types of anthropogenic disturbance. Due to increased focus on sage-grouse, I expected most research on sage-grouse winter habitat to have been published in the last 10 years (2013–2022). I conducted a second review to identify publications that have identified habitat characteristics documented to influence sage-grouse winter survival.

METHODS

I followed general systematic review guidelines (Centre for Evidence-Based Conservation 2013) to ensure transparency and repeatability in my review. I set my temporal range for the last 46 years (1977–2022) to document the growth in literature on sage-grouse winter habitat. I gathered literature using combinations of search terms "sage-grouse," "habitat selection," "survival," and "winter" in Google Scholar and Web of Science (Table 1.1). I also used older synthesis papers (Connelly et al. 2000, Crawford et al. 2004, Connelly et al. 2011) to find older publications that did not appear in online search results. I defined *a priori* criteria for inclusion to require the species of focus to be adult greater sage-grouse (not juvenile greater sage-grouse or Gunnison sage-grouse [*C. minimus*]; Table 1.1). For articles describing habitat selection, I required that methods include use-available habitat selection tests (*t*-tests) or models, such as logistic regression (Manly et al. 2002), conditional logistic regression (Boyce 2006), or boosted regression trees (Elith et al. 2008; Table 1.1). For articles about survival analysis, I required the methods to include either Kaplan-Meier estimates (Rich et al. 2010), known-fate models (Program MARK; White and Burnham 1999) or Cox proportional hazards regression (Cox 1972; Table 1.1). I included grey literature (reports and theses) but excluded synthesis papers and papers that used resource selection functions (RSFs) from other reports. I assessed each study that met the inclusion criteria and extracted the following information: study location, method type, and main findings regarding winter habitat selection or survival.

RESULTS

I identified 32 published studies that reported winter resource selection models and 7 studies that published winter survival models. Of the published RSF studies, sage-grouse locations from Wyoming were included in the most studies (11 or 35.5%); Colorado was second (6 studies or 19.4%); and Utah was third (5 studies or 16.5%). Other states/provinces included California, Idaho, Montana, Nevada, Oregon, North Dakota, and South Dakota and Alberta (Table 1.2; Figure 1.1). Nineteen (59.4%) of the winter habitat selection publications were published in the last 10 years (Figure 1.2) and 17 (53.1%) reported a form of anthropogenic disturbance as a significant predictor of sage-grouse winter habitat use (Table 1.3). I excluded some well-cited papers on wintering sage-grouse because they failed to meet my use-availability methodology criteria for including habitat selection studies (e.g., Beck 1977). Study lengths ranged from 1 to 15 years, with a median of 3 years (Table 1.2). The most common effects in sage-grouse winter habitat included selection for greater sagebrush cover (either land cover type or percent canopy cover), flatter topography, and avoidance of pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.)/forest or other non-shrubland cover types (Table 1.2). Preferred sagebrush species, heterogeneity in shrub species cover, and shrub heights varied the most in reported selection or avoidance (Table 1.2). Of the 17 publications that incorporated anthropogenic features, sage-grouse exhibited some level of avoidance in 16 of them (Table 1.3).

Of the 7 studies that reported winter survival rates, 3 included locations from Wyoming; one included locations from Wyoming, Idaho, and Utah; and Colorado, Montana, or Oregon accounted for one study each (Table 1.4). Out of these 7, only 5 attributed winter survival to some kind of environmental factor. Winter survival rates ranged from 67.4% (during a 2-week period, Anthony and Willis 2010) to 100% (seasonal survival rate, Wik 2002; Table 1.4). Average length of study was about 3 years (Table 1.4). Winter weather conditions were most reported as impacting survival, with 2 studies reporting negative effects of periods of extreme minimum temperatures, high snow depth, and high precipitation (Moynahan et al. 2006, Anthony and Willis 2010), compared to one study that reported no effect (Zablan et al. 2003). One study found higher survival of grouse that wintered inside their breeding ranges (Dinkins et al. 2017), compared to one study that found no effect of migration (Cardinal and Messmer 2016). Greater heterogeneity in sagebrush cover and lower heterogeneity shrub cover were associated with higher winter survival in Wyoming (Smith et al. 2014). Anthropogenic disturbance was not found to be a significant predictor of winter survival in 2 studies (Smith et al. 2014, Pratt and Beck 2019).

CONCLUSIONS OF SYSTEMATIC REVIEW

I found that 59.4% of sage-grouse winter habitat selection publications had been published in the last 10 years (2013–2022; Figure 1.2) and 53.1% (17) of 32 published habitat selection studies reported avoidance of a form of anthropogenic disturbance (Table 1.3). Much of the increase in winter sage-grouse research can be attributed to improved modeling procedures and GPS technology that provides researchers with expanded capabilities to conduct research remotely during winter conditions. Common effects I found in published studies of sage-grouse winter habitat selection included selection for undisturbed sagebrush land cover, flatter topography, and avoidance of pinyon-juniper/forest, and other non-shrubland cover types (Table 1.2).

Very few studies connected winter habitat use with survival outcomes (Table 1.4). Two studies attributed depressed survival rates to severe winter weather (Moynahan et al. 2006, Anthony and Willis 2010). Only one study connected fitness with specific habitat characteristics (Smith et al. 2014). If sage-grouse are able to detect and avoid low-quality habitat, then fitness consequences of surface disturbance may be difficult to detect until densities of disturbance push sage-grouse onto marginal winter habitat (Smith et al. 2014). Greater understanding of habitat characteristics that buffer winter sage-grouse survival may improve efforts to conserve high-quality habitat for sage-grouse in increasingly fragmented landscapes (Anthony and Willis 2010, Dzialak et al. 2013).

Sage-grouse populations continue to decline in most parts of their range (Coates et al. 2021a). Literature on sage-grouse winter habitat suggests that current methods of protecting sage-grouse habitat delineated by breeding ranges are insufficient for protecting more migratory sage-grouse populations (Fedy et al. 2012, Dinkins et al. 2017, Smith et al. 2016b, 2019). Beers and Frye (2022) found Random Forest modeling in the southern margins of sage-grouse range was more effective than RSFs at predicting habitat for out-of-sample regions but both effectively predicted habitat selection within-region. Parsons et al. (2022) found use of RSF analysis for identifying priority habitat resulted in the most spatially efficient footprint for protecting habitat for all three seasons (breeding, summer, and winter), a conclusion that has been supported by other research (Walker et al. 2016, Heinrichs et al. 2019, Pratt et al. 2019). Resource selection modeling has been utilized in many wintering populations across sage-grouse range and provides useful information for defining high-use habitat (Table 1.2). Conservation plans for sage-grouse should consider all seasonal habitat requirements to conserve declining populations in rapidly changing landscapes (Heinrichs et al. 2019, Smith et al. 2019).

DISCUSSION

Greater sage-grouse is a species of conservation concern across the Intermountain West of North America. Sage-grouse populations have declined 30.7% in the last 17 years and 80.7% in the last 53 years (Coates et al. 2021a). Most declines in sage-grouse are attributed to loss of habitat. Once expansive tracts of sagebrush shrublands have retracted with growing demand for domestic energy and expanding development. Federal and state agencies are tasked with managing public lands to fulfill growing economic demand while sustaining healthy populations of sage-grouse and other iconic wildlife.

One challenge to managing disturbance to core sage-grouse areas is their partially migratory behavior, meaning a proportion of individuals in many populations may be non-migratory or migrate between two or three separate seasonal ranges (Fedy et al. 2012; Pratt et al. 2019). Sage-grouse winter habitat often has a smaller spatial footprint than other seasonal ranges (Smith et al. 2016, Dinkins et al. 2017), suggesting that loss of habitat within core wintering range could have an impact on winter survival disproportionate to the spatial extent of disturbance (Dzialak et al. 2013, Smith et al. 2014, Dinkins et al. 2017). Wintering areas also contain flocks of individuals that breed in dissimilar areas (Smith et al. 2019), as far away as 240 km (Newton et al. 2017). Therefore, degradation to sage-grouse winter habitat could negatively affect the year-round success of populations far beyond the spatial extent of winter ranges (Smith et al. 2016b, Dinkins et al. 2017).

RESEARCH FOCUS

Sage-grouse winter ranges have received less focus and protection than other seasonal ranges, based on the assumption that winter survival is usually high and less important than breeding success for maintaining stable populations (Connelly and Braun 1997, Doherty et al. 2010, 2011, Pratt et al. 2019). Winter ranges are often thought to be similar (spatially and in habitat) to breeding habitat, so conservation of breeding areas is often assumed to also conserve winter habitat (Doherty et al. 2010). Prior research raised concern over the ability of conservation areas delineated by sage-grouse breeding habitat to protect winter habitat (Fedy et al. 2012, Dinkins et al. 2014, Smith et al. 2016*b*). In Wyoming, these concerns prompted research to develop guidelines to manage sage-grouse in winter concentration areas (Smith et al. 2021). The primary objective of my thesis was to evaluate whether these proposed guidelines could be effectively applied in regions in Wyoming where there exists little information on local sage-grouse behaviors and habitat selection. My second objective addressed the commonly held assumption that sage-grouse are not affected by winter weather conditions as long as snow depth does not exceed vegetation height (Connelly et al. 2000, Crawford et al. 2004). I investigated how sage-grouse select winter habitat in response to various daily weather conditions, a temporal scale of winter resource selection that has been rarely explored for sage-grouse (but see Dzaliak et al. 2012).

My thesis focused on multi-scale winter habitat ecology of greater sage-grouse (*Centrocercus urophasianus*) in the Red Desert of southcentral Wyoming, using GPS location data from winters 2018/2019, 2019/2020, and 2020/2021. My research encompassed 1) validation of management guidelines for winter concentration areas as the second phase to a state-wide analysis, 2) habitat selection and behavior within home- and population-range scales as influenced by winter weather conditions, and 3) a fine-scale evaluation of microhabitat within home- and population-range scales during winter 2020/2021. My results suggest that current conservation strategies do not sufficiently protect sage-grouse winter habitat and winter habitats characteristics should be expressly incorporated in conservation plans for sage-grouse populations in rapidly changing landscapes.

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TABLES AND FIGURES

Table 1.1. Inclusion criteria for greater sage-grouse winter studies in a systemic review of known environmental and anthropogenic features associated with winter habitat selection or winter survival.

Inclusion category	Criteria
Literature	Published articles, reports, and theses that reported original data
Animals	Adult greater sage-grouse (*Centrocercus urophasianus*)
Temporal range	1977–2022
Spatial range	North America
Habitat methodology	Use versus available habitat selection t-test or models (use-available logistic regression, conditional logistic regression, or boosted regression trees)
Survival methodology	Kaplan-Meier survival estimates, Known-fate analyses, or Cox proportional hazard regression models

Table 1.2. Summary of literature on adult greater sage-grouse winter habitat selection influenced by environmental features from 1977 to 2022. Effects are signified as selection (+), avoidance (–), and differing context-dependent (+/–) for topographic, vegetation, and proximity to lek variables.

			Winter Habitat Variables													
			Leks[a]	Topography[b]				Vegetation[c]								
			Proximity to Leks	Elevation	Rough terrain	Thermal aspects	Topographic position	Sagebrush cover	Big sagebrush	Short sagebrush species	Other sagebrush	Shrub height	Heterogeneity	Juniper/forest	Riparian/Mesic	Sparse shrub/ bare ground
Study	Location	Years														
Boswell 2017	UT	2013–2016			–				+/–	+/–				–		
Beers and Frey 2022	UT	2014–2020			+/–			+						–		
Carpenter et al. 2010	Alberta	1999–2003			–			+								
Coates et al. 2016	CA, NV	1998–2014		–	–		+/–	+					+/–	–	–	
Coates et al. 2020	CA, NV	1998–2014		–			–	+		+			+/–	–	–	
Connelly 1982	ID	1977–1981						+	+	+		+		–		
Doherty et al. 2008	MT, WY	2003–2006			–			+						–	–	
Dzialak et al. 2012	WY	2008–2011			–			+				+			–	
Dzialak et al. 2013	WY	2007–2008				+		+	+			+				–
Fedy et al. 2014	WY	2001–2010			–			+						–		
Frye et al. 2013	ID	2010–2011							–		+					
Hagen et al. 2011	OR	1989–1992			–	+			–	+			+			
Hanf et al. 1994	OR	1988–1993						–	–	+	+					
Hansen et al. 2016	UT	2011–2016				–		+		+						
Homer et al. 1993	UT	1889–1990			–				+			+				–
Naugle et al. 2006	WY	2005–2006						+						–		
Parsons et al. 2022	SD	2006–2017			–			+								
Remmington & Braun 1985	CO	1980–1982							+		–					

Rice et al. 2016	CO	2010–2012		–			+						+	
Robertson 1991	ID	1987–1990					+			+				
Row et al. 2022	WY	1998–2010			–		+					–		
Schoenberg et al. 1982	CO	1979–1980				+/–	+				+			
Schuyler et al. 2022	OR, NV	2013–2019			–		+							
Smith et al. 2014	CO, WY	2007–2009					+	+		–	–			
Smith et al. 2016b	WY	2011–2014			–		+	+						
Smith et al. 2019	WY	2017	+				+			–				
Smith et al. 2021	WY	2008–2020	+		–	+/–	+			+		–		
Swanson et al. 2012	ND, SD	2005–2007					+			–	+		–	
Walker et al. 2016	CO	2006–2010			–		+				–	–		–
Walker et al. 2022	CO	2006–2014					+				–	–		–
Welch et al. 1988	UT	1984–1985							+/–					

[a]Proximity to leks represented distance to high density breeding areas, as represented by average male sage-grouse attendance.

[b]Topographic variables included elevation, rough terrain (measured by terrain roughness index or standard deviation of slope), and topographic position (on ridges or in depressions).

[c]Sagebrush cover included canopy cover (%) and sagebrush land cover type. Big sagebrush indicates selection for *A. tridentata wyomingensis* for cover or foraging. Short sagebrush indicates selection for black sagebrush (*A. nova*) or low sagebrush (*A. arbuscula*) for cover or foraging. Other sagebrush shrub species included mountain big (*A. tridentata vasevana*) and basin big (*A. tridentata tridentata*). Shrub height variables included height of sagebrush, height of all shrubs, and height of shrubs relative to snow depth. Heterogeneity represented mixed cover of sagebrush, other shrubs, or grasslands. Juniper/forest represented pinyon-juniper or forested land cover. Sparse shrub/bare ground represented xeric or bare land cover. Riparian/mesic represented riparian land cover, distance to water, and NDVI.

Table 1.3. Summary of literature on adult greater sage-grouse (*Centrocercus urophasianus*) winter habitat selection influenced by anthropogenic features from 1977 to 2022. Effects are signified for anthropogenic disturbance as selection (+), avoidance (–), and differing context-dependent trends (+/–).

			Anthropogenic disturbance variables[a]						
			Agriculture	Energy development	Major roads	Mining	Minor roads	Press disturbance	Wildfire
Study	Location	Years							
Boswell 2017	UT	2013-2016	+/–						
Carpenter et al. 2010	AB	1999-2003		–			–		
Doherty et al. 2008	MT, WY	2003-2006		–					
Dzialak et al. 2012	WY	2008–2011		–				–	
Dzialak et al. 2013	WY	2007–2008		–					
Fedy et al. 2014	WY	1994–2010	–		–				
Hansen et al. 2016	UT	2011–2016		–	–				
Naugle et al. 2006	WY	2005–2006		–	–				
Parsons et al. 2022	SD	2006–2017			–				
Pratt and Beck 2019	WY	2011–2015				–			
Rice et al. 2016	CO	2010–2012	–						
Row et al. 2022	WY	1998–2010	–	–	–				
Smith et al. 2014	CO, WY	2007–2009		–					
Smith et al. 2019	WY	2017		+					
Smith et al. 2021	WY	2008–2020		–	–			–	
Schuyler et al. 2022	OR, NV	2013–2019							–
Walker et al. 2022	CO	2006–2014		–	–				

[a]Agriculture represented cropland cover. Energy development included oil and natural gas wells or well pads and transmission lines. Major roads represented paved rights or higher density of roads. Mining represented bentonite mine disturbance, both active and reclaimed locations. Minor roads represented unpaved to two-track roads. Press disturbance represented consistent human activity levels beyond initial disturbance.

Table 1.4. Summary of literature on adult greater sage-grouse winter survival. Survival rates and effects for habitat and weather variables that influence survival rates are signified as increasing (+) or decreasing survival (–), or no effect (None).

Study	Location	Years	Survival rate (%)[a]	Anthropogenic disturbance	Migration	Protected areas	Sagebrush cover heterogeneity	Total shrub cover heterogeneity	Weather conditions
Anthony and Willis 2010	OR	1989-1992	67.4–98.4						–
Cardinal and Messmer 2016	ID, UT, WY	2010-2012	83.0		None				
Dinkins et al. 2017	WY	2008-2015	86.0		–	+			None
Moynahan et al. 2006	MT	2001-2004	91.0–98.6						–
Pratt and Beck. 2019	WY	2011–2015	92.0	None					
Smith et al. 2014	CO, WY	2007-2010	83.6–95.9	None			+	–	
Wik 2002[b]	ID	1999–2001	85.0–100						

[a] Reported winter survival rates or ranges of rates.

[b]The Kaplan-Meier staggered entry method was used to estimate survival, but did not associate survival with any environmental factor.

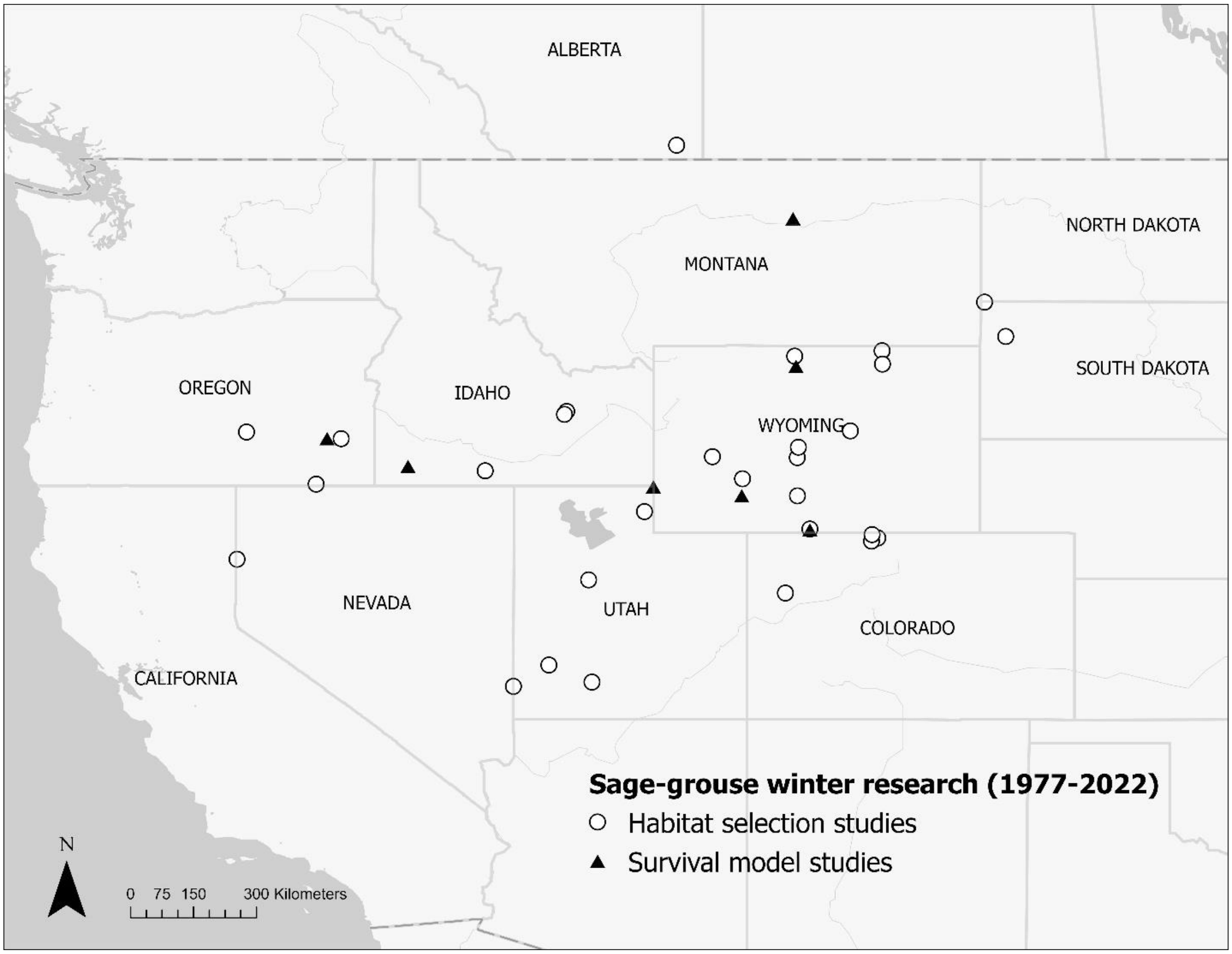

Figure 1.1 Locations of study areas conducting research on greater sage-grouse winter habitat selection and winter survival published between 1977 and 2022.

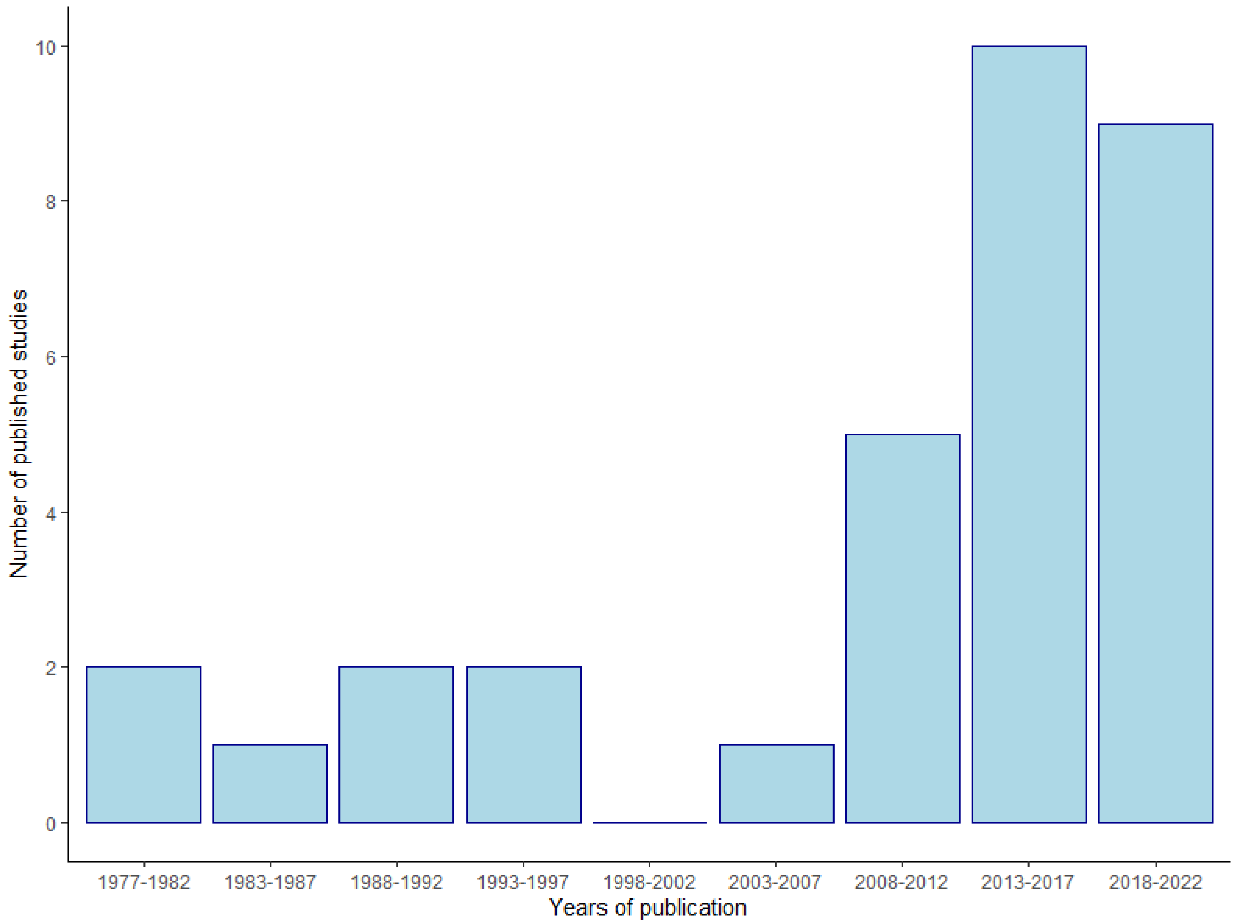

Figure 1.2. Number of published studies on greater sage-grouse winter habitat selection, grouped in 5-year bins (1977–2022).

CHAPTER 2: EVALUATING RECOMMENDED SURFACE DISTURBANCE GUIDELINES WITHIN GREATER SAGE-GROUSE WINTER CONCENTRATION AREAS

In the form for manuscripts submitted to the *Journal of Wildlife Management and Wildlife Monographs*

ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*, hereafter 'sage-grouse') is a species of conservation concern across 11 western states and 2 Canadian provinces, where populations have declined mainly as a result of habitat loss and degradation. In the eastern portion of the range of sage-grouse, state and federal agencies are tasked with balancing a booming energy economy while conserving stable grouse populations. In Wyoming, disturbance is limited within Core Areas, which represent sage-grouse breeding habitat. Recommendations were recently developed for limiting disturbance within sage-grouse winter habitat, which are necessary to conserve sage-grouse populations throughout their annual cycle. These management recommendations were developed using habitat selection models derived from sage-grouse GPS locations across 6 regional populations in Wyoming. We used a region in the Southern Red Desert of Wyoming to test the validity and applicability of these models for regions with little data. We also compared sage-grouse habitat selection in the Southern Red Desert with the nearby Northern Red Desert region to determine whether regional differences support the use of regional models over statewide models. Similar to the statewide and near-region models, anthropogenic covariates improved habitat selection models in the Southern Red Desert over models with only environmental variables. We found similar trends in habitat selection between the Southern Red

Desert, near-region, and statewide models. Sage-grouse in the Southern Red Desert exhibited lower thresholds for avoidance of anthropogenic features than either the near-region or statewide models. The statewide model better predicted sage-grouse habitat selection at the home-range scale and the near-region model better predicted habitat selection within home ranges. Similar trends in avoidance behavior towards small amounts of surface disturbance across Southern Red Desert, near-region, and statewide models lends support to the recommendations to limit new surface disturbance below a small level of total disturbance in sage-grouse winter concentration areas.

KEYWORDS *Centrocercus urophasianus*, energy development, RSF, sage-grouse, winter habitat, Wyoming

INTRODUCTION

Changes in traditional land use and energy development will continue to be an enduring challenge to wildland management in the 21st century (Newbold et al. 2015). Western states are expected to experience the greater proportion of energy development in the US during the next 20 years (Trainer et al. 2016). In Wyoming, the intensity and extent of energy development (oil, gas, and wind) rose in the last ten years to unprecedented levels, primarily in sagebrush (*Artemisia* spp.) steppe (EIA 2022). Quantifying impacts of increasing energy development on sagebrush steppe ecosystems is necessary for state and federal agencies to make informed decisions toward fulfilling economic demand while sustaining wildlife populations. Habitat selection models can be used to inform development guidelines for protecting wildlife habitat by revealing patterns of selection or avoidance and predicting selection based on concurrent levels of disturbance. It is necessary to assess these models across different populations and vegetation communities to ensure that landscape variability does not exclude regionally used habitat from model predictions and thence from management protections (Coe et al. 2012).

Greater sage-grouse (*Centrocercus urophasianus,* hereafter 'sage-grouse') is a species of conservation concern across the Intermountain West of North America. Sage-grouse populations have declined 30.7% in the last 17 years and 80.7% in the last 53 years (Coates et al. 2021). Wyoming is considered a stronghold for sage-grouse (Knick et al. 2003), and southwest Wyoming is the only region, range-wide, where average finite rate of increase (lambda [λ]) was estimated to exceed 1.0 over the last 30 years (Coates et al. 2021). Concern over this declining charismatic species has heavily influenced modern land management policy in the western United States. In Wyoming, the Greater Sage-Grouse Core Area Protection Executive order (order 2019–3; hereafter "Sage-Grouse Executive order") designated Core Areas for sage-grouse conservation, with a 5% cap on surface disturbance per 2.6 km^2 (State of Wyoming 2019). However, this level of surface disturbance is often exceeded within individual projects inside Wyoming's 31 Core Areas (Gamo et al. 2017). Core Areas were delineated by breeding density areas (Doherty et al. 2011) and are more effective at protecting nesting and early brood-rearing locations than summer or winter habitat, with winter habitats being least protected (Fedy et al. 2012, Dinkins et al. 2017, Smith et al. 2016).

Sage-grouse have distinct seasonal habitat requirements during spring (breeding and nesting), summer/autumn (late-brood rearing), and winter (Pratt et al. 2019, Schroeder et al. 2021). Many sage-grouse populations are partially migratory, meaning a proportion of individuals in a population may be non-migratory or migrate between two or three separate seasonal ranges (10 to greater than 200 km apart; Fedy et al. 2012, Cardinal and Messmer 2016, Newton et al. 2017). Of these seasonal ranges, winter ranges are least likely to be encompassed within Core Areas (Fedy et al. 2012, Smith et al. 2016). High fidelity of sage-grouse for wintering areas (Schroeder et al. 2021) means disturbance outside Core Areas that limit wintering sage-grouse to marginal habitat could decrease winter survival and negatively impact sage-grouse populations that breed within Core Areas (Dinkins et al. 2017). The Sage-Grouse Executive Order (SGEO) calls for designation of protected winter concentration areas where seasonal disturbance is prohibited between 1 December and 14 March (State of Wyoming 2019). Currently, only the Alkali Creek and Alkali Draw Winter Concentration Areas (WCA) have been officially designated, both of which encompass approximately 142 km^2 in Sublette County in southwestern Wyoming (Wyoming Game and Fish 2022). Current seasonal protections in the Wyoming SGEO are insufficient to protect important winter habitat (Smith et al. 2016), considering sage-grouse and other species tend to avoid energy development and infrastructure during winter beyond the initial building activity (Doherty et al. 2008, Holloran et al. 2015, Reinking et al. 2019, Northrup et al. 2021, MacNearney et al. 2021).

The Wyoming Sage-Grouse Implementation Team, which is tasked with providing recommendations relative to the Wyoming Governor's SGEO, requested information through the WCA Subcommittee concerning sage-grouse winter habitat selection and if thresholds exist where sage-grouse respond to anthropogenic disturbance. Our research is the second phase of a larger effort to answer these questions (Smith et al. 2021). Phase 1 used existing datasets of sage-grouse GPS locations from 6 regions across Wyoming, digitized anthropogenic surface disturbance maps, and snow data to model winter habitat selection and avoidance patterns of disturbance state-wide. Phase 1 found variation in winter habitat selection between the pooled regions but a general statewide trend towards areas with gentle topography that were dominated by sagebrush land cover and absent of juniper (*Juniperus* spp.) land cover (Smith et al. 2021). Concerning anthropogenic disturbance, Phase 1 reported avoidance of press disturbance (disturbance sustained after initial disturbance such as energy field infrastructure and roads; Morrison et al. 2008) and all surface disturbance in both within-home-range and population-range scale selection. Statewide grouse-use locations did not exceed ~7% surface disturbance within any analysis window up to 10 km, and average surface disturbance (%) from all oil and gas development and active oil and gas development did not exceed 1% at grouse-use locations. The proportion of sage-grouse use locations were lower than the proportion of available habitat within all study regions when surface disturbance exceeded 3.8% for all disturbance types and scales assessed.

Results from Phase I formed the basis for developing disturbance management guidelines. The purpose of Phase II is to validate results of Phase I modeling and determine if the statewide model accurately described sage-grouse winter habitat selection and anthropogenic avoidance in regions not considered in that model. We used out-of-sample data from the Southern Red Desert to compare the predictive ability of both the statewide model and the nearest regional model (Northern Red Desert) and assess whether near-region data were more effective in predicting sage-grouse habitat selection between similar regions. We used the same methods utilized in Phase 1 to create a model for winter habitat selection using environmental and anthropogenic covariates at 2 scales of selection in the Southern Red Desert. The second order, or population-range scale, assessed selection across multiple winter home ranges of GPS-marked grouse, and the third order, or home-range scale, assessed selection within individual winter home ranges (Johnson 1980). Because sage-grouse winter habitat has been shown to be relatively similar across their range, we predicted that sage-grouse winter range selection trends in the Southern Red Desert would align with general trends evidenced in the statewide model but will be most similar to the nearby Northern Red Desert model. By comparing results of the novel area model to the near-region and statewide resource selection models, we determined whether state-wide or region-specific models were more appropriate for creating disturbance management plans for regions where habitat selection may be context-dependent.

STUDY AREA

Phase I utilized sage-grouse location data from existing datasets from 6 studies within Wyoming that each had unique research objectives and study area boundaries (Figure 2.1). The 6 pooled regions ranged in mean surface disturbance from 2.8% to 16.6% (Table 2.1). The Northern Red Desert region was the nearest region to the Phase II study area, located between Wamsutter and Rawlins, Wyoming, and north of Interstate 80 (Dzialak et al. 2013, Smith et al. 2021).

The Phase II study area was in the Southern Red Desert, located within Sweetwater and Carbon counties, Wyoming, with capture locations restricted to an area bordered by Interstate 80 to the north, Colorado to the South, Sierra Madre Range to the east, and Kinney Rim to the west. Sage-grouse in our study area nested within and between the South Rawlins and Powder Core Areas (Wyoming Game and Fish 2015) and wintered in lower elevations between these Core Areas. There have been multiple documented winter flocks with more than 50 birds in our study area, which fulfills the requirements for a winter concentration area under the SGEO (Smith et al. 2019, State of Wyoming 2019). We gathered location data across three winters: 2018/2019, 2019/2020, and 2021/2022. Comparing these winters with the previous 30 years in our study area (1988–2022; PRISM 2022), average winter temperatures fell within the 29th, 31st, and 31st percentiles, respectively. Winter precipitation, compared to the previous 30 years, fell within the 63rd, 91st, and 66th percentiles, respectively (PRISM 2022).

The study area encompassed ~10,500 km^2, comprised mostly of BLM-managed land (71%), private land (26%) and state of Wyoming land (3%). The study area was categorized as cold arid-steppe (Kottek et al. 2006) with elevation ranging from 1,800–3,300 m (USGS 2016) and annual precipitation ranging from 22–40 cm (30-yr average, PRISM Climate Group 2020). Dominant shrubs included Wyoming big sagebrush (*A. tridentata wyomingensis;* Table 2.1), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus spp.*), and saltbushes (*Atriplex spp.*). Shrub assemblies occurred across a gradient of soil and precipitation, dominated by sandy loams but including sand dunes and alkali complexes (Soil Survey Staff 2015). The study area contained regions of active oil and gas extraction, retired oil and gas development, and proposed areas of new development. Total surface disturbance was 4.0% (Table 2.1). Other dominant land uses in the study area included cattle and sheep grazing and recreation.

METHODS

Capture and GPS Locations

We captured and radio-marked adult female sage-grouse using spotlight and hoop-net methods (Giesen et al. 1982, Wakkinen et al. 1992) around leks during spring or at roost sites during summer or winter. We fitted each grouse with a rump-mounted GPS transmitter (GPS PTT [GeoTrack, Apex, North Carolina, USA], ~37 g total weight; or Bird Solar [e-obs GmbH, Grunwald, Germany], ~30 g total weight). GeoTrak transmitters uploaded GPS locations to satellites used by the ARGOS system (Woods Hole Group, Largo, Maryland, USA) every 3 days, and were programmed to acquire 4 locations per day from 1 November to 14 March (at 0000, 0900, 1200, and 1500 MST), 5 locations per day from 15 March to 30 April and 25 August to 30 October (at 0000, 0700, 1000, 1300, and 1600 MST), and 6 locations per day from 1 May to 24 August (at 0000, 0600, 0900, 1200, 1500, and 1800 MST). We programmed Bird Solar transmitters to collect at least one location every 10–15 minutes and stored locations onboard to be downloaded manually in the field or by fixed-wing aircraft. For this analysis, we subset location data collected from Bird Solar transmitters to be consistent with location data collected from GeoTrak transmitters. We redeployed recovered transmitters after mortality events during the following spring or winter. By doing so, we maintained active transmitters on females until spring 2021, providing location data across 3 winters (2018/2019, 2019/2020, and 2020/2021). All sage-grouse capturing and monitoring protocols were approved by the University of Wyoming Institutional Animal Care and Use Committee (protocol 20170324AP00266-03 and protocol 20200317JB00413-02) and Wyoming Game and Fish Department Chapter 33 permits (numbers 1160 and 1303).

We used individual-specific seasonal classifications of winter range arrival and departure dates to determine grouse locations used for subsequent analyses. We assigned grouse locations as winter locations by first identifying seasonal ranges of migratory grouse using a combination of contour levels of a utilization distribution from individual grouse locations and then calculating displacement (Pratt et al. 2017). We calculated a 95% utilization level to identify and delineate large concentrations of use, for the lifespan of each individual, from a dynamic Brownian bridge movement model (Kranstauber et al. 2012). To determine whether non-overlapping utilization distributions were seasonally dependent, we visually inspected plots of net-squared displacement (Bunnefeld et al. 2011) for characteristic 'plateaus' (i.e., displacement was larger between seasonal ranges than within seasonal ranges).

Landscape Predictor Variables

We explored predictor variables that described topography, vegetation, and anthropogenic landscape features (Table 2.). We calculated a heat load index (0–1), an index of solar radiation, to estimate areas that were hotter and drier compared to cooler and wetter (McCune and Keon

2002; Geomorphometry and Gradient Metrics, Evans et al. 2014). We used a 10-m digital elevation model (U.S. Geological Survey 2011) to calculate slope and standard deviation of slope, as an index of ruggedness (Grohmann et al. 2011) within a 5 x 5-pixel moving window. For vegetation predictors, we estimated percent big sagebrush canopy cover and sagebrush height from remotely sensed products (Xian et al. 2015). We calculated the proportion of sagebrush-dominated landscape (hereafter sagebrush) from the LANDFIRE Existing Vegetation Type raster dataset (LANDFIRE 2014). Sagebrush was restricted to Great Basin xeric mixed sagebrush shrubland, Intermountain basins big sagebrush shrubland, Columbia Plateau low sagebrush steppe, Intermountain basins big sagebrush steppe, and Intermountain basins montane sagebrush steppe identified from LANDFIRE (Donnelly et al. 2017). We also used LANDFIRE to generate the proportion of juniper (*Juniperus* spp.)-dominated landscapes (hereafter juniper). Juniper was restricted to Colorado Plateau pinyon (*Pinus* spp.)-juniper woodland, Great Basin pinyon-juniper woodland, Intermountain basins juniper savanna, Rocky Mountain foothill limber pine (*P. flexilis*)-juniper woodland, southern Rocky Mountain pinyon juniper woodland, and southern Rocky Mountain juniper woodland and savanna identified by LANDFIRE (2014).

We quantified surface disturbance following the Density/Disturbance Calculation Tool and the State of Wyoming Executive Order 2015-4 guidelines detailing sage-grouse protection within Core Areas (State of Wyoming 2015). We first gathered available data from the Wyoming Geographic Information Science Center at the University of Wyoming (http://www.uwyo.edu/wygisc/) and completed heads-up digitizing in areas that were not yet completed. We processed GIS data with ArcGIS Desktop v. 10.6, (http://www.esri.com/). Disturbance included any human alterations that resulted in vegetation removal, including improved roads (gravel and paved), access roads, energy infrastructure (e.g., oil and gas wells, wind turbines, and bentonite or coal mines), railroads and associated infrastructure, human dwellings and associated development, man-made reservoirs (e.g., evaporation pits), general electrical disturbance (e.g., overhead power lines), and other surface disturbance. Where possible, we time-stamped disturbance for each year to account for ongoing activities in some areas. We obtained data about active, plugged, and abandoned wells from the Wyoming Oil and Gas Conservation Commission (WYGCC 2018), that included location, status, and date when drilling was initiated. We used National Agriculture Imagery Program and Environmental Systems Research Institute world imagery to inspect and time-stamp disturbance when other information was not available.

We identified the operative scales for predictor variables, excluding Euclidean distance-based variables, using 8 circular regions: 0.1-km radii (0.03 km^2), 0.2-km radii (0.13 km^2), 0.4-km radii (0.50 km^2), 0.8-km radii (2.01 km^2), 1.6-km radii (8.04 km^2), 3.2-km radii (32.17 km^2), 6.4-km radii (128.68 km^2), and 10.0-km radii (314.16 km^2). The circular regions we assessed had relevance to previous research evaluating winter sage-grouse resource selection and existing management stipulations (Doherty et al. 2008, Carpenter et al. 2010, Dzialak et al. 2013, Smith et al. 2014, 2016, 2019, Walker et al. 2016).

Data Analysis

We modeled resource selection functions (RSFs) for sage-grouse at the scale of the population range (second-order selection; Johnson 1980) and within winter home ranges (third-order selection; Johnson 1980) using binomial generalized mixed models with package lme4 in R (Bates et al. 2015). To compare results from Phase II to statewide and the near-region models, we followed the same methods for analyzing data as Phase I, with two exceptions. First, Phase II did not incorporate breeding density metrics because some of our locations occurred in Colorado and information about lek locations and maximum numbers of males per lek were not available. Second, Phase II also lacked snow depth variables for all three years in this region to evaluate the relationship between resource selection and snow covariates. In all models, we used individual bird nested within year to account for individual variation and possible variation in individuals across years (Gillies et al. 2006). We considered 4 models of environmental covariates to predict sage-grouse winter habitat selection and used the most parsimonious model as the baseline to evaluate 5 additional models that included anthropogenic disturbance covariates. The null model contained only topographic covariates and the full model contained all topographic and vegetative covariates.

Prior to developing our candidate models, we performed initial variable screening by removing unsupported predictor variables when single variable models had Akaike's Information Criterion (AIC) scores that were greater than random intercept only models. All variables were centered and Z-transformed to ensure model convergence (Becker et al. 1988). When considering variables across multiple circular regions, we selected the variable scale that had the lowest AIC score. We then used a variable subset approach (Arnold 2010) to develop our nested candidate models to determine the most parsimonious environmental model (Table 2.2). Our null model contained only topographic covariates and then we explored all vegetation variable combinations within topography predictors separately. We did not allow variables in the same model when $|r| > 0.6$. We allowed each model to compete and considered candidate models within 4 AIC (Burnham and Anderson 2002) from the top model to be competitive.

Once we identified the top environmental model, we employed it as the base model(s) for evaluating potential anthropogenic disturbance and density thresholds on sage-grouse winter resource selection. We compared all anthropogenic variables that were retained after initial variable screening criterion, as described above. We compared 5 disturbance models containing covariates in the most predictive base environmental model, plus those describing potential anthropogenic impacts. We included covariates describing total surface disturbance, press disturbance, all surface disturbance resulting from oil and gas development, surface disturbance resulting from active oil and gas development, and oil and gas well pad density (Table 2.2). In addition, we included predictors that measured Euclidean distance to major and minor roads. We interpreted each anthropogenic model compared to environmental models, suggesting that multiple forms of anthropogenic surface disturbance could influence sage-grouse winter resource selection, then we used the most predictive anthropogenic model for interpretation of model coefficients. We used AIC to determine the most predictive model. Once the most predictive anthropogenic models were identified, we re-ran similar models that included all circular regions for each type of anthropogenic surface disturbance. Our intent was to determine the circular region for each disturbance type where disturbance was no longer predictive of sage-grouse winter resource selection. In addition, we used the most relevant anthropogenic covariates to identify potential threshold levels where sage-grouse winter use diverged from the amount of surface disturbance in available habitat. Finally, we included Euclidean distance to disturbance (e.g., oil and gas well pads or roads) in the most predictive anthropogenic model by including distance to the same disturbance type identified in the anthropogenic model to assess model improvement. We reasoned that inclusion of Euclidean distance would aid with identifying thresholds of response by sage-grouse to disturbance.

Validation

We compared thresholds of avoidance between the statewide, near-region, and Southern Red Desert models within the 8 circular regions used in our analyses. We compared common trends and differences between the Southern Red Desert and the other two models by assessing patterns in coefficients across each circular scale. To validate the statewide and near-region models using the out-of-sample data in the Southern Red Desert (~45,000 locations), we predicted selection across the Southern Red Desert study area using coefficients from each population-range and home range model. We then reclassified the resulting map into 5 equal-area bins using percentile breaks at 20% intervals. We extracted the reclassified landscape bin values to the Southern Red Desert sage-grouse location data and considered the models predictive if >50% of locations fell within the highest 2 bins, or probability >0.6 (Smith et al. 2019, Sawyer et al. 2007).

RESULTS

There were 44,968 locations from 90 individual grouse identified within winter habitat in the Southern Red Desert. The median date of arrival and departure of grouse from winter range in the Southern Red Desert was 10 November and 20 March, respectively, which fell within the statewide range in median dates of 17 October–29 November and 28 February–21 March for arrival and departure, respectively (Smith et al. 2021).

Winter Range (Second Order or Population-Range Scale) Resource Selection

The null environmental model included heat load index within 3.2 km, slope (%) within 0.1 km, and standard deviation of slope within 0.2 km. The full environmental model, which included sagebrush canopy cover (%) within 10.0 km, sagebrush land cover within 0.4 km, sagebrush height (cm) within 0.1 km, and proportion of juniper land cover within 0.4 km, was the most predictive model describing environmental covariates correlated with sage-grouse selection of winter ranges (ΔAIC = 23,908; Table 2.3). In general, sage-grouse selected areas with lower heat load index, lower slopes, and lower variability in slope (Table 2.4). Selection for vegetation included selection for areas with less sagebrush canopy cover at the largest scale (10.0 km) we evaluated, but sagebrush-dominated land cover with taller sagebrush and less juniper at a local scale (0.1 km and 0.4 km, respectively; Table 2.4).

All anthropogenic models including forms of surface disturbance and well pad density were more informative than the base environmental model (Table 2.3). The most parsimonious model included all surface disturbance within 6.4 km, distance to roads, and distance to major roads (Table 2.3). Other models included anthropogenic covariates describing press disturbance, well pad density, active oil and gas disturbance, and all oil and gas disturbance within 10.0 km. Coefficients from the top model indicated that the relative probability of selection of sage-grouse winter seasonal ranges decreased as all surface disturbance increased within 10.0 km (Figure 2.2). Sage-grouse avoided press disturbance and all surface disturbance once circular regions exceeded 1.6 km and 0.4 km, respectively (Figure 2.2). Avoidance of all oil and gas, and active oil and gas disturbance was evident within circular regions up to 0.8-km radii (Figure 2.2). Avoidance of greater well pad density was evident within circular regions up to 1.6-km radii (Figure 2.2). Across all disturbance types and circular regions, mean surface disturbance (%) at grouse-use locations did not exceed ~2.5% surface disturbance (Figures 2.3). Sage-grouse use locations did not occur in areas exceeding ~1% active oil/gas disturbance (Figure 2.4).

Within Winter Range (Third Order or within Home-Range Scale) Resource Selection

The null environmental model included heat load index within 0.4 km and slope (%) within 0.1 km. The full environmental model, which also included sagebrush canopy cover (%) within 0.1 km, sagebrush land cover within 0.1 km, and juniper land cover within 0.4 km, was the most predictive model describing environmental covariates correlated with sage-grouse selection of winter habitat within home ranges (ΔAIC = 4,484; Table 2.5). In general, sage-grouse selected areas within home ranges with lower heat load index and lower slopes (Table 2.6). Selection for vegetation included selection for areas at local scales with greater sagebrush canopy cover and sagebrush-dominated land cover (0.1 km), and with less juniper land cover (0.4 km; Table 2.6).

All anthropogenic models containing forms of surface disturbance and well pad density were more informative than the base environmental model (Table 2.5). The most parsimonious model included all surface disturbance within 0.4 km and distance to roads (Table 2.5). Other models included anthropogenic covariates describing well pad density within 0.8 km, active oil and gas disturbance within 0.4 km, oil and gas disturbance within 0.4 km, and press disturbance within 1.6 km (Table 2.5). Coefficients from the top model suggested that the relative probability of selection of sage-grouse for habitat within winter home ranges decreased as all surface disturbance increased within 0.4 km (Figure 2.4). In the Southern Red Desert, sage-grouse avoided press disturbance up to radii of 0.4 km and all surface disturbance once circular regions exceeded 6.4 km (Figure 2.5). Avoidance of all oil and gas disturbance, and active oil and gas disturbance was evident across all circular regions we assessed (Figure 2.5). Avoidance of greater well pad density was also evident across all circular regions (Figure 2.5). Across all disturbance types and circular regions, mean surface disturbance (%) at grouse-use locations did not exceed approximately 2.5% for all surface disturbance (Figure 2.6). Sage-grouse use locations did not occur in areas exceeding ~1% active oil/gas disturbance (Figure 2.7).

Validation

Comparison of the predicted probability of selection showed that at both population-range and home-range scales the statewide and near-region models were predictive. At the population-range scale, the statewide model best predicted winter habitat home range selection, with 74% of Southern Red Desert sage-grouse locations in winter falling in areas with a predicted probability

>0.6 (on a 0 to 1 scale), compared to 64% in the near-region model (Figure 2.8). At the home-range scale, the near-region model was a slightly stronger predictor, with 66% of locations having a predicted probability >0.6, compared to 64% from the statewide model (Figure 2.8). At the population-range scale, 15% of locations fell in areas that the statewide model predicted relative selection probability of 0.0, which indicates that the statewide model failed to predict some areas that sage-grouse were using in the Southern Red Desert.

DISCUSSION

We used out-of-sample data located in the Southern Red Desert, Wyoming, to assess the ability of near-by region and statewide models to predict sage-grouse winter habitat selection and response to anthropogenic disturbance. Our assessment will serve to validate the applicability of management approaches to be applied to areas in Wyoming with no sage-grouse winter location data. Our results support the notion that regional variation in sage-grouse selection of habitats during winter is dependent on specific environmental conditions and amounts of existing disturbance. The degree of use by sage-grouse deviated from available winter habitat at low levels of surface disturbance, irrespective of study region or scale, which lends support for the approach taken by Wyoming's Core Area policy to limit new surface disturbance below a small level of total disturbance (State of Wyoming, 2015).

The Southern Red Desert model of sage-grouse winter habitat selection followed similar trends, at both population-range and home-range scales, to the near-region and statewide models (Table 2.6). Our results were consistent with other published trends that reported sage-grouse winter in areas with gentle topography that are dominated by sagebrush land cover and absent of juniper land cover (Doherty et al. 2008, Carpenter et al. 2010, Smith et al 2014, Coates et al. 2020).

Our results support our prediction that baseline environmental factors for sage-grouse winter habitat selection were similar across regions with some regional variability (Table 2.6). For instance, the main deviation from the statewide model that both the Northern Red Desert and Southern Red Desert shared was a tendency of sage-grouse to select cooler-facing northern slopes instead of warmer-facing southern slopes at both population-range and home-range scales (Table 2.6). This was consistent with what other studies reported for sage-grouse in the Northern Red Desert (Dzialak et al. 2013). Our results agree with Phase 1 modeling and other research that anthropogenic disturbance is a significant predictor of sage-grouse winter habitat selection but with regional differences in avoidance depending on existing disturbance (Table 2.6; Doherty et al. 2008, Holloran et al. 2015, Smith et al. 2014, 2019, Row et al. 2022). These results are also consistent with findings on sage-grouse avoidance of energy development during other seasons (Walker et al. 2010, 2022; Kirol et al. 2015). In all three models, greater tolerance for surface disturbance within larger circular regions indicates that sage-grouse selected winter home ranges (population-range scale) with lower surface disturbance at smaller scales where surface disturbance within quality winter habitat (home-range scale) fell below thresholds of avoidance (Figure 2.2, 2.5). Similar to the statewide and near-region models, thresholds of avoidance in the Southern Red Desert were lowest for percent surface disturbance from active oil and gas disturbance at both scales assessed (Figures 2.4 and 2.7).

We used an out-of-sample validation method because it provides better information regarding broader-scale predictive power than in-sample model validation (Tredennick et al. 2021). Out-of-sample validation has been effective at predicting suitable habitat in novel areas for other species (e.g., Lepidopterans, Binzenhofer et al. 2005; elk [*Cervus canadensis*], Sawyer et al. 2007; and little owl [*Athene nactua*], Fattebert et al. 2018). In some contexts, resource selection functions (RSF) are not robust for application in different populations due to regional adaptations and behavior (Boyce et al. 2002). In other contexts, non-local models may be better for conservation purposes because RSFs generated from local populations may result in over-fit models that fail in broader-scale applications (Wan et al. 2019). However, in the case of the Southern Red Desert, the statewide model was the best predictor of sage-grouse habitat selection in the Southern Red Desert at the population selection scale (Figure 2.8), supporting our prediction of baseline environmental features for winter habitat. At the home-range scale, 15% of sage-grouse locations fell within areas the statewide model predicted a 0% chance of selection, and the near-region model had a slightly higher total percentage of locations above our 0.6 probability threshold (Figure 2.8). These results suggest that the statewide model did not fully capture regional differences in sage-grouse winter selection at small scales and supports our prediction of some regional variation in habitat selection. Previous reports of sage-grouse winter habitat selection included both flat topography (Doherty et al 2008) or ridges (Beck 1977); short sagebrush (Hagen et al. 2011) or draws with tall, dense sagebrush (Braun et al. 2005); homogenous landscapes dominated by sagebrush (Carpenter et al. 2010) or mixed shrub communities (Hagen et al. 2011, Coates et al. 2016) and even cropland landcover (Coates et al. 2016). These reported differences may demonstrate adaptations to local landscapes and weather patterns. Our results suggest that scale of selection is important in prediction applications and support use of within-region models for predicting small-scale, local habitat selection.

Because of regional differences, we recommend caution when setting disturbance thresholds at a statewide level. Underlying environmental conditions and percentage of alternative winter habitat may determine the strength of sage-grouse response to anthropogenic disturbance (Gill et al. 2001) and the risk of creating population sinks (Keagy et al. 2005). In the Southern Red

Desert, where total surface disturbance was lower than most other regions included in the statewide model (second to Southern Wind/Sweetwater Basins; Table 2.1), mean surface disturbance at grouse-use locations did not exceed 2.5%. This is in comparison to 4.7% in the Northern Red Desert and 7% statewide (Table 2.1). There are a few possible reasons for the variation in avoidance thresholds. Functional responses of sage-grouse occupying areas with higher disturbance may demonstrate reduced sensitivity in habitat near energy development, which has been observed in cougars (*Puma concolor;* Knopff et al. 2014) and mule deer (*Odocoileus hemionus*; Northrup et al. 2021). Alternatively, in areas with the greatest disturbance (Bighorn Basin and Green River Basin had 12.2% and 16.6% surface disturbance, respectively), sage-grouse may already be relegated to habitat closer to disturbance than they would otherwise select through the reduction of available habitat. Reduction of available habitat more than surface disturbance density may have survival consequences for sage-grouse similar to other sagebrush obligate songbirds (LeBeau et al. 2014, Hethcoat and Chalfoun, 2015). More research is needed to determine the fitness outcomes for sage-grouse that live in closer proximity to energy development.

We recommend consideration of regional differences in habitat quality when setting levels of permitted disturbance. Location of disturbance within regions and proximity to high-quality winter habitat may be as important as total surface area in qualifying the impact of anthropogenic disturbance (Edge and Fortin 2020). In the Northern Red Desert, habitat that provides critical cover for sage-grouse during severe winter conditions was distributed patchily and constrained to 7–18% of the landscape (Dzialak et al. 2013). Therefore, disturbance to habitat necessary to surviving severe winters could impact populations disproportionate to the extent of disturbance or the degree of selection by sage-grouse during mild winters (Dzialak et al. 2013). In the Southern Red Desert, Kirol et al. (2015) reported that reduction of source populations was most likely caused by encroachment of energy development, and Smith et al. (2014) reported that winter habitat characterized as high occurrence–low risk for sage-grouse encompassed only 17.1% within the Southern Red Desert. Disturbance within patches that are high occurrence and low risk is more likely to negatively impact winter sage-grouse populations than areas where occurrence is low. Further research into fitness consequences may elucidate the relative impact of surface disturbance on sage-grouse populations between regions.

MANAGEMENT IMPLICATIONS

Our analysis of the Southern Red Desert in comparison with statewide and near-region resource selection function models supports the notion that sage-grouse select baseline environmental conditions that can be predicted at broad scales in regions with little data. Regional variation in sage-grouse selection of habitats during winter should be expected on more local levels, dependent on specific environmental conditions and amounts of existing disturbance. Efforts to apply recommendations for total surface disturbance should consider coverage of existing winter habitat whenever that information is available. While the effectiveness of limiting the amount of surface disturbance for sage-grouse is not well studied, our results suggest that the 5% surface disturbance cap within Sage-Grouse Core Areas (State of Wyoming 2019) is too high for winter habitats in many regions of Wyoming. Our results also suggest that, in addition to total density of disturbance, proximity to disturbance may also influence sage-grouse avoidance of available habitat. Overall, our findings lend support for Wyoming's Core Area policy (State of Wyoming 2019) that limits development projects to a low level of surface disturbance within sage-grouse winter habitat falling within core areas.

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Table 2.1. Characteristics of sagebrush and surface disturbance within the novel study area (Southern Red Desert) and each of the 6 study regions used to assess greater sage-grouse winter resource selection, Wyoming, 2008–2018 (Smith et al. 2021). Values represent mean characteristics within each study region defined by a minimum convex polygon surrounding all seasonal grouse use locations.

Percentage	**Southern Red Desert**	**Northern Red Desert**	**Northern Wind and Sweetwater Basins**	**Southern Wind and Sweetwater Basins**	**Bighorn Basin**	**Green River Basin**	**Tongue and Powder Basins**
Sagebrush canopy cover[a]	7.3	8.5	7.6	10.4	5.8	11.2	11.5
Sagebrush land cover[b]	55.9	63.4	57.8	71.2	37.4	46.6	26.2
Press disturbance	2.1	3.1	2.4	2.1	9.9	14.6	4.4
All disturbance	4.0	4.7	7.9	2.8	12.2	16.6	4.4
All oil and gas disturbance	0.56	1.0	0.28	0.09	0.07	0.78	0.20
Active oil and gas disturbance	0.38	0.83	0.23	0.06	0.06	0.75	0.19

[a]Percent canopy cover of big sagebrush developed by Xian et al. (2015).

Table 2.2. Variables used in models evaluating greater sage-grouse winter habitat selection at the population-range (second order) and home-range (third order) scales.

Variable name	Description/source
Topographic	
Heat load index (HLI)	HLI approximates an index of coolest to warmest aspects (0-1; McCune and Keon 2002)
Slope	Mean slope (%) calculated from a 10-m digital elevation model (U.S. Geological Survey 2011)
Standard deviation of slope (SlopeSD)	Index of topographic ruggedness calculated as the standard deviation of slope within a 5 x 5-pixel moving window (Grohmann et al. 2011)
Breeding density	
Distance (km) to nearest occupied lek (EucLeks)[a]	Euclidean distance to nearest lek (km). Lek locations from Wyoming Game and Fish Department lek database (Wyoming Game and Fish Department 2012)
Maximum male lek count (Males)[a]	Maximum male lek counts over the preceding 10 years within each circular region (Smith et al. 2019)
Vegetation	
Sagebrush cover (Sage)	Percent canopy cover of big sagebrush developed by Xian et al. (2015)
Proportion of sagebrush (SageProp)	Proportion of sagebrush land cover (LANDFIRE 2014). Sagebrush was restricted to Great Basin xeric mixed sagebrush shrubland, Intermountain basins big sagebrush shrubland, Columbia Plateau low sagebrush steppe, Intermountain basins big sagebrush steppe, and Intermountain basins montane sagebrush steppe identified from LANDFIRE (Donnelly et al. 2017)
Sagebrush height (sageH)	Height of sagebrush (cm) developed by Xian et al. (2015)
Proportion of juniper (Juniper)	Proportion of juniper land cover (LANDFIRE 2014). Juniper was restricted to Colorado Plateau pinyon-juniper woodland, Great Basin pinyon-juniper woodland, inter-mountain basins juniper savanna, Rocky Mountain foothill limber pine juniper woodland, southern Rocky Mountain pinyon juniper woodland, and southern Rocky Mountain juniper woodland and savanna identified from LANDFIRE
Snow	

Length of core snow season (SnowCore)[a]	Length (days) of the core snow season defined as the period with the longest continuous snow cover exceeding 1 cm (Liston and Elder 2006)
Daily snow depth (SnowDaily)[a]	Daily snow depth (m; Liston and Elder 2006)
Maximum snow depth (SnowMax)[a]	Maximum snow depth (m) for each year (Liston and Elder 2006)
Mean snow depth (SnowMean)[a]	Mean snow depth (m) during winter for each year specified for each study area by timing of presence on winter range
Sagebrush height above snow (SageSnow)[a]	Mean sagebrush height (SageH; Xian et al. 2015) subtracted from Mean snow depth (SnowMean; Liston and Elder 2006)
Anthropogenic	
Distance to roads (EucRoads)	Euclidean distance (km) to roads, excluding 2-tracks, and US or interstate roads (O'Donnell et al. 2014)
Distance to major roads (EucMajRoads)	Euclidean distance (km) to US or interstate roads (O'Donnell et al. 2014)
Total surface disturbance (AllDisturb)	Bare ground (%) resulting from vegetation removal
Press disturbance (Press)	Surface disturbance (%) sustained after initial disturbance (Morrison et al. 2008) such as roads and energy infrastructure but not pulse disturbances such as fire or mechanical and chemical treatments
Active oil and gas development (ActiveOg)	Surface disturbance (%) resulting from active oil and gas development (well pads, oil and gas structures, evaporation pits, etc.)
All oil and gas development (AllOg)	Surface disturbance (%) resulting from oil and gas development (well pads, oil and gas structures, evaporation pits, etc.) including abandoned and interim reclamation disturbance
Oil and gas well pad density (WellDens)	Number of oil and gas well pads within each circular analysis region (WYGCC 2018)

[a]Variable was not used in Phase II (Southern Red Desert) modelling because accurate information on this metric was unavailable.

Table 2.3. Candidate models using environmental and anthropogenic covariates to explain sage-grouse winter range selection (population-range scale selection) using data from the Southern Red Desert of Wyoming, 2018–2021.

	Model fit statistics [a]		
Model	**K**	**ΔAIC**	**w_i**
Environmental[b] + Roads[c] + $AllDisturb_{6.4km}$	12	0.00	1.00
Environmental[b] + Roads[c] + $Press_{10.0km}$	12	3880.39	0.00
Environmental[b] + Roads[c] + $WellDens_{10.0km}$	12	6472.08	0.00
Environmental[b] + Roads[c] + $ActiveOg_{10.0km}$	12	6558.01	0.00
Environmental[b] + Roads[c] + $AllOg_{10.0km}$	12	6816.05	0.00
Environmental[b]	9	25115.93	0.00

[a]Number of parameters (*K*), change in Akaike's Information Criterion score from the top model (ΔAIC) and Akaike weights (w_i).

[b]Environmental model parameters include heat load index within 3.2 km ($HLI_{3.2km}$), slope (%) within 0.1 km ($slope_{0.1km}$), standard deviation of slope ($SlopeSD_{0.2km}$), sagebrush cover (%) within 10.0 km ($Sage_{10.0km}$), proportion of sagebrush within 0.4 km ($SageProp_{0.4km}$), sagebrush height (cm) within 0.1 km ($SageH_{0.1km}$), and proportion of juniper within 0.4 km ($Juniper_{3.2km}$).

[c]Roads parameters include EucMajRoads and EucRoads.

Table 2.4. Parameter estimates with 95% confidence intervals for predictor variables describing greater sage-grouse resource selection within population-range and home-range scales in the Southern Red Desert, Wyoming, 2018–2021.

				95% CI	
Parameter[a]	**Selection scale**	**Scale (km)**	**Estimate**	**Lower**	**Upper**
Topography					
HLI	Population	3.2	-0.03	-0.05	-0.01
	Home-range	0.4	-0.10	-0.12	-0.09
Slope	Population	0.1	-0.65	-0.69	-0.61
	Home-range	0.1	-0.42	-0.44	-0.41
Vegetation					
Sage	Population	10.0	-0.45	-0.47	-0.42
	Home-range	0.1	0.41	0.40	0.43
SageProp	Population	0.4	0.69	0.67	0.71
	Home-range	0.1	0.11	0.10	0.12
Juniper	Population	0.4	-0.94	-1.03	-0.85
	Home-range	0.4	-0.16	-0.18	-0.14
Anthropogenic					
EucRoads	Population	NA	-0.11	-0.13	-0.10
	Home-range	NA	0.03	0.01	0.04
EucMajRoads	Population	NA	-0.93	-0.94	-0.91
	Home-range	NA	NA	NA	NA
AllDisturb	Population	6.4	-0.90	-0.92	-0.87
	Home-range	0.4	0.11	0.10	0.11

[a]Parameter estimates obtained from models with centered and scaled variables. Parameters included heat load index within 0.4 km (HLI0.4km), slope (%) within 0.1 km (Slope0.1km), sagebrush cover (%) within 0.1 km (Sage0.1km), proportion of sagebrush within 0.1 km (SageProp0.1km), proportion of juniper within 0.4 km (Juniper0.4km), Euclidean distance to roads (EucRoads), and all disturbance within 0.4 km (ActiveOg0.4km).

Table 2.5. Candidate models using environmental and anthropogenic covariates to explain sage-grouse habitat selection within winter home ranges (third-order selection) using data from the Southern Red Desert of Wyoming, 2018–2021.

	Model fit statistics [a]		
Model	**K**	**ΔAIC**	**w_i**
Environmental[b] + Roads[c] + $AllDisturb_{0.4km}$	9	0.00	1.00
Environmental[b] + Roads[c] + $WellDens_{0.8km}$	9	212.70	0.00
Environmental[b] + Roads[c] + $ActiveOg_{10.0km}$	9	428.77	0.00
Environmental[b] + Roads[c] + $AllOg_{0.4km}$	9	460.73	0.00
Environmental[b] + Roads[c] + $Press_{1.6km}$	9	543.83	0.00
Environmental[b]	7	646.68	0.00

[a]Number of parameters (*K*), change in Akaike's Information Criterion score from the top model (ΔAIC) and Akaike weights (w_i).

[b]Environmental model parameters include heat load index within 3.2 km ($HLI_{3.2km}$), slope (%) within 0.1 km ($slope_{0.1km}$), standard deviation of slope ($SlopeSD_{0.2km}$), sagebrush cover (%) within 10.0 km ($Sage_{10.0km}$), proportion of sagebrush within 0.4 km ($SageProp_{0.4km}$), sagebrush height (cm) within 0.1 km ($SageH_{0.1km}$), and proportion of juniper within 0.4 km ($Juniper_{3.2km}$).

[c]Roads parameters include EucMajRoads and EucRoads.

Table 2.6. Scales (radii size) and effects in parameter estimates for predictor variables describing winter greater sage-grouse resource selection from data pooled statewide (2008–2018), from the near-region Northern Red Desert (2009–2014), and from the Southern Red Desert study area (Phase II, 2018–2021), Wyoming. Parameters were derived from the most parsimonious model describing environmental and anthropogenic covariates that influenced resource selection within the population and within winter home ranges by sage-grouse. Scales and trends of all surface disturbance predictors were included for comparison.

		Statewide		Northern Red Desert		Southern Red Desert	
Parameter	Selection scale	Scale	Effect	Scale	Effect	Scale	Effect
Topography							
HLI	Population	0.8	+	10.0	–	10.0	–
	Home-range	10.0	+	0.1	–	0.4	–
Slope	Population	0.2	–	0.1	–	0.1	–
	Home-range	0.1	–	0.1	–	0.1	–
SlopeSD	Population	NA	NA	NA	NA	NA	–
	Home-range	NA	NA	NA	NA	NA	–
Vegetation							
Sage	Population	0.1	+	1.6	+	10.0	–
	Home-range	0.1	+	0.1	+	0.1	+
SageProp	Population	0.4	+	0.4	+	0.4	+
	Home-range	0.4	+	0.2	+	0.1	+
SageH	Population	NA	NA	NA	NA	0.1	+
	Home-range	NA	NA	NA	NA	NA	NA
Juniper	Population	3.2	–	3.2	–	0.4	–
	Home-range	0.2	–	3.2	–	0.4	–
Anthropogenic							
EucRoads	Population	NA	–	NA	+	NA	–[a]
	Home-range	NA	–	NA	+	NA	+[a]
EucMajRoad	Population	NA	+	NA	+	NA	–[a]
	Home-range	NA	+	NA	NA	NA	NA
Press	Population	1.6	–	0.2	–	10.0	–
	Home-range	0.2	–	0.1	–	1.6	+
AllDisturb	Population	3.2	–	10.0	–[a]	6.4	–[a]
	Home-range	3.2	–	1.6	+	0.4	+[a]
WellDens	Population	NA	NA	NA	NA	10.0	–
	Home-range	NA	NA	NA	NA	0.8	–
AllOG	Population	10.0	–	0.4	–	10.0	–
	Home-range	0.4	–	0.2	–	0.4	–
ActiveOG	Population	10.0	–[a]	0.4	–	10.0	–
	Home-range	0.4	–[a]	0.4	–[a]	0.4	–

[a]Surface disturbance covariate included in the most predictive model

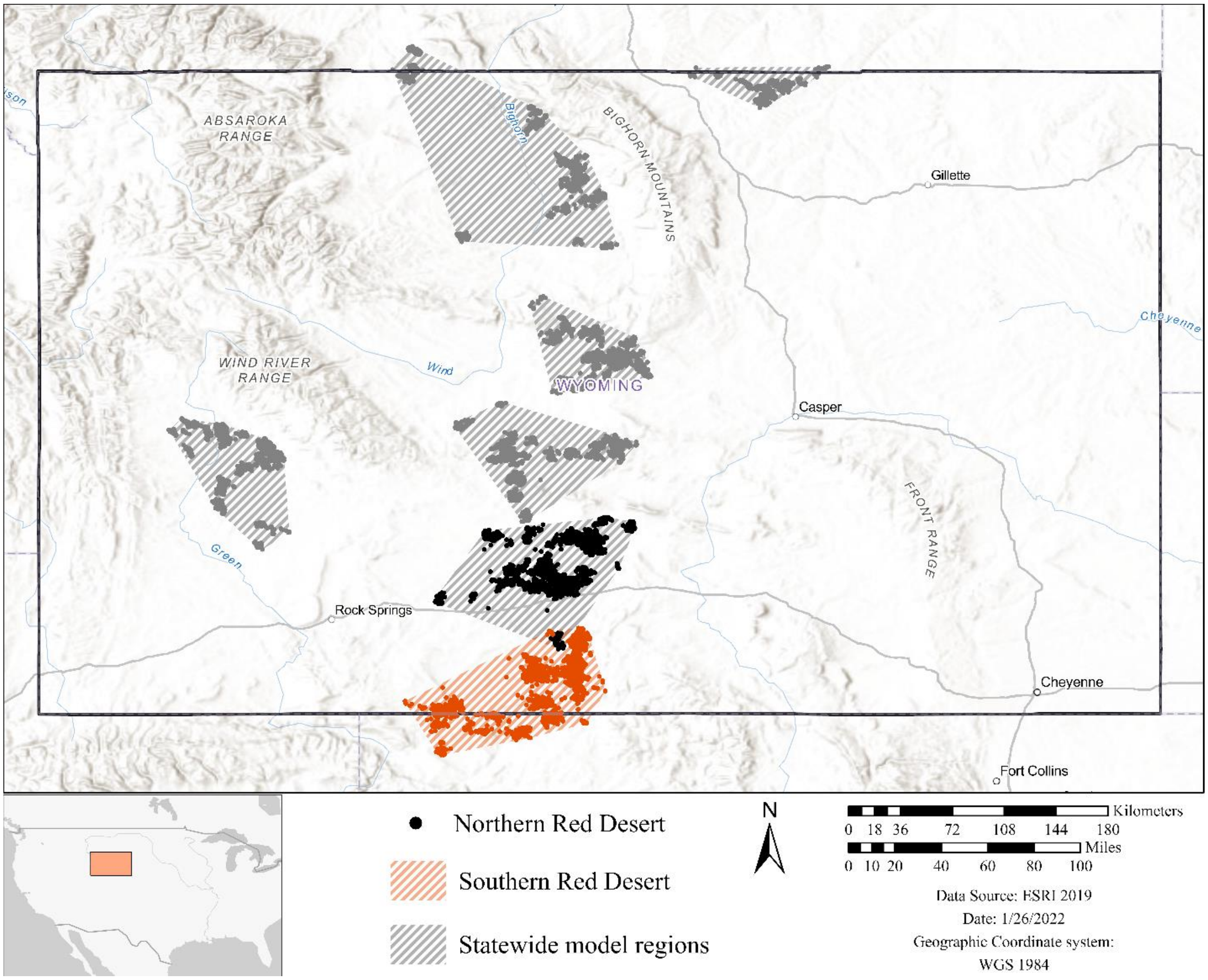

Figure 2.1. Greater sage-grouse locations from GPS datasets in 7 regions in Wyoming, USA, 2008–2018. 6 regions, including the Northern Red Desert, were used in resource selection function analyses for sage-grouse winter habitat (Phase I). Locations from the Southern Red Desert were used as out-of-sample data to test the effectiveness of the statewide model to predict sage-grouse winter habitat selection in regions outside the dataset (Phase II).

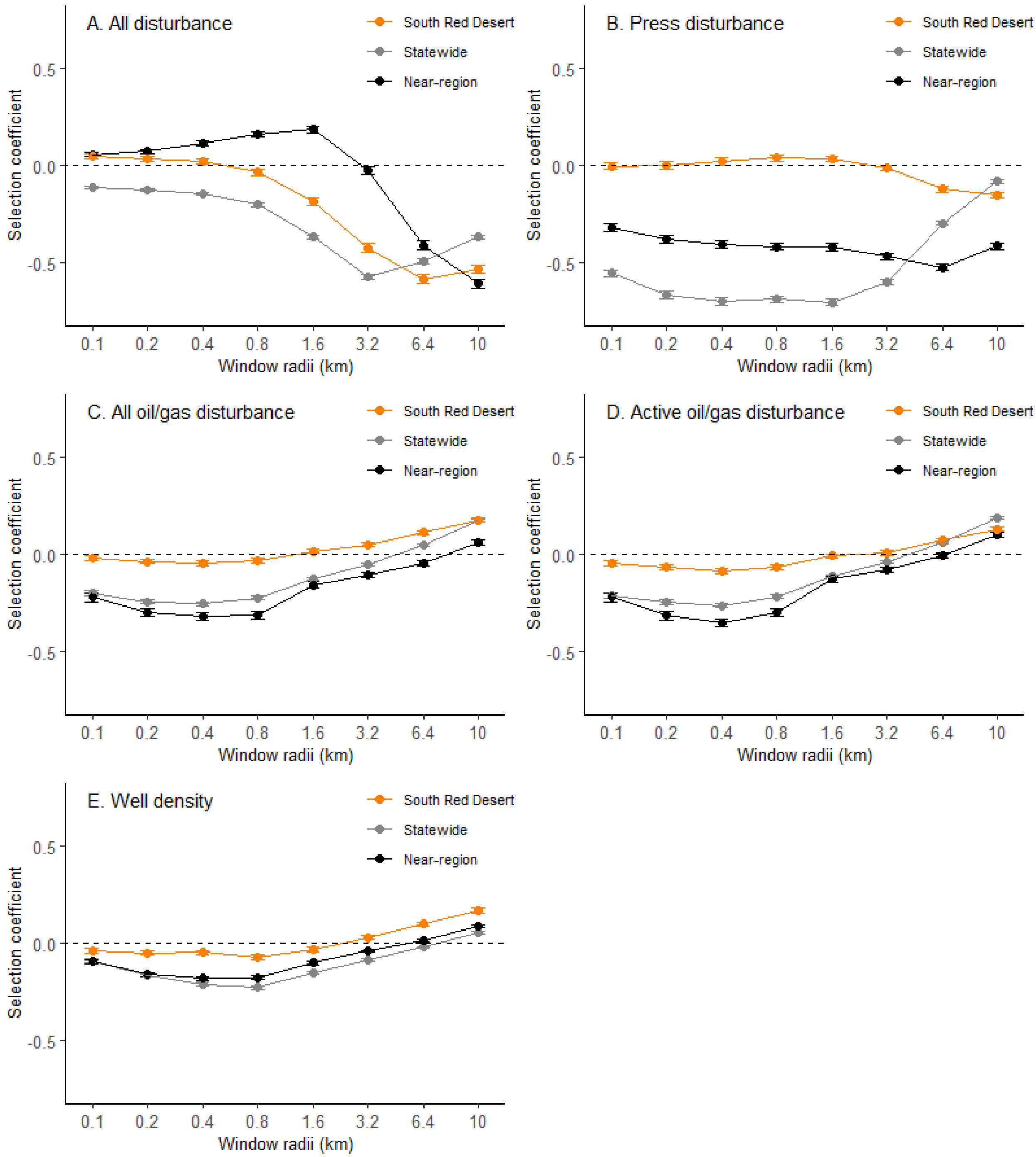

Figure 2.2. Comparison of greater sage-grouse resource selection coefficients used to evaluate selection of winter ranges **(population-range scale selection)** for all surface disturbance (A), press disturbance (B), all oil and gas surface disturbance (C), active oil and gas surface disturbance (D), and oil and gas well pad density © in the Southern Red Desert (2018–2021), Northern Red Desert (near-region; 2009–2014) and within 6 study regions across Wyoming (statewide; 2008–2018).

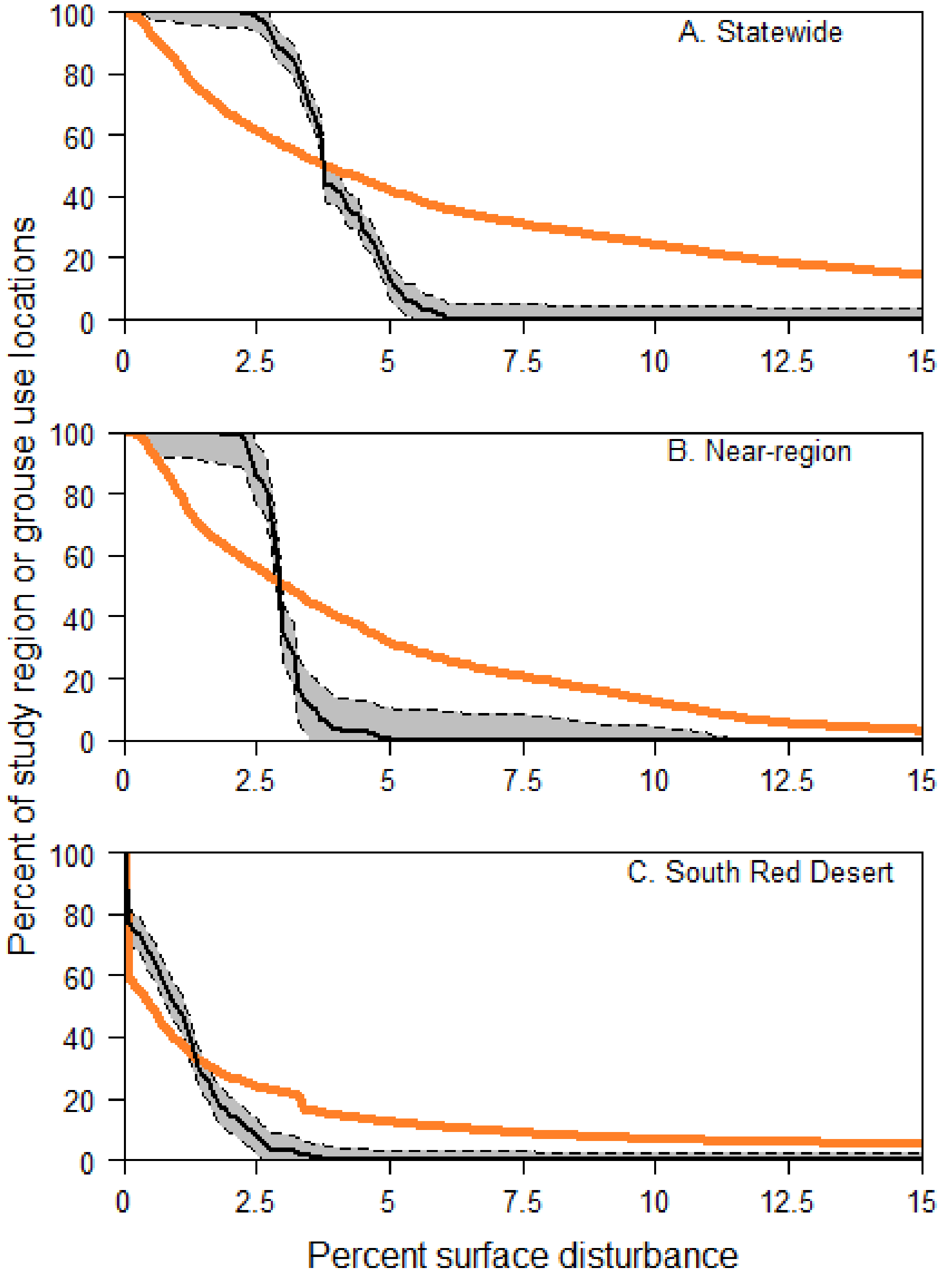

Figure 2.3. Potential disturbance thresholds for greater sage-grouse from 6 study regions, Wyoming, 2008–2018 (Statewide; A), the Northern Red Desert study region, 2009–2014 (Near-Region; B) and the Southern Red Desert study region, 2018–2021 (C). The red line represents the percent of available habitat in a 100% minimum convex polygon around all winter grouse use locations (**population scale analysis**; Y-axis) with the indicated amount of disturbance or greater (X-axis) for all surface disturbance within 10.0 km. The black line represents the percent of grouse-use locations across differing levels of disturbance within the same region sizes.

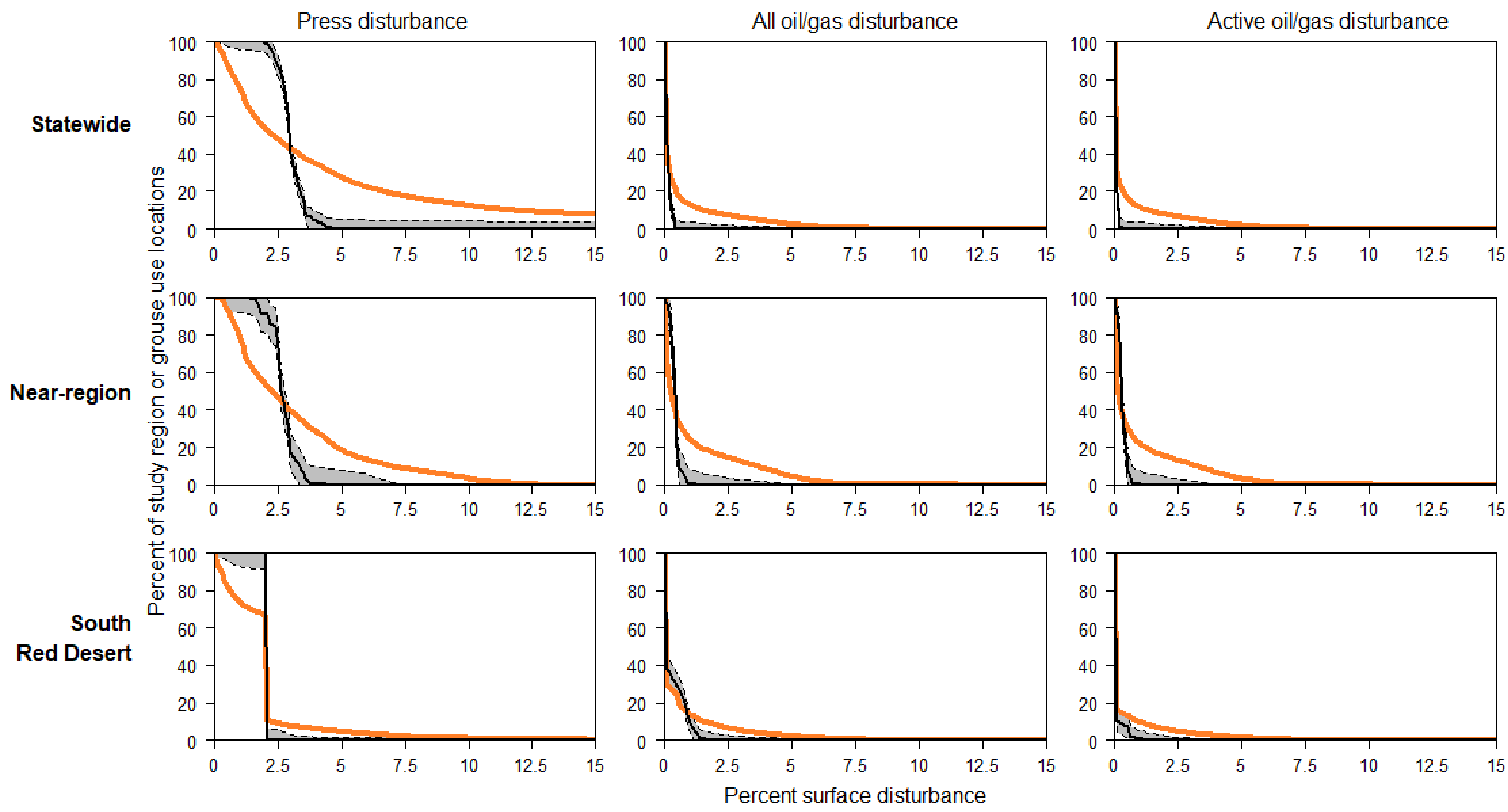

Figure 2.4. Potential disturbance thresholds for greater sage-grouse within 6 study regions, 2008–2018 (Statewide), the Northern Red Desert, 2009–2014 (Near-region) and in the Southern Red Desert, Wyoming study region, 2018–2021. The red line represents the percent of available habitat in a 100% minimum convex polygon around all year-round grouse use locations (**population-range scale analysis**; Y-axis) with the indicated amount of disturbance or greater (X-axis) for press disturbance within 3.2 km (A), all disturbance within 0.8 km (B), all oil and gas disturbance within 0.8 km (C), and active oil and gas disturbance within 0.8 km (D). The black line represents the percent of grouse-use locations across differing levels of disturbance within the same region sizes.

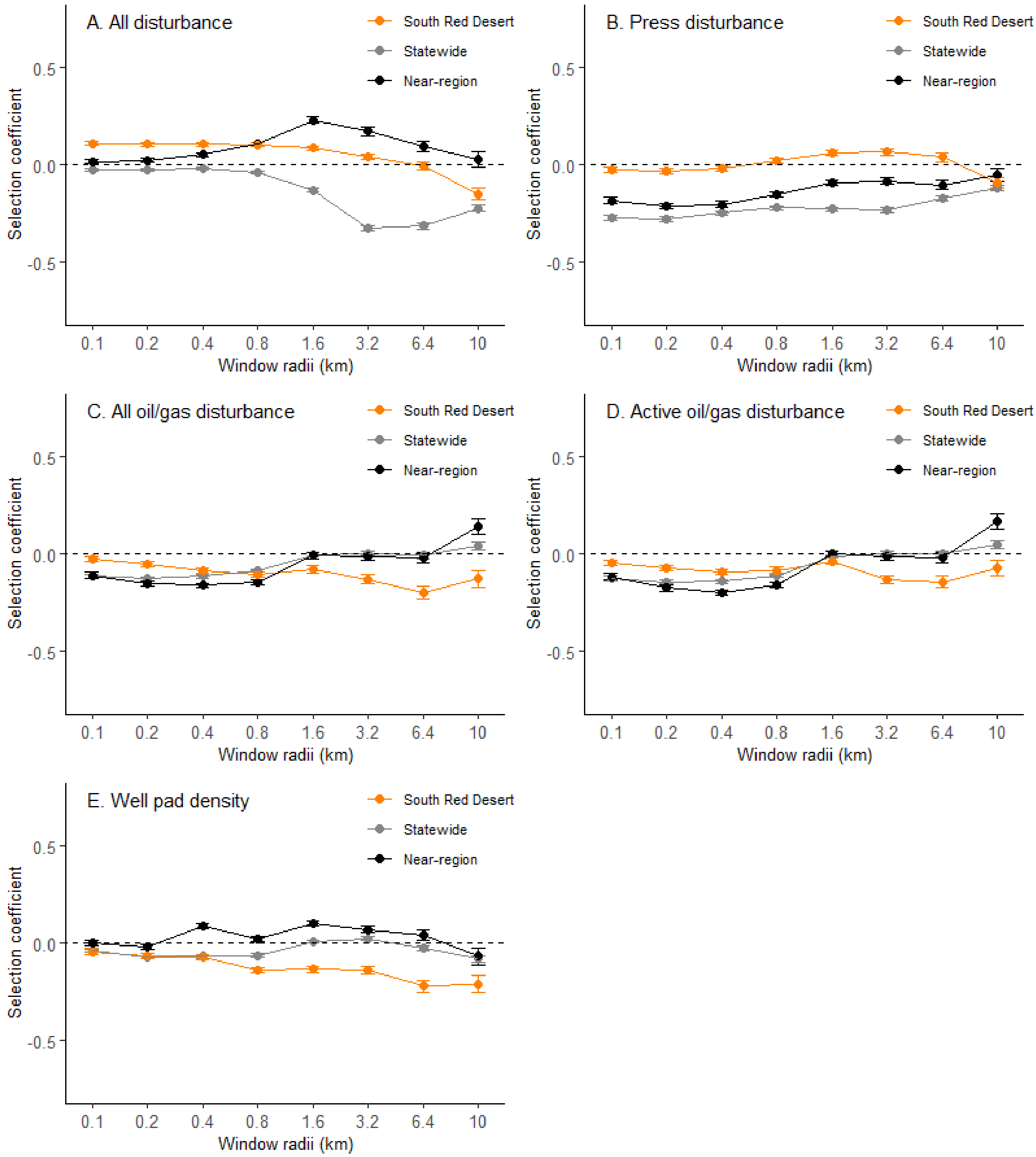

Figure 2.5. Comparison of greater sage-grouse resource selection coefficients used to evaluate selection of habitat within winter home ranges for all surface disturbance (A), press disturbance (B), all oil and gas surface disturbance (C), active oil and gas surface disturbance (D), and oil and gas well pad density (E) in the Southern Red Desert (2018–2021), Northern Red Desert (near-region; 2009–2014) and within 6 study regions across Wyoming (statewide; 2008–2018).

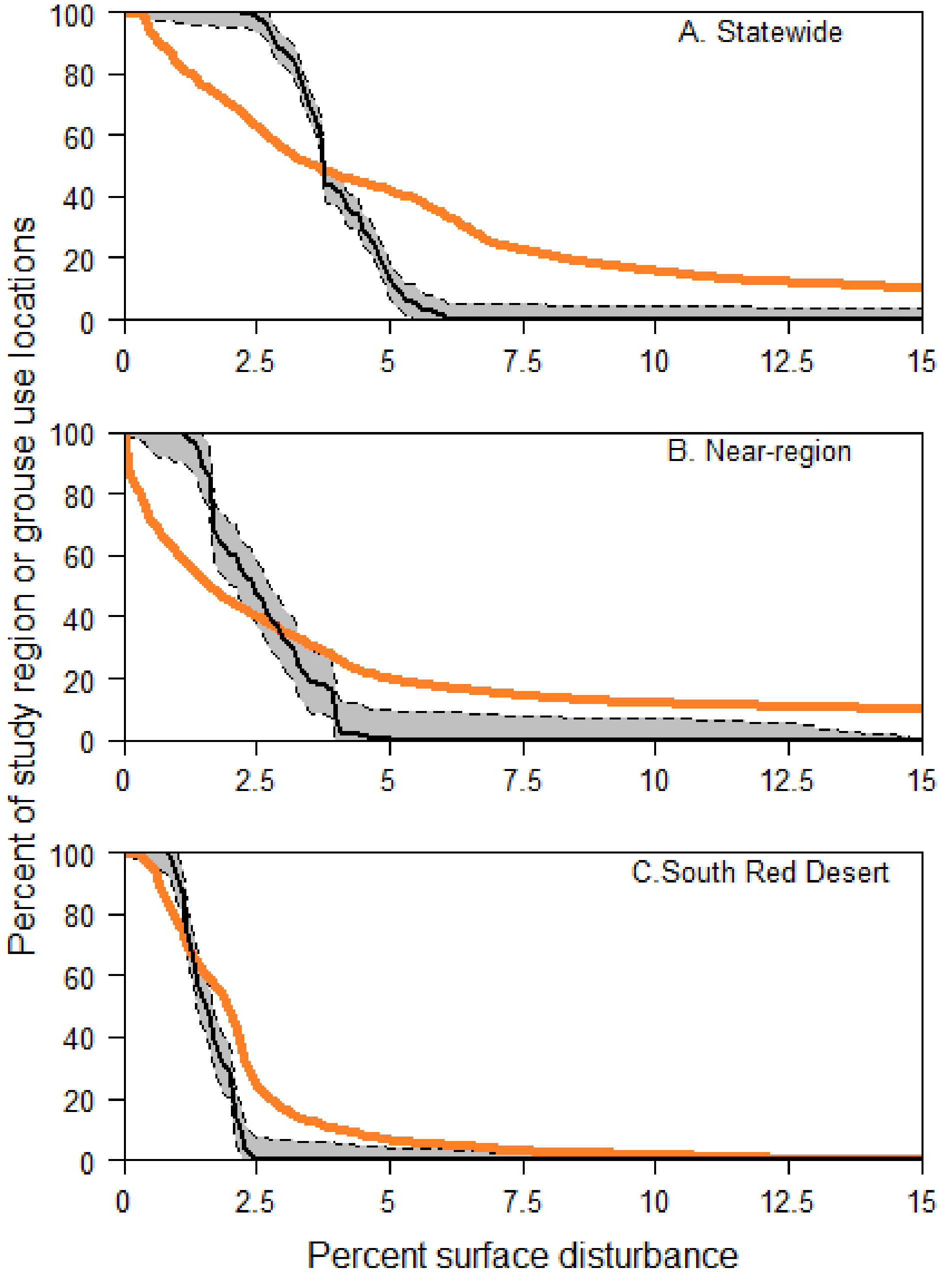

Figure 2.6. Potential disturbance thresholds for greater sage-grouse from 6 study regions, Wyoming, 2008–2018 (Statewide; A), the Northern Red Desert study region, 2009–2014 (B) and the Southern Red Desert study region, 2018–2021 (C). The red line represents the percent of available habitat in a 100% minimum convex polygon around all winter grouse use locations (**home-range scale analysis**; Y-axis) with the indicated amount of disturbance or greater (X-axis) for all surface disturbance within 10.0 km. The black line represents the percent of grouse-use locations across differing levels of disturbance within the same region sizes.

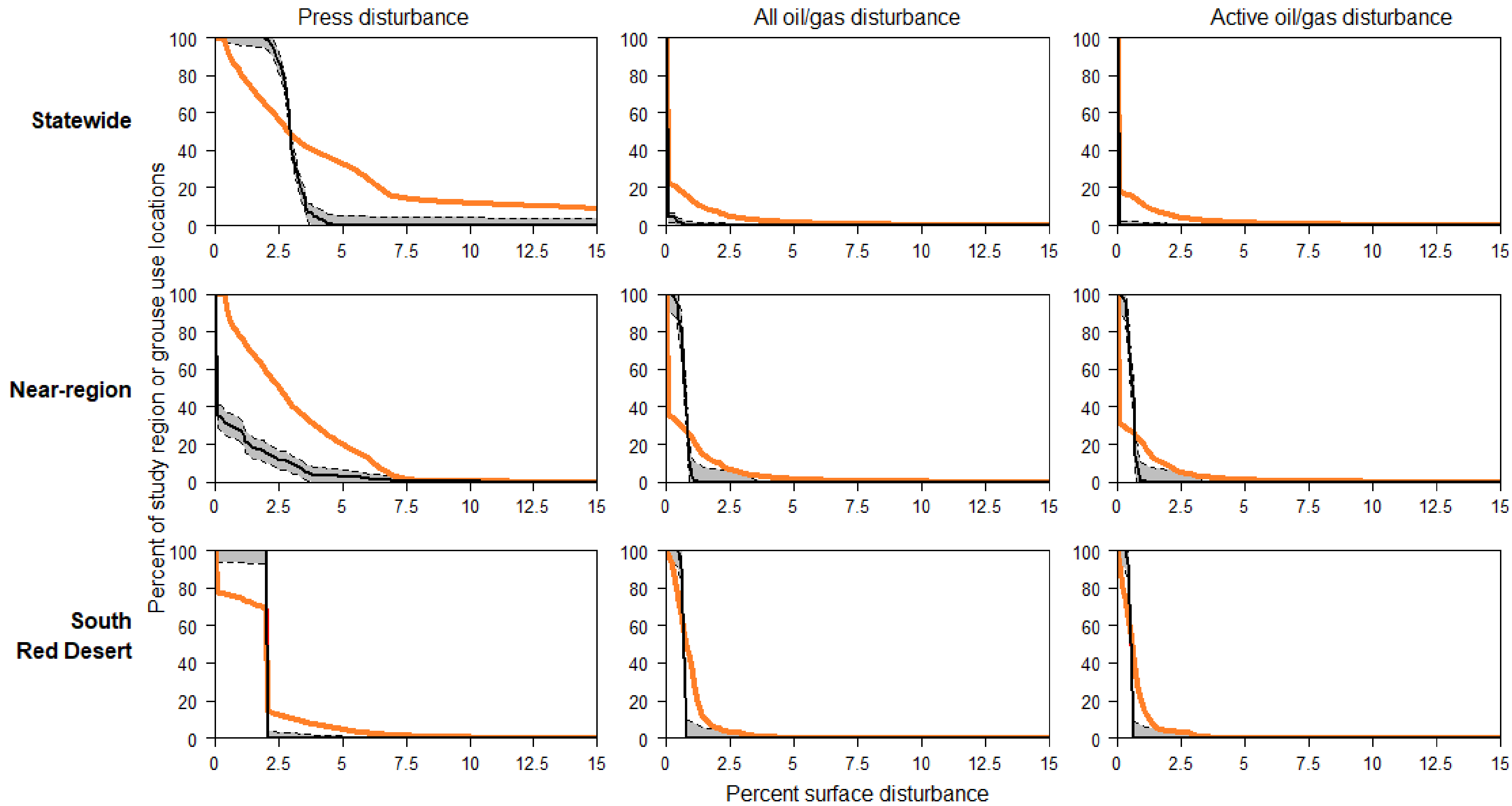

Figure 2.7. Potential disturbance thresholds for greater sage-grouse within 6 study regions, 2008–2018 (Statewide), the Northern Red Desert, 2009–2014 (Near-region) and in the Southern Red Desert, Wyoming study region, 2018–2021. The red line represents the proportion of available habitat in a 100% minimum convex polygon around all year-round grouse use locations (**home range scale analysis**; Y-axis) with the indicated amount of disturbance or greater (X-axis) for press disturbance within 3.2 km (A), all disturbance within 0.8 km (B), all oil and gas disturbance within 0.8 km (C), and active oil and gas disturbance within 0.8 km (D). The black line represents the proportion of the grouse-use locations across differing levels of disturbance within the same region sizes.

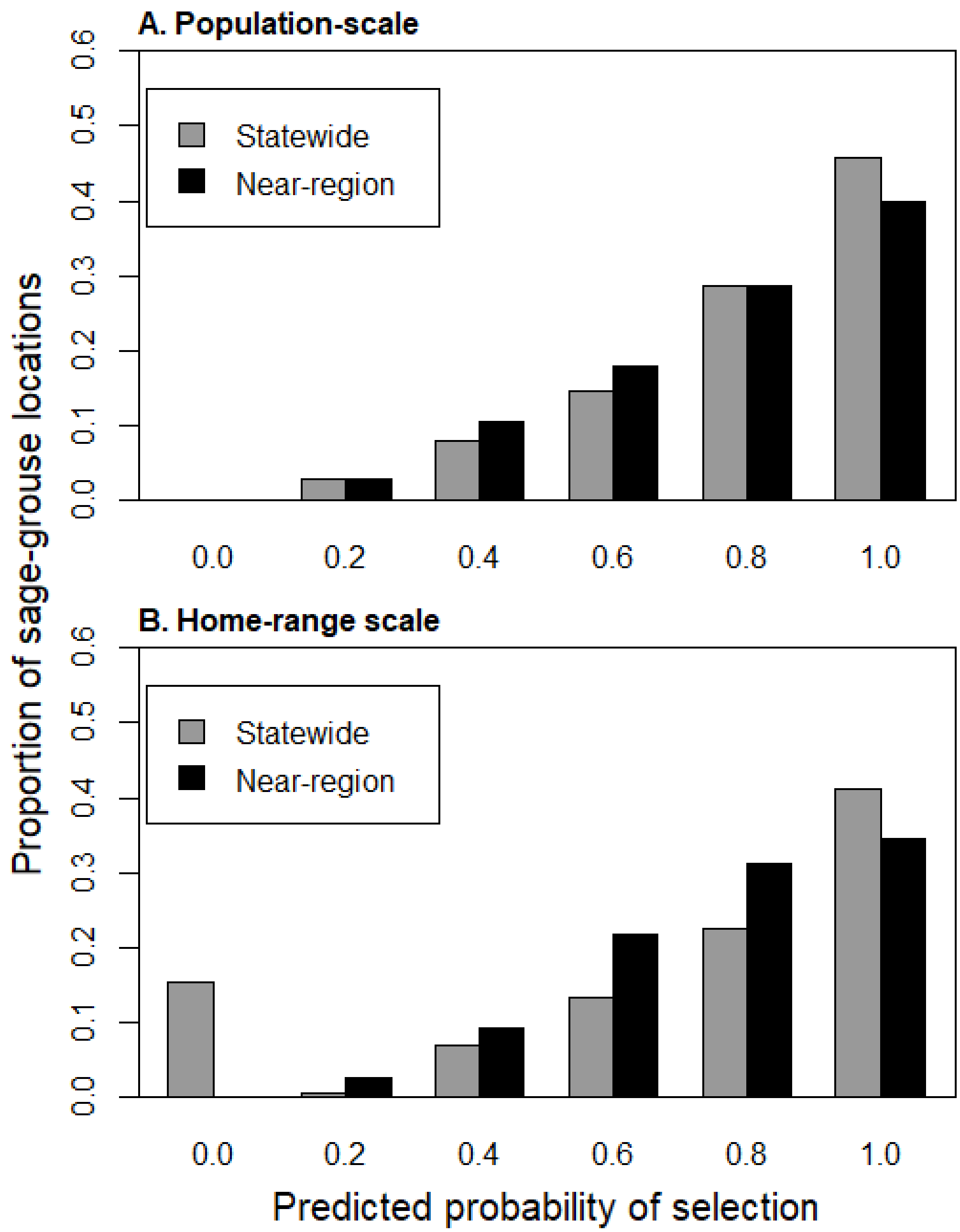

Figure 2.8. Probability of sage-grouse winter habitat occurrence as predicted by a statewide and near-region model at sage-grouse locations in the Southern Red Desert, Wyoming, 2018–2021. Resource Selection Function models at the population-range and home-range scales were binned into 5 quantiles using percentile breaks at 20% intervals. Predicted relative probability of occurrence (X-axis) and mapped across the Southern Red Desert study area. The Y-axis represents the proportion of sage-grouse locations that fell within each predicted probability bin.

CHAPTER 3: INFLUENCE OF WINTER WEATHER ON HABITAT SELECTION AND BEHAVIOR OF GREATER SAGE-GROUSE

In the form for manuscripts submitted to *Ecosphere*

ABSTRACT

For non-hibernating species within temperate climates, survival during severe winter conditions often depends on individuals' behavioral response and availability of refugia. Refugia is defined as habitats to which species retreat or persist in and which provide temporal resistance to populations under changing environmental conditions. Conserving refugia habitat is important for maintaining sustainable landscapes, but identifying such habitat can be logistically difficult and complex. Our research provides an example of how synthesized but biologically relevant weather information can be used to identify important relationships between wildlife behavior and constantly changing snowy landscapes. We assessed the behavioral responses of greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse") to winter weather conditions modeled at the daily scale. Sage-grouse are well-adapted to winter in cold desert shrublands, but their winter behavior is not well understood, and thus far winter habitat selection has only been modeled at the season-long scale. By comparing habitat selection and behavior across fine temporal scales, we found that sage-grouse responded to daily weather conditions by selecting refugia habitat more than altering daily activity levels. Our results suggest that, in addition to landscape features, sage-grouse selected home ranges at the population scale for warmer wind chill temperatures and greater windspeed. Within home ranges, sage-grouse appeared to respond to harsher weather (lower wind chill temperature and high wind speeds) by selecting greater sagebrush cover and leeward sides of ridges. Our research underlines the importance of examining winter habitat at narrower temporal scales than the entire winter season to identify

important refugia features that may only be used periodically. Additional research into quantifying weather refugia for wintering sage-grouse populations may provide greater insight to the future sustainability of winter ranges.

KEY WORDS: *Behavior, greater sage-grouse, habitat selection, resource selection function, SnowModel, weather, winter*

INTRODUCTION

Climatic seasonality is intrinsic to the annual life cycles of most temperate vertebrates. In regions with pronounced seasons, animals time reproduction, migration, hibernation, habitat use, and more with weather conditions (Humphries et al. 2002, Guerra and Reppert 2013, Sunde et al. 2014, Selonen et al. 2016). Within each season, unusually severe weather events (often measured by large swings above or below long-term averages of temperature or precipitation) can impact vital rates and have carry-over effects on fitness in subsequent seasons (Harrison et al. 2011, Williams et al. 2014, Londe et al. 2021). Winter in temperate zones is often a time of greatest energetic demand and mortality for vertebrate species (Martinka 1967, Gray and Prince 1988). Animal populations where survival in winter is limited by availability of resources are particularly vulnerable to severe weather (Payne and Wilson 1999, Altwegg et al. 2006, Giraudoux et al. 2019). Severe winter weather can create ecological bottlenecks for populations that must concentrate on spatially restricted patches of remaining food and cover (Barrett et al. 1982, Morrison et al. 2003, Coulson et al. 2001). The severity of these bottlenecks often depends on the presence of refugia, defined as sites that biota will retreat or persist in and which provide temporal resistance to populations under changing environmental conditions (Samways 1990, Keppel et al. 2012, Shipley et al. 2020). Conservation of landscapes with specific characteristics that animal populations select to survive severe winter conditions is necessary for landscape sustainability amid a changing climate and variable weather conditions (Dzialak et al. 2013, Adam et al. 2015, Zuckerberg and Pauli 2018).

During winter, animals respond to shifting snow and weather characteristics on a daily and even hourly basis. Snow and weather conditions can impact thermoregulation of wildlife (Merritt 1995, Gilbert et al. 2008, Shipley et al 2021), movements and behaviors (Stien et al 2010, Richard et al. 2014, Butler et al. 2019, Pedersen 2021, Sheppard et al 2021), and foraging availability and effort (Sonerud 1986, Dumont et al. 2005, Visscher et al. 2006). Effective evaluation of relationships between animal behavior and winter conditions was historically hampered by a lack of technical expertise and technology to capture the complex and dynamic nature of snowfall and microclimate at a scale relevant to ecology. Measurements of weather conditions were limited to a few local metrics that are logistically easy to measure (e.g., local temperature and snow depth; Leckenby and Adams 1986, Lishawa et al. 2007) or generalized across an area via weather stations. Modern meteorological modeling technology provides a greater abundance of microclimate information at finer spatial and temporal resolutions for ecological applications (Pedersen et al. 2021, Reinking et al. 2022).

We used greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse) as an example of how synthesized but biologically relevant weather information can be used to identify important relationships between winter weather and wildlife behavior (Reinking et al 2022). Because reported sage-grouse winter survival rates typically range from 80% to 100% (Wik 2002, Moynahan et al. 2006, Smith et al. 2014, Cardinal and Messmer 2016), winter behavior and habitat selection has been largely overlooked compared to other seasonal periods. A repeated assumption is that as long as snow depths do not exceed available sagebrush cover, winter weather will have minimal effect on sage-grouse populations (Call and Maser 1985, Connelly 2000, Crawford et al. 2004). Yet, sage-grouse are not immune to the pressures of winter conditions. Sage-grouse can tolerate nighttime temperatures of -10°C with minimal expense of endogenous reserves (Sherfy et al. 1994), but the metabolic costs of thermoregulation for sage-grouse increase at temperatures below -5°C and wind speeds greater than 1.5 m/s (Sherfy and Pekins 1995). The energetic cost of surviving prolonged periods of severe winter weather can result in higher mortality events for sage-grouse, as reported in two studies (Moynahan et al. 2006, Anthony and Willis 2010). Habitat that can minimize energetic expense during harsh winter days would likely buffer fitness for sage-grouse. Such habitat may be used only during the harshest periods and avoided during mild days. Modeling sage-grouse winter resource selection at broad, season-long scales, which is common, may mask the impact of severe weather events, resulting in conclusions that weather has no effect on sage-grouse winter habitat or survival (Zablan 2003). Understanding the relationship between winter weather and habitat selection may give insight into habitat refugia that might buffer sage-grouse survival during severe weather conditions.

We predicted that sage-grouse would respond to winter weather in two ways: either by selecting refugia habitat or by lowering their activity level to conserve thermogenic output. For our first objective we asked: Do sage-grouse change their daily habitat selection based on current weather and snow conditions? To answer this question, we compared two alternative hypotheses: 1) that only shrub availability relative to snow depth determines habitat selection, as suggested by Call and Maser (1985) and others (Hupp and Braun 1989, Connelly et al. 2000, Crawford et al. 2004); and 2) daily weather conditions affect the way sage-grouse select or interact with other habitat features. We predicted that snow levels would affect habitat selection even if weather does not play a role. Therefore, support for hypothesis 1 would indicate that daily weather played no role in winter habitat selection, while support for hypothesis 2 would indicate that sage-grouse altered habitat selection for types of refugia depending on prevailing weather conditions.

For our second objective, we asked whether sage-grouse alter their activity levels in response to daily weather conditions. We reasoned that sage-grouse may change their behavior in response to weather conditions even if weather was not predictive of habitat selection. To answer this question, we compared 2 hypotheses against a baseline model of landscape predictors (topography and vegetation) to explain daily activity levels: 1) snow levels influenced the activity levels depending on other occupied habitat features; and 2) weather conditions influenced activity levels depending on occupied habitat characteristics (topography, vegetation, and snow levels). Support for hypothesis 2 over hypothesis 1 could indicate that sage-grouse altered activity levels in response to weather conditions depending on if the current occupied areas provided shelter. We predicted that sage-grouse activity would decrease during harsh winter days while they sought shelter in areas with greater shrub cover. Our research will provide new insight into the behavioral adaptations and refugia habitat that enable sage-grouse and other vertebrates to withstand adverse winter conditions.

STUDY AREA

Our study area included portions of Sweetwater and Carbon counties, Wyoming, and Moffet County, Colorado. The study area encompassed 9,687 km^2, comprised of BLM-managed (73%), private (24%) and state of Wyoming (3%) land. Sage-grouse winter ranges occurred in areas categorized as cold arid-steppe (Kottek et al. 2006). Elevation within the study area ranged from 1,600–3,300 m (USGS 2016) and annual precipitation ranged from 20.0–63.0 cm (PRISM Climate Group 2022). Dominant shrubs included Wyoming big sagebrush (*A. tridentata* *wyomingensis*), saltbushes (*Atriplex spp*.), greasewood (*Sarcobatus vermiculatus*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*). Shrub assemblies occurred across a gradient of soil and precipitation, dominated by sandy loams but including sand dunes and alkali complexes (Soil Survey Staff 2015).

We gathered location data across two winters: 2018/2019 and 2019/2020. Comparing these winters with the previous 30 years in our study area (1988 to 2022; PRISM 2022), average winter temperatures fell within the 29th and 31st percentiles, respectively. Winter precipitation, compared to the previous 30 years, fell within the 63rd and 91st percentiles, respectively (PRISM 2022).

METHODS

Capture and Monitoring

We captured and radio-marked adult female sage-grouse using spotlight and hoop-net methods (Giesen et al. 1982, Wakkinen et al. 1992) around leks during spring or at roost sites during summer and winter. We fitted female sage-grouse with rump-mounted GPS transmitters (GPS PTT [GeoTrack, King George, Virginia, USA], ~37 g total weight; or Bird Solar [e-obs GmbH, Grunwald, Germany], ~30 g total weight). GeoTrak transmitters uploaded GPS locations to satellites used by the ARGOS system (Woods Hole Group, Largo, Maryland, USA) every 3 days, and were programmed to acquire 4 locations per day from 1 November to 14 March (at 0000, 0900, 1200, and 1500 hours MST). Bird Solar transmitters were programmed to collect one location every 10 minutes and stored locations onboard to be downloaded manually in the field or by fixed-wing aircraft. Incorporated in the E- transmitters was an accelerometer, which measured the force of gravity on the body in relation to the ground. During each location acquired, the accelerometer measured the acceleration (G) along x, y, and z planes across 5 seconds. Our goal was to download data from Bird Solar transmitters every 3 months in fall/winter. We redeployed recovered transmitters after mortality events during the following spring or winter. All sage-grouse capturing and monitoring protocols were approved by University of Wyoming Institutional Animal Care and Use Committee (protocol 20170324AP00266-03) and Wyoming Game and Fish Department Chapter 33-1160 permit.

Landscape and Weather Variables

We explored predictor variables that described topography, vegetation, snow, and weather landscape features for both our resource selection models and behavioral models (Table 1). We calculated a heat load index, an index of solar radiation, to estimate areas that are hotter and drier compared to cooler and wetter (0–1; McCune and Keon 2002; Geomorphometry and Gradient Metrics, Evans et al. 2014). We used a 30-m digital elevation model (U.S. Geological Survey 2011) to calculate Terrain Ruggedness Index (Wilson et al. 2007) and Terrain Position Index (De Reu et al. 2014). We used 30-m resolution sagebrush and shrub fractional component and height datasets from the National Land Cover Database (Xian et al. 2015, Dewitz 2021. We calculated the proportion of juniper (*Juniperus* spp.)-dominated landscapes (hereafter "juniper") from the LANDFIRE Existing Vegetation Type raster dataset (LANDFIRE 2016). Juniper was restricted to Colorado Plateau pinyon (*Pinus edulis*)-juniper woodland and Rocky Mountain foothill limber pine (*P. flexilis*)-juniper woodlands (LANDFIRE 2016).

We defined our winter season to be 1 December–15 March. This was considered the core winter period when all sage-grouse were expected to be on winter range and severe weather events were most likely to occur. We confirmed occupancy of winter ranges by visually inspecting GPS locations for migration movements. We generated weather and snow variables for winters 2018/2019 and 2019/2020 using MicroMet and SnowModel (Liston and Elder 2006a,b, and Appendices in Liston et al. 2020). MicroMet and SnowModel are detailed numerical process models that produce weather and snow variables that evolve realistically across space and through time. MicroMet spatially downscales basic meteorological information including air temperature, precipitation, relative humidity, wind speed, and wind direction (Liston and Elder 2006a). Using this downscaled meteorological forcing, SnowModel simulates the interactions between weather and landscape characteristics to produce realistic snow and environmental information at wildlife-relevant spatiotemporal scales (Liston and Elder 2006b; and Appendices in Liston et al. 2020). Meteorological inputs consisted of North American Land Data Assimilation System, Version 2 (NLDAS-2) forcing data (Cosgrove et al. 2003). Landscape inputs included topography (United States Geological Survey [USGS] 3D Elevation Program Digital Elevation Model; Stoker and Miller 2022) and land cover type (North American Land Change Monitoring System [NALCMS] 30-m, 2015 land cover; USGS 2020). Land cover data also integrated 270 field observations of vegetation height across our study area to ensure snow holding depths congruent with field observations. SnowModel produced spatially explicit distributions of weather and snow variables at the daily temporal resolution and 30-m × 30-m spatial resolution. SnowModel variables included mean air temperature (C°), mean wind-chill temperature (C°), mean wind speed (m/s), snow depth (cm), whether vegetation protrudes above snow (binary, 1 = vegetation protrudes above snow level, 0 = vegetation does not protrude), height of vegetation above snow depth (cm), and blizzard conditions (i.e., blizzarding), defined as the mass of snow blowing in the air at ground level per unit width per unit time (kg/m/s; Liston and Sturm 1998, Liston et al. 2007, Liston and Hiemstra 2011).

Resource Selection Function Model

We modeled sage-grouse winter habitat selection within individual home ranges using paired logistic regression (clogit; Gail et al. 1980, Therneau 2000, Therneau and Grambsch 2015) in the R package “survival.” We subset Bird Solar transmitter locations to 4 per day to match locations collected by GeoTrak transmitters. Then we paired 15 available locations within each bird’s winter home range with each use location by corresponding date. We reasoned that a 15:1 ratio was a sufficiently large sample size to avoid significant numerical integration error (Northrup 2013). After forming our model, we validated this assumption by comparing coefficients from our model with coefficients from models with ratios of 1:1, 4:1, 8:1, and 12:1 to confirm convergences of estimated parameter coefficients (Northrup 2013).

To identify the operative scales for predictors, we extracted all landscape and weather variables to sampled locations using 8 circular regions: 0.1-km radii (0.03 km^2), 0.2-km radii (0.13 km^2), 0.4-km radii (0.50 km^2), 0.8-km radii (2.01 km^2), 1.6-km radii (8.04 km^2), 3.2-km radii (32.17 km^2), 6.4-km radii (128.68 km^2), and 10.0-km radii (314.16 km^2). Our aim was to identify the scale sage-grouse most likely selected landscape features. Each circular region considered had relevance to previous research evaluating sage-grouse winter resource selection (Doherty et al. 2008, Carpenter et al. 2010, Dzialak et al. 2013, Smith et al. 2014, 2016, 2019, 2021, Walker et al. 2016). We extracted weather variables (Table 1) to sampled locations or home ranges by corresponding date and across our 8 circular regions. We centered and Z-transformed all variables to ensure model convergence (Becker et al. 1988) and make main effects and interactions more interpretable (Schielzeth 2010). Then we identified the most likely operative scale within each variable category by selecting the variable that had the lowest AIC score in single-variable models. Prior to developing our models, we performed initial variable screening by removing unsupported predictor variables when single variable models had AIC scores greater than random intercept-only models. We did not allow variables in the same model when $|r| > 0.6$. We removed variables from our pool step-wise by highest Variance Inflation Factor (VIF).

We used information theoretic procedures (Burnham and Anderson 2002) to compare our two alternative hypotheses to a baseline model of landscape characteristics, and we ranked each model by Akaike's Information Criterion (AIC; Akaike 1973). We built our models in three steps, building from the top model from the previous step. First, we modeled sage-grouse selection using only topography and vegetation predictors (Landscape model) by using the top model generated with the dredge function from the "MuMIn" R package (Barton and Barton 2015). For step 2, we added variables representing aspects of snow depth, preserving the variables from the landscape model, to assess our hypothesis that sage-grouse select habitat within home-ranges for current snow characteristics (Landscape + Snow model). For each snow variable, we considered the top 3 interactions with landscape variables that individually improved AIC. We considered a maximum of 3 interactions was reasonable given our sample size. For step 3, we added weather variables (Landscape + Snow + Weather model), dependent on whether each weather variable improved AIC. For each weather variable, we considered a maximum of 3 interactions with landscape variables that each improved AIC individually over the non-interaction model.

After determining the best model for sage-grouse habitat selection within individual winter home ranges (third-order scale, Johnson 1980), we modeled habitat selection with random "available" points generated at the population scale (second order, Johnson 1980). We defined the population scale using the area encompassing winter home ranges for all GPS-marked grouse. This was to determine whether the same variables that influenced sage-grouse use within home-ranges also played a role in home range selection. We allowed operative scales for each parameter to differ from the home range model and only removed parameters if $|r| > 0.6$.

Behavioral Model

To describe daily sage-grouse behavior, we considered four metrics calculated from Bird Solar transmitters from winters 2018/2019 and 2019/2020: average hourly step length (avg.step), home range area (area.d), distance between night roost locations (dist.) and standard deviation of acceleration (SD.acc). To calculate daily average step length, we subset daily locations to each hour between civil twilights. We calculated daily home range areas using 100% minimum convex polygons (MCP) around each bird's daily locations. For the size of each bird's daily range, an MCP was more capable of capturing daily area than other estimates of home range (e.g., Brownian bridge or kernel density) that require a higher minimum area that covers multiple raster cells (minimum sage-grouse daily home range was 2 m^2, smaller than the resolution of most remotely sensed datasets). We measured roost distance as Euclidean distance between first and last location for each day, representing the distance between each day's roost sites. Lastly, we calculated the daily standard deviation of the magnitude of acceleration (estimated across 5 seconds during each location fix) using the formula:

$$1. \qquad SD.acc = \sqrt{(SDX_2 + SDY_2 + SDZ_2)}$$

SDX_2, SDY_2, and SDZ_2 represent the standard deviations of acceleration along the X, Y, and Z planes respectively. We used principal components analysis (principal function in the R package "psych;" Revelle 2010) to incorporate response variables into an index representing daily sage-grouse activity. We used the first component for our daily sage-grouse activity index (DSA), provided the eigenvalue > 1.0.

Because sage-grouse may respond to environmental changes across days (Pratt et al. 2017), we calculated all weather variables (Table 1) with a “linear predictor” that used α as a weighting factor of the current day’s weather value relative to previous days (Gienapp et al. 2005). We considered values for α in increments of 0.1. An $\alpha = 1.0$ represented the current day’s value while $\alpha = 0.1$ acted as a smoothing parameter representing a trend over the last 30 days (Figure 1 in Gienapp et al. 2005). We started calculations from 30 days prior to 1 December, the first day of each winter. For the blizzard variable, we also considered direct blizzard values of one day before and one day after each day, to assess whether sage-grouse changed activity in response to impending precipitation or the previous day’s snowfall. For temperature variables, we used the slope between each day’s value and the previous 2 days to measure the rate of warming or cooling trends. We also considered day length (hours between civil twilights) as a potential predictor of sage-grouse activity.

We extracted weather, snow, and landscape variables to each daily home range, averaged and weighted by the proportion of cells overlapped by the polygon. Because the activity index could not be less than 0 and we predicted variation in activity to be proportional to parameters, as is common with biological data, we considered both a generalized mixed-effect model with gamma distribution (link = log) and a linear distribution with the response log-transformed. We compared residual plots to determine the best-fit distribution. Prior to building our models, we removed predictor variables when single variable models had AIC scores that were greater than random intercept only models. Then we determined the operative temporal scale by selecting the α for each variable with the lowest AIC score in single-variable models. We used a variable subset approach (Arnold 2010) to determine the most parsimonious behavioral model for each alternative hypothesis, by AIC score, and we used bird ID as a random mixed effect (interclass correlation coefficient = 0.18). We removed highly correlated variables ($|r| > 0.6$) stepwise by highest Variance Inflation Factor (VIF). First, we created a Landscape-only model using topography and vegetation covariates. Next, we created a Landscape + Snow model (hypothesis 1) by adding snow variables (snow depth, binary vegetation, height of vegetation above snow level, and blizzard conditions with $\alpha < 0.5$) depending on whether they improved AIC. For each snow variable, we considered the one interaction with landscape variables that best improved AIC. For our Landscape + Snow + Weather model (hypothesis 2) we added weather variables (air temperature, wind chill temperature, wind chill trend, windspeed, and blizzard conditions with $\alpha > 0.5$) representing recent weather trends rather than landscape features. For each weather variable, we considered the one interaction with the landscape variables that most improved AIC.

RESULTS

Habitat Selection Model

For the habitat selection model, we used 16,376 locations from 37 female sage-grouse during winters 2018/2019 and 2019/2020. The top model describing sage-grouse habitat selection within winter home ranges included interactions between landscape, snow, and weather variables (AIC = 83453.0, Akaike's weight [w_i] = 1.0). The second-best model was the Landscape + Weather model (ΔAIC =300.9, w_i = 0.0) and the Landscape-only model was third (ΔAIC = 3076.1, w_i = 0.0). Comparison of model coefficients produced by 1:1, 1:4, 1:8, and 1:12 ratios of use: availability with our top model confirmed that the coefficients are stable at the 1:15 ratio (Figure 3.1). Our final model contained 20 parameters; compared to our sample size, this represented 1.85 birds per parameter, 25.5 location days per parameter, and 818.8 use locations per parameter.

Within the home-range scale, sage-grouse selected cooler aspects (HLI at grouse use locations ranged from 0.67 to 0.74), flatter topography, higher on ridges, greater sagebrush canopy cover and height, and lower proportion of juniper land cover. In the Landscape + Snow model, the binary variable was selected to represent vegetation availability in relation to snow depth; it included interactions between the binary vegetation variable and $Sage_{0.1km}$, $TRI_{0.1km}$, and $TPI_{0.8km}$. 75% of sage-grouse use locations occurred in areas with TRI< 3.0 within 0.1 km, and predicted avoidance for rough terrain was greater when the proportion of protruding vegetation was low (Figure 3.2). Fifty-percent of sage-grouse use locations occurred between -5.6 and 6.4 TPI, but predicted selection for hilltops was greater where proportion of available vegetation was high (Figure 3.2). Seventy-five percent of sage-grouse use locations occurred in <13.3% sagebrush canopy cover within 0.1 km, but sage-grouse showed stronger selection for areas up to 100% sagebrush canopy cover (Figure 3.2). Predicted selection for greatest sagebrush canopy cover was strongest when the proportion of protruding vegetation was near 0 (Figure 3.2).

Blizzard conditions (kg/m/s) within 0.8 km, windspeed (m/s) within 0.1 km, and wind chill (°C) within 0.1 km represented the weather variables in the Landscape + Snow + Weather model. Within the home-range scale, sage-grouse selected areas with lower blizzarding conditions and lower windspeed (Table 3.2). Predicted avoidance of rough terrain was strongest during high blizzarding events and when windspeed was high (Figure 3.3). Predicted avoidance of juniper cover was also greatest during high blizzarding events (Figure 3.3). During high windspeeds, sage-grouse appeared to select areas higher on ridges and cooler aspects (Figure 3.3). Sage-grouse did not appear to select for wind chill directly, but wind chill affected habitat selection for other features. During very cold wind chill days, sage-grouse selected cooler aspects and greater sagebrush canopy cover (Figure 3.3), and during mild temperature days, sage-grouse appeared to select higher ridges (Figure 3.3).

When we applied the same parameters to sage-grouse winter habitat selection at the population scale (second order; Johnson 1980), we found similar trends for most parameters, including interactions, and variation in operative scale in only a few variables (Table 3.2). At the population scale, selection for topography and sagebrush canopy cover were very similar to the home-range scale (Table 3.2). Avoidance of juniper was much stronger at the population scale (Table 3.2). Sage-grouse selected home ranges with lower proportions of available vegetation, warmer wind chill temperatures and greater wind speeds, which differed from selection within home-range scales (Table 3.2).

Behavioral Model

We used 27,117 sage-grouse locations from 29 female sage-grouse, subset to an hourly fix rate during daytime hours, to estimate 3,219 daily home ranges from winters 2018/2019 and 2019/2020. The daily average of step-length ranged from 1.6 m to 1,462.2 m with a mean of 130.6 m. Distance between roost sites ranged from 1.1 m to 7,515.8 m with a mean of 716.7 m. Daily home range area ranged from 1.0 m^2 to 14.2 km^2, with an average of 0.1 km^2. Daily standard deviation of acceleration ranged from 0.01 to 0.74 with a mean of 0.43. There was one extreme outlier day removed from the sample after we determined that bird flew to her breeding area mid-winter and then returned within one day.

In our PCA of sage-grouse activity metrics, principal component 1 (PC1) included all four movement variables and 61.3% of the variation. Principal components 1 and 2 accounted for

82.3% of the total variation (Figure 3.4). We used PC1 as our daily sage-grouse activity index (DSA), weighted by individual factor loadings in the formula:

2. $$DSA = 0.904(avg.step) + 0.855(dist) + 0.808(area.d) + 0.148(SD.acc)$$

We found that $Bnry_{\alpha=1.0}$ was correlated ($|r|$ >0.6) with $Snod_{\alpha = 0.6}$ and $Prot_{\alpha = 1.0}$, and $Snod_{\alpha = 0.6}$ was also correlated with $Prot_{\alpha = 1.0}$ and $Bliz_{\alpha = 0.1}$. Sage, Sageht, Shrub and Shrubht were all correlated with each other. Removing variables step-wise by highest VIF resulted in $Bliz_{\alpha = 0.1}$ and $Bnry_{\alpha=1.0}$ representing the snow variables and Shrubht representing vegetation in the models (Table 3.3). $Bliz_{\alpha = 0.1}$ and $Bnry_{\alpha=1.0}$ were moderately correlated (r = -0.52), but removing either one from the model did not largely affect the coefficient estimate of the other so both were retained. The only weather variable that improved the model over the intercept-only model was the rate of wind chill change over 3-days (Chil.trend3). The Landscape + Snow + Weather (hypothesis 2) was the best-fit model for our data (AIC = 8389.5, w_i = 0.972). The second-best model was the Landscape + Snow model (ΔAIC = 7.1, w_i = 0.027), and third was the Landscape-only model (ΔAIC = 234.9, w_i = 0.001). The final model included interactions between Bliz $_{\alpha = 0.1}$ and TPI, $Bnry_{\alpha = 0.1}$ and Juniper, and Chil.trend3 and Shrubht. Our final behavioral model had 10 parameters and represented 2.9 individual birds per parameter and 321.9 daily home ranges per parameter.

Daily sage-grouse activity levels increased in areas with greater blizzard conditions over the previous month (Bliz $_{\alpha = 0.1}$), greater proportion of juniper land cover (Juniper), more rugged terrain (TRI) and higher terrain positions (TPI; Table 3.3). Daily activity decreased in areas with greater shrub height (Shrub), greater proportion of vegetation above snow level ($Bnry_{\alpha = 1.0}$), and warming wind chill trends (Chil.trend3). Predicted sage-grouse daily activity increased with higher TPI if month-long blizzard conditions were also high (Figure 3.5). Predicted daily activity increased with shrub height if the proportion of available vegetation was near 0 or if the wind chill trend was warming (Figure 3.5). Predicted daily activity decreased in taller shrubs if the proportion of available vegetation was high or if the wind chill trend was cooling (Figure 3.5).

DISCUSSION

We employed synthesized daily weather information, vegetation characteristics, and topographic characteristics to evaluate whether greater sage-grouse responded to winter weather by altering habitat selection or activity levels. We conducted our study during winters that included unusually high snow depth (63rd percentile in 2018/2019 and 91st percentile in 2019/2020 compared to the 30-year average), which provided an opportunity to assess the commonly held assumption that weather has no effect on wintering sage-grouse as long as snow depth does not exceed vegetation height (Call and Maser 1985, Connelly et al. 2000, Crawford et al.2004). We found that the proportion of available vegetation above snow level was a significant predictor of winter habitat selection, as previously reported (Call and Maser 1985, Connelly 2000, Crawford 2004). This also agrees with other reports that sage-grouse select taller sagebrush species during winters with greater snow depth (Hanf et al. 1994). We also found strong evidence to support our prediction that sage-grouse would select daily habitat based on both snow and weather conditions. Daily blizzarding conditions, proportion of vegetation above snow level, wind chill temperature, and windspeed also affected how sage-grouse selected habitat within home ranges and home range selection at the population scale (Table 3.2). Comparison between the home range and population range scales suggest that sage-grouse were selecting home ranges that were generally warmer and flat (lower TRI) but with hillsides (greater TPI) where greater wind speeds could expose the sagebrush (Table 3.2).

Our purpose in modeling daily activity was to provide an alternative method of measuring behavior as it may respond to daily weather conditions. Therefore, we refrained from prescribing activity levels as positive or negative effects of daily weather as we lacked information about stress hormone levels or foraging energetics. Higher daily activity levels could be a result of sage-grouse responding in advance of changing weather conditions, to disturbance from a predator, or in proximity to human activity. Alternatively, low daily activity levels could be the result of a favorable foraging patch, such as represented by greater proportion of vegetation above snow (Table 3.3); or it could represent a harsh blizzard day when sage-grouse were sheltering in a snow burrow (behavior documented during winter 2019/2020; Back et al. 1987). We found some evidence to support our prediction that sage-grouse would have lower daily activity levels (DSA) as a result of seeking shelter from weather conditions: activity levels declined in greater shrub heights during 3-day cooling trends (Figure 3.5). However, we found that daily activity levels were more responsive to general snow conditions relative to other landscape features rather than to daily weather. Our results indicate that sage-grouse respond to winter weather conditions by seeking refugia and less through changing daily activity levels.

Our results provide insight to how sage-grouse selected frequently-reported winter habitat characteristics in response to adverse weather conditions. Juniper land cover is typically avoided by sage-grouse (Doherty et al. 2008, Coates et al. 2016, 2020), and our results show that sage-grouse avoided juniper land cover much stronger where blizzarding conditions were also high (Figure 3.2). Sage-grouse typically select areas for sagebrush cover (Beck 1977, Carpenter et al. 2010, Smith et al. 2021). During the coldest days in the Southern Red Desert or when snow depths made most vegetation inaccessible, sage-grouse selected areas with up to 100% sagebrush canopy cover (Figures 3.2 and 3.3). Sage-grouse typically avoid rough topography (Carpenter et al 2010, Coates et al. 2020, Smith et al. 2016, 2021, Walker et al. 2016), but in the Southern Red Desert this avoidance was greatest when wind speed or blizzarding conditions were high (Figure 3.3) or the proportion of vegetation above snow was low (Figure 3.2). Despite the general selection for flatter areas, sage-grouse appeared to utilize ridges for shelter from harsh weather. The wind blew from the south/southeast during 84% of days during the study period. During periods of high wind speed and cold wind chill, sage-grouse moved away from the prevailing wind towards the cooler northernly aspects and higher ridgelines (Figure 3.3).

Our study underscores the importance of examining winter habitat at narrower temporal scales than the entire winter season. In the Southern Red Desert, 75% of used locations within sage-grouse winter home ranges had <15% sagebrush canopy cover (Figure 3.2). If we had only considered selection for sagebrush cover at a season-long scale, we most likely would have overlooked the periods of extreme cold and high snow levels when sage-grouse selected greater sagebrush canopy of up to 100% (Figure 3.3). Smaller temporal scales are necessary for identifying refugia habitat that may be expected to buffer winter survival disproportionate to spatial extent or frequency of use (Dzialak et al. 2013, Adam et al. 2015).

The ability of sage-grouse populations to withstand severe weather may vary regionally depending on the proportion of available refugia habitat. If sage-grouse are unable to select refugia from severe weather, it may explain the high mortality reported in some winters (Moynahan et al. 2006, Anthony and Willis 2010). Alternatively, the presence of adequate refugia may explain why weather was found to not have a significant impact on winter survival in other regions (Zablan et al. 2003, Dinkins et al. 2017). Our results lend support to the idea that landscape sustainability for species that rely on high annual survival may depend on habitat that populations select when weather conditions are most limiting (Maron et al. 2015). Climate change is predicted to reduce the range of sagebrush in the West through a combination of reduced snow melt and shifting precipitation patterns leading to drier, hotter summers and increased fire frequency (Ziska et al. 2005, Homer et al. 2015, Palmquist et al. 2016). If sagebrush cover is reduced, sage-grouse could lose important habitat during winter as well as breeding seasons (Wolf and Broughton 2016). As sage-grouse habitat becomes increasingly fragmented and lost by climate change and human development (Walker et al. 2020), additional research into quantifying weather refugia for wintering sage-grouse populations may provide important information and support for the cultivation and preservation of sagebrush for sage-grouse winter habitat (Beck et al. 2009, Poessel et al. 2022).

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TABLES AND FIGURES

Table 3.1. Variables used in models evaluating greater sage-grouse winter habitat selection and daily activity, with literature sources for variables that have been predictive of sage-grouse winter habitat selection or survival.

Variable name	Description	Predicted selection response	Literature
Topographic			
Heat load index (HLI)	HLI approximates an index of coolest to warmest aspects (0-1; McCune and Keon 2002)	Positive or negative	Hupp and Braun 1989, Dzialak et al. 2013, Smith et al. 2021
Terrain Position Index (TPI)	Difference between location and mean elevation of surrounding cells (De Reu et al. 2013)	Positive	Hupp and Braun 1989, Coates et al 2016,
Terrain Roughness Index (TRI)	Terrain relief (Wilson et al. 2007)	Negative	Doherty et al. 2008, Coates et al. 2016, Hagen et al. 2011
Vegetation			
Juniper land cover (Juniper)	Proportion of pinyon-juniper land cover (LANDFIRE 2016).	Negative	Coates et al. 2020, Smith et al. 2021
Sagebrush canopy cover (Sage)	Percent canopy cover of big sagebrush	Positive	Doherty et al. 2008, Hansen et al. 2016, Smith et al. 2021
Shrub canopy cover (Shrub)	Percent canopy cover of all shrub species	Positive	Hagen et al. 2011
Sagebrush height (Sageht)	Mean height (cm) of sagebrush	Positive	Dzialak et al. 2013, Smith et al. 2021
Shrub height (Shrubht)	Mean height (cm) of all shrub species	Positive or negative	Dzialak et al. 2013, Smith et al. 2016, Coates et al. 2020
Protruding vegetation height (Prot)	Height (cm) of vegetation protruding above snow depth	Positive	Smith et al. 2021

Vegetation above snowdepth (Bnry)	A binary variable representing whether the vegetation protrudes above the snow	Positive	Hupp and Braun 1989
Weather			
Blizzard (Bliz)	Daily mean of mass of snow blowing in the air and at ground level (kg/m/s) developed by Liston, G. and A. Reinking (2021, unpublished manuscript)		–
Air temperature (Tair)	Mean daily air temperature (degrees Celsius).	Positive	Moynahan et al. 2006, Anthony and Willis 2010, Dinkins et al. 2017
Wind-chill temperature (Chil)	Mean daily wind-chill temperature (°C) meant to convey how cold it feels, based on air temperature (Tair) and windspeed (Wspd)	Positive	Sherfy and Pekins 1995, Moynahan et al. 2006, Anthony and Willis 2010
3-day trend in wind-chill (Chil.trend)	Slope of the line for wind-chill values between 3 previous consecutive days		–
Windspeed (Wspd)	Daily mean wind speed (m/s)	Negative	Sherfy and Pekins 1995
Snow depth (Snod)	Daily depth of snow (cm)	Positive or negative	Moynahan et al. 2006, Anthony and Willis 2010

[a]Parameter included only in sage-grouse activity model

Table 3.2. Parameter estimates for predictor variables from conditional logistic regression models that describe daily winter resource selection by greater sage-grouse within home ranges (third-order selection) and within population range (second-order selection) in the Southern Red Desert, Wyoming, winters 2018/2019 and 2019/2020.

Parameter[a]	Selection order	Operative scale	Estimate	P-value
Topography				
HLI	Home range	1.6 km	-0.25	<0.001
	Population	1.6 km	-0.48	<0.001
TPI	Home range	0.8 km	0.17	<0.001
	Population	0.8 km	0.26	<0.001
TRI	Home range	0.1 km	-0.37	<0.001
	Population	0.1 km	-0.60	<0.001
Vegetation				
Jun	Home range	0.4 km	-0.72	<0.001
	Population	0.8 km	-1.85	<0.001
Sage	Home range	0.1 km	0.16	<0.001
	Population	0.1 km	0.23	<0.001
Snow				
Bnry	Home range	0.1 km	0.65	<0.001
	Population	10.0 km	-0.43	<0.001
Weather				
Bliz	Home range	0.8 km	-0.72	<0.001
	Population	0.1 km	-0.15	<0.001
Chil	Home range	0.1 km	-0.02	0.917
	Population	10.0 km	0.54	<0.001
Wspd	Home range	0.1 km	-0.25	0.002
	Population	0.1 km	0.45	<0.001
Interactions				
Bnry x TPI	Home range		0.11	<0.001
	Population		0.09	<0.001
Bnry x TRI	Home range		-0.26	<0.001
	Population		-0.46	<0.001
Bnry x Sage	Home range		-0.06	<0.001
	Population		-0.45	<0.001
Bliz x Jun	Home range		-0.64	<0.001
	Population		-0.70	<0.001
Bliz x TRI	Home range		-0.10	<0.001
	Population		-0.10	<0.001
Chil x HLI	Home range		0.05	<0.001
	Population		0.05	<0.001
Chil x TPI	Home range		0.03	<0.001
	Population		0.03	<0.001
Chil x Sage	Home range		-0.07	<0.001
	Population		-0.07	<0.001
Wspd xHLI	Home range		-0.15	<0.001
	Population		-0.08	<0.001
Wspd x TPI	Home range		-0.04	<0.001
	Population		0.07	<0.001
Wspd x TRI	Home range		0.08	0.005
	Population		-0.08	<0.001

[a]Parameter estimates obtained from model with centered and scaled variables. Landscape parameters were measured within operative scales (radii around each location) and included heat load index (HLI), terrain roughness index (TRI), terrain position index (TPI) sagebrush (A. tridentata) canopy cover (%; Sage), and proportion of juniper land cover class (Juniper). The proportion of area where vegetation protrudes above snow depth (0-1; Bnry) represented the snow parameters. Weather parameters included blizzarding conditions (snow kg/m/s; Bliz), wind chill temperature (°C; Chil), and windspeed (m/s; Wspd). For each snow and weather variable, a maximum of three interactions were considered that individually improved AIC over the non-interaction model.

Table 3.3. Parameter estimates with 95% confidence intervals for predictor variables describing greater sage-grouse daily activity index (ln[DSA]) in the Southern Red Desert, Wyoming, winters 2018/2019 and 2019/2020.

		95% CI		
Parameters[a]	**Estimate**	**Lower**	**Upper**	**P-value**
Topography				
TRI	0.15	0.11	0.18	<0.001
TPI	0.20	0.16	0.24	<0.001
Vegetation				
Shrubht	-0.10	-0.14	-0.07	<0.001
Juniper	0.06	0.03	0.09	<0.001
Snow				
$Bnry_{\alpha=1.0}$	-0.20	-0.24	-0.16	<0.001
$Bliz_{\alpha=0.1}$	0.04	0.001	0.09	<0.001
Weather				
Chil.trend3	-0.03	-0.06	0.002	0.07
Interactions				
$Bnry_{\alpha=1.0}$ x Shrubht	-0.18	-0.22	-0.15	<0.001
$Bliz_{\alpha=0.1}$ x TPI	0.04	0.004	0.08	0.029
Chil.trend3 x Shrubht	0.05	0.02	0.08	0.003

[a]Parameter estimates include terrain roughness index (TRI), terrain position index (TPI), percent shrub canopy cover (Shrub), and proportion of pinyon-juniper land cover (Juniper), and month-long (α = 0.1) blizzarding (snow kg/m/s) trends within daily home ranges. For each snow and weather variable, we considered the top interaction that improved the AIC score over the non-interaction model.

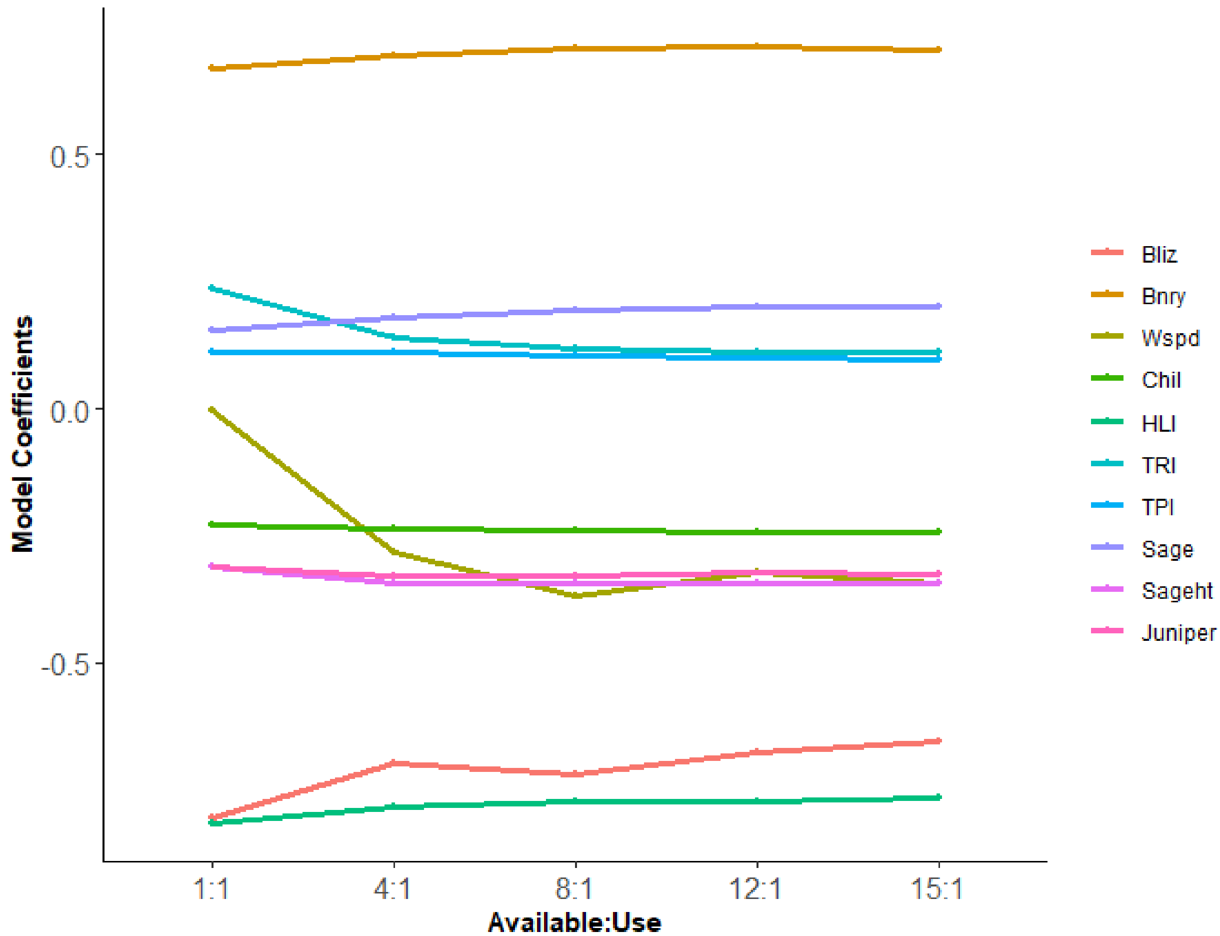

Figure 3.1. Comparison of model coefficients from the home range (third order) conditional logistic model to confirm coefficient convergence in greater sage-grouse resource selection modeling, Southern Red Desert, Wyoming, winters 2018/2019 and 2019/2020.

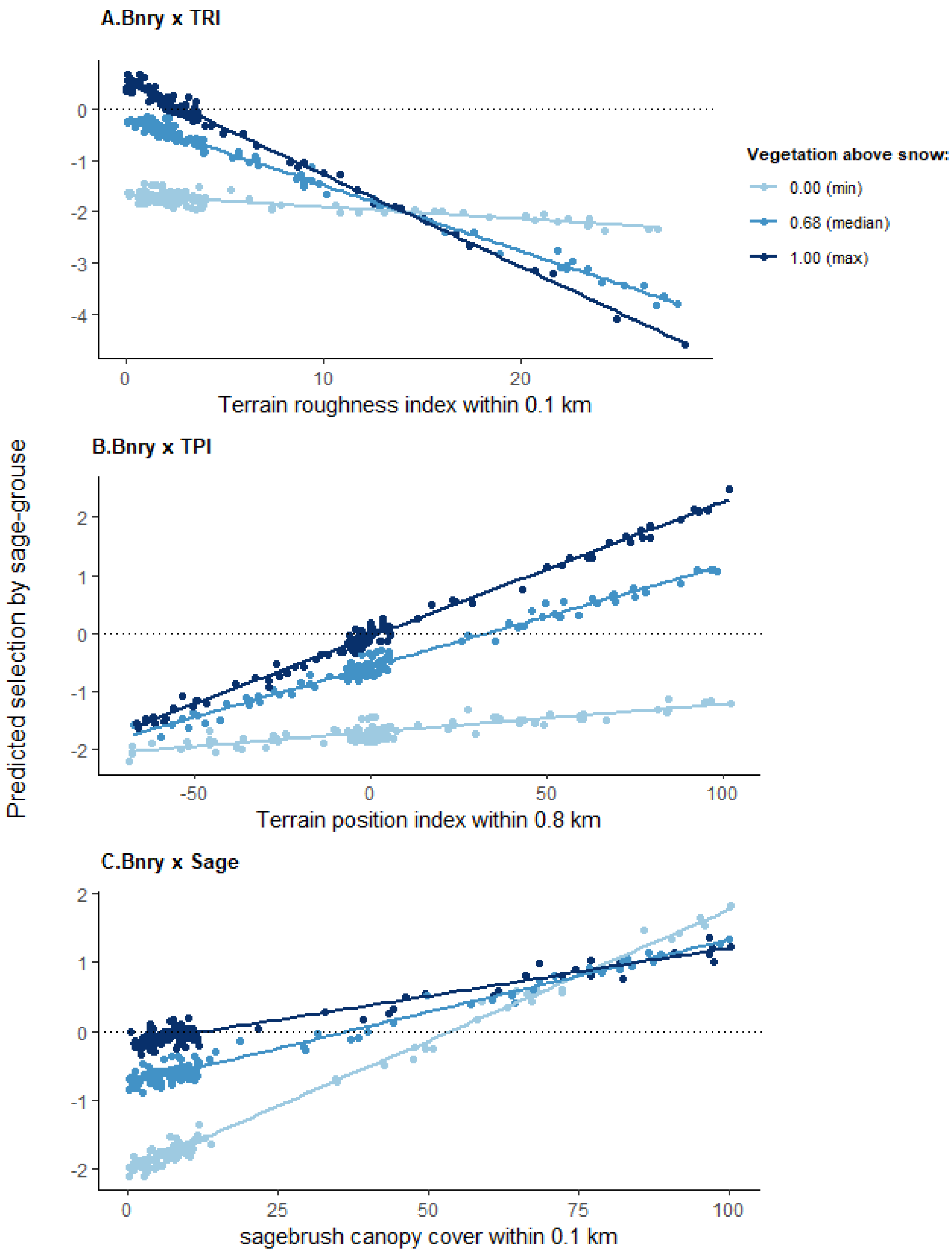

Figure 3.2. Predicted sage-grouse winter resource selection response to the interaction between the proportion of area with vegetation protruding above snow (0/1; Bnry) within 0.1 km and other vegetation and other landscape characteristics from the 2018/2019 and 2019/2020 winters in the Red Desert of southcentral Wyoming. Landscape characteristics included terrain

roughness index (TRI) within 0.1 km, terrain position index (TPI) within 0.8 km, and percent sagebrush canopy cover (Sage) within 0.1 km. Predicted selection response was calculated on a new dataset using 20 groups of 1:15 use versus available locations. Bnry variables in the new dataset set to minimum, median, and max values. Terrain and vegetation values in the new data set were randomly sampled equally from the 1st, 2nd, 3rd, and 4th quantiles of observations from the original dataset.

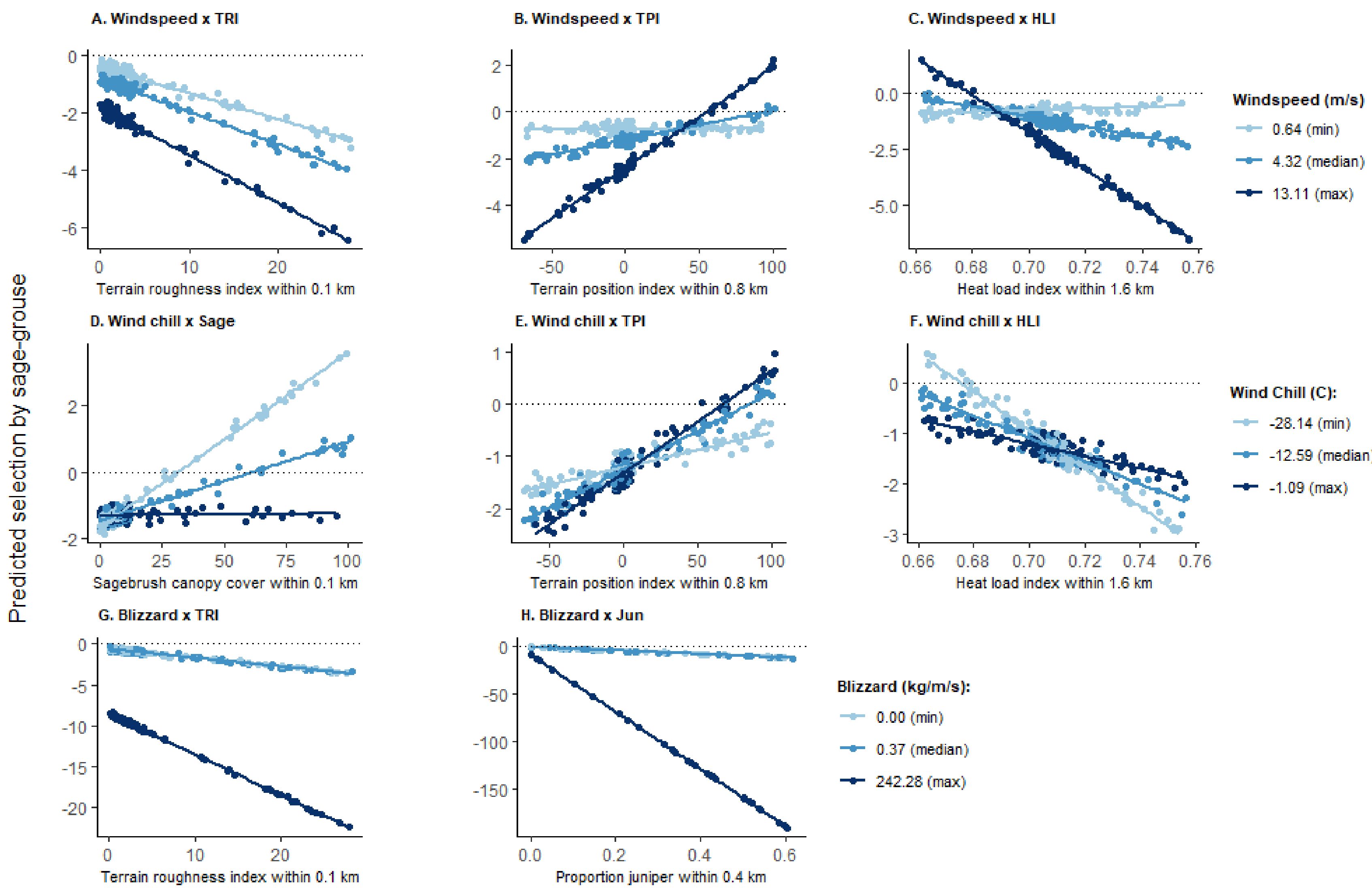

Figure 3.3 Predicted sage-grouse winter resource selection response to the interaction between weather and landscape variables on a daily temporal during the 2018/2019 and 2019/2020 winters in Red Desert of southcentral Wyoming. Predicted selection response was calculated on a new dataset using 20 groups of 1:15 use versus available locations. The weather variables of wind speed (m/s; Wspd)

within 0.1 km, wind chill (°C; Chil) within 0.1 km, and blizzard conditions (kg/m/s snow; Bliz) were set to their respective minimum, median, and maximum values from the original observation dataset. Landscape parameter values in the new data set were randomly sampled equally from the 1st, 2nd, 3rd, and 4th quantiles of observations from the original dataset. Landscape characteristics included terrain roughness index (TRI) within 0.1 km, terrain position index (TPI) within 0.8 km, and percent sagebrush canopy cover (Sage) within 0.1 km. All variables not included in each interaction were set to their respective mean values.

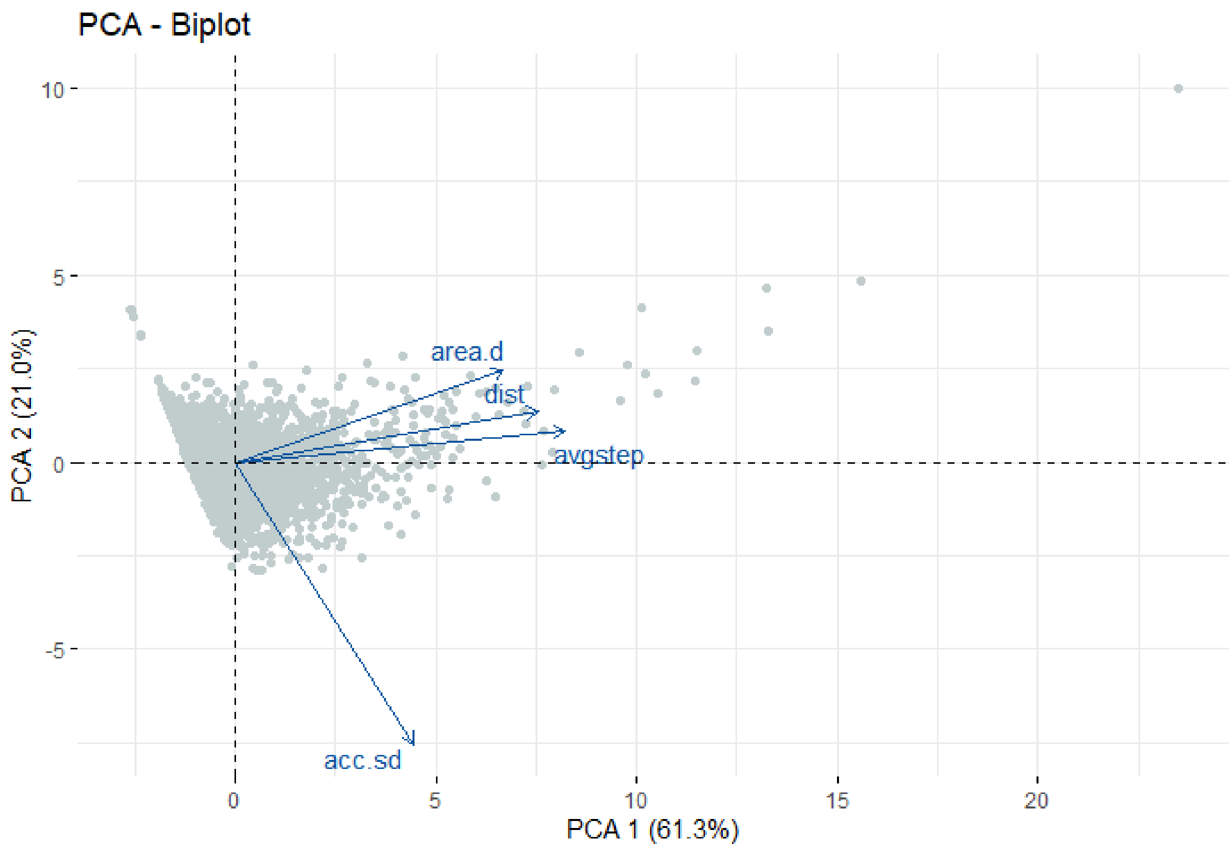

Figure 3.4. Biplot of principal components analysis of sage-grouse daily winter movement metrics in the Southern Red Desert, Wyoming, winters 2018/2019 and 2019/2020.

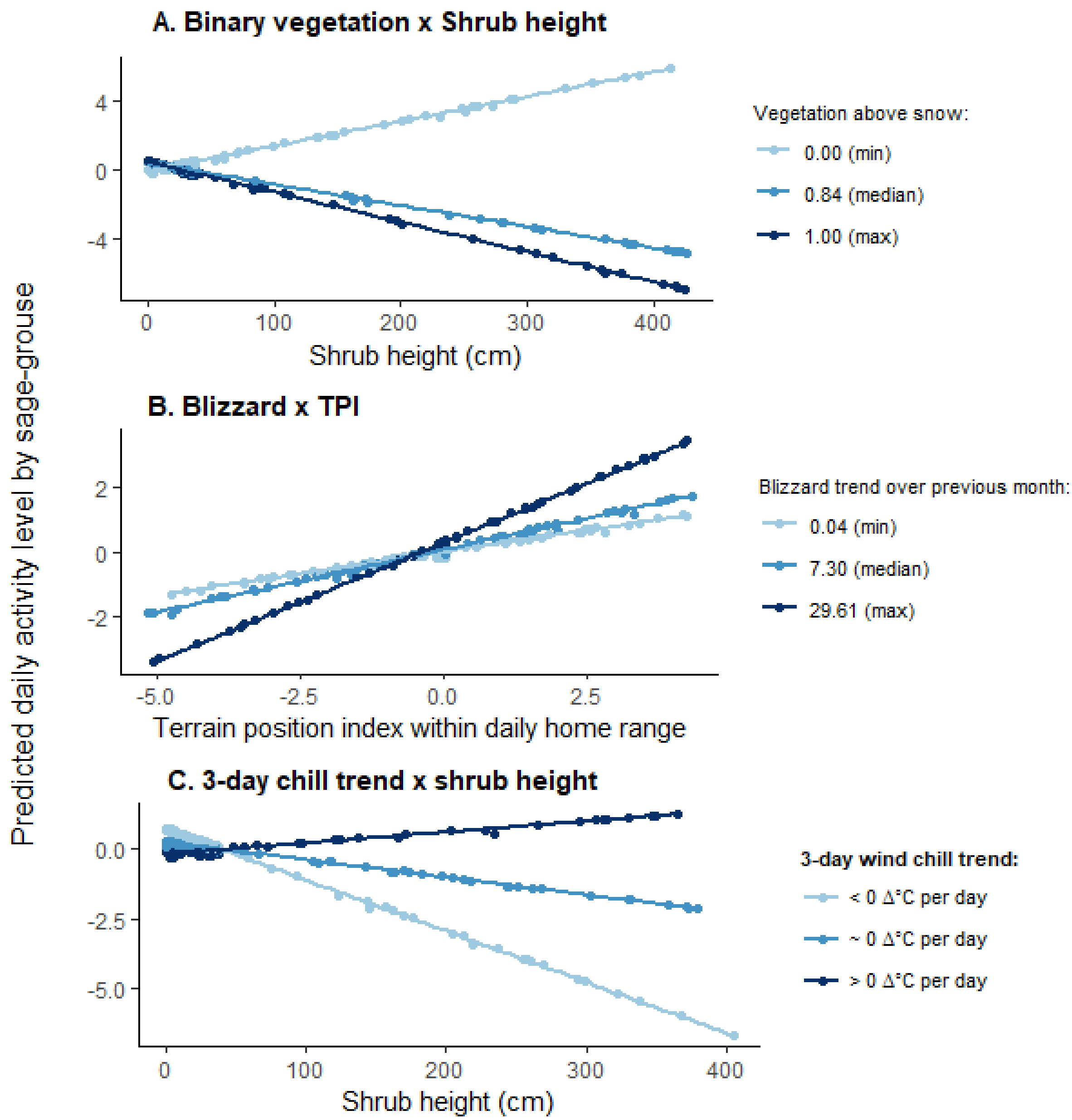

Figure 3.5. Interaction trends in predicted daily sage-grouse activity response to snow variables and landscape characteristics in the Southern Red Desert, Wyoming, winters 2018/2019 and 2019/2020. Snow variables included month-long trends in blizzard conditions (kg/m/s; Blizzard) and proportion daily home range with vegetation protruding above snow depth (0-1; Binary vegetation). The weather variable was the rate of change in wind chill temperature over 3-day periods (Chil.trend3). Landscape variables included shrub height (cm) and terrain position index (TPI) within each daily home range. Predicted selection response was calculated on a new dataset (n = 320) with all non-interacting variables set to mean values. For each interaction, we set the snow and weather variables to minimum, median, and maximum values. Terrain and vegetation values in the new data set were randomly sampled equally from the 1st, 2nd, 3rd, and 4th quantiles of observations from the original dataset.

APPENDIX A: WINTER MICROHABITAT SELECTION BY GREATER SAGE-GROUSE WITHIN HOME AND POPULATION RANGES

In the form for manuscripts submitted as Research Notes to *Rangeland Ecology and Management*

ABSTRACT

Limited resource availability constrains habitat selection during winter for wildlife that inhabit temperate landscapes. Most studies of habitat selection by greater sage-grouse (*Centrocercus urophasianus* ‘sage-grouse’) have focused on breeding and summer habitat. Fewer studies have evaluated winter resource selection by sage-grouse, especially at the microhabitat scale, than have focused on breeding and summer habitat. We focused on the microhabitat scale during winter when available habitat is constrained by snow conditions. We designed our study to characterize winter microhabitat selection at second (population) and third order (within home range) scales. We predicted habitat characteristics at grouse use locations would be more similar to paired random locations within the home range than to random locations within the population range. We also predicted that, because sage-grouse select specific habitat characteristics, there would be fewer differences when comparing random available locations between the home and population range than comparisons of used and available habitat. In summer 2020, we measured shrub characteristics and herbivore dung counts at 90 sage-grouse locations from the previous 2019/2020 winter in northwest Colorado and southcentral Wyoming, USA and compared them to 90 paired, available locations within grouse home ranges and 90 randomly available and unpaired locations within the population range. We found no support for our first prediction, with equal differences (6/10) in shrub characteristics between grouse use versus home range random locations and grouse use versus population random locations (based on paired t-tests and student's t-tests, adjusted by the Bonferroni correction, respectively). We found strong support for our second prediction, with 0/10 differences in shrub characteristics between random locations in the home range compared to population range. Wintering sage-grouse selected areas of higher big sagebrush (*Artemisia* spp. Nutt.) and overall canopy cover, big sagebrush height, and visual obstruction compared to random locations within home and population ranges. Sage-grouse dung piles were 7.0- and 9.9-times higher at used locations than random locations within home or population ranges, respectively. Conservation of sage-grouse wintering microhabitat in the Red Desert should focus on areas of greater concealment cover, particularly dominated by big sagebrush, which corresponds with habitat requirements during nesting and brood-rearing.

Key Words: *Centrocercus urophasianus*; home-range-scale habitat selection; population-scale habitat selection; shrubs; winter habitat

INTRODUCTION

Limited resource availability makes habitat selection during winter challenging for temperate wildlife species. Most studies of habitat selection by greater sage-grouse (*Centrocercus urophasianus*) have focused on breeding and summer habitat (Connelly et al. 2011). There are fewer studies designed to better understand winter resource selection by sage-grouse, especially at the microhabitat scale (but see Hagen et al. 2011). We focused on the microhabitat scale during winter when grouse habitat selection is likely constrained to above-snow vegetation. We designed our study to characterize winter microhabitat selection at the second order (population) and third order (within home range) scales (Johnson 1980). We established two predictions to guide our analyses. First, we predicted habitat characteristics at used locations would be more similar to paired random locations within home ranges than to random locations within the population range. Second, because sage-grouse select specific habitat characteristics, we predicted there would be fewer differences when comparing random available locations between the home and population range than comparisons of used and available habitat. Better understanding these relationships will aid in understanding winter habitat needs by sage-grouse, thus improving conservation of this imperiled rangeland species.

METHODS

Study Area

Our study area was located on the border of Wyoming (67%) and Colorado (33%) within Sweetwater and Carbon counties, Wyoming, and Moffat County, Colorado. The study area encompassed 4,660 km^2, comprised mostly of BLM-managed land (85%), private land (10%), and state land (5%). Our study area was categorized as cold arid-steppe (Kottek et al. 2006) with elevation ranging from 1,800–2,500 m (USGS 2016) and the 33-year (1988–2021) mean winter precipitation ranged from 11.7–39.8 cm (PRISM Climate Group 2022). During core months (1 Dec–28 Feb) of winter 2019/2020, mean accumulated precipitation was in the 91st percentile compared to the 30-year average and in the 31st percentile for mean winter temperature (PRISM 2022). Shrub assemblies in our study area occurred across a gradient of soil and precipitation, dominated by sandy loams but including sand dunes and alkali complexes (USDA Soils Conservation Service 2020). We identified 21 shrubs to species or genera. Dominant shrubs included big sagebrush (*A. tridentata* Nutt.), greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.), shadscale saltbush (*Atriplex confertifolia* [Torr. & Frém.] S. Watson), and yellow rabbitbrush

(*Chrysothamnus viscidiflorus* [Hook.] Nutt.). We identified 7 sub-shrub species with birdfoot sagebrush (*A. pedatifida* Nutt.), Gardner's saltbush (*Atriplex gardneri* [Moq.] D. Dietr.), and winterfat (*Krascheninnikovia lanata* [Pursh] A. Meeuse & Smit) being most common.

Capture and Monitoring

We captured and radio-marked adult female sage-grouse using spotlight and hoop-net methods (Giesen et al. 1982; Wakkinen et al. 1992) around leks during spring or at roost sites during summer or winter. All sage-grouse capturing and monitoring protocols were approved by the University of Wyoming Institutional Animal Care and Use Committee (protocol 20170324AP00266-03) and Wyoming Game and Fish Department Chapter 33-1160 permit. We fitted adult female sage-grouse with rump-mounted GPS transmitters (22-g GPS PTT [GeoTrack, King George, Virginia, USA] and 15-g Bird Solar [e-obs GmbH, Grunwald, Germany], total weight ~32g). GeoTrak transmitters uploaded GPS locations to satellites used by the ARGOS system (CLS America, Largo, Maryland, USA) every 3 days, and were programmed to acquire 4 locations per day from 1 November to 14 March at 0000-, 0900-, 1200-, and 1500-hours MST. We programmed Bird Solar transmitters to collect a location every 10 minutes and stored locations onboard to be downloaded manually in the field or by fixed-wing aircraft.

Microhabitat Measurements

To obtain microhabitat conditions, we sampled vegetation at sage-grouse winter use locations from winter 2019/2020. We defined winter as 1 December–March 15, when we confirmed through visual inspection of GPS locations that all marked grouse were occupying winter ranges. We used snow depth data from the Cow Creek Wyoming weather station (Bureau of Land Management NWS ID 482011) to broadly categorize days between 1 December 2019 and 14 March 2020 as low, moderate, and high snow depth (0–25, 26–75, and 76–99 percentile, respectively). For each marked grouse, we randomly selected at least one day during each snow depth period. This approach provided greater temporal independence between locations. For each use point we paired an available point randomly generated within that bird's winter home range, which we estimated using a 99% kernel density estimator in the "adehabitatHR" package of R (version 4.1.2; Calenge 2011; Fig. 1). We estimated the population range using a 99% kernel density estimator (KDE) for all bird locations, then randomly generated an equal number of available points at the population scale (Fig. 1). In generating available locations, we first excluded any areas we defined as 'non-habitat' such as exposed rock, open water, human development, and deciduous forest (LANDFIRE 2016).

Sampling microhabitat locations during winter was not logistically feasible; however, we reasoned that shrub characteristics selected by grouse during the preceding winter should not change by the following summer. Thus, during summer 2020 (26 May–20 Aug), we visited each location to measure shrub characteristics and dung counts at microhabitat plots (Table 1). We did not measure herbaceous vegetation or ground cover because sage-grouse consume sagebrush exclusively in winter (Wallestad and Eng 1975) and winter microhabitat selection is focused on shrub-meditated structural characteristics (Hagen et al. 2011).

We assessed winter microhabitat characteristics at used and available plots using two 50-m transects (100-m total) that intersected at the center and extended in the cardinal directions from the center of the location. We defined sub-shrubs as shrub species with typical height at maturity less than 3 dm. We measured canopy cover by species along each 50-m transect using the line-intercept method (Canfield 1941). Every 2.5 m along the transect line, we recorded the height of the nearest shrub. To estimate species richness, we recorded every shrub (to species when possible and to genus when not) rooted within 1 m of the right side of each transect line

(100 m^2 total). Shrub characteristics included overall shrub height (shrubs and sub-shrubs combined), big sagebrush height, non-sagebrush height (shrubs and sub-shrubs combined), overall canopy cover (all shrubs and sub-shrubs), sagebrush canopy cover, non-sagebrush shrub canopy cover, sub-shrub canopy cover, species richness, and whether big sagebrush was present (0 or 1) at the location (Table 1). We considered big sagebrush separately because it is as an important characteristic of sage-grouse winter habitat (Hagen et al. 2011; Dzialak et al. 2013; Smith et al. 2014, 2021) and range-wide (Connelly et al. 2011). We used a Robel pole to measure visual obstruction (to the nearest 0.5 dm; Robel et al. 1970) by visually observing shrub obstruction of the pole from 4 m away and 1 m from the ground along the transect at 0, 10, 15, 20, 25, 30, 35, 40, and 50 m intervals.

At each sampling location we recorded piles of dung from sage-grouse, native ungulates (elk [*Cervus elaphus*], mule deer [*Odocoileus hemionus*], and pronghorn [*Antilocapra Americana*]), feral horses, and cattle within 2 m on each side of each 50-m transect line (400 m^2 total). Dung piles represented general degree of use during winter, so we did not include fresh dung to ensure deposition during the previous winter or spring.

Statistical Analysis

Within home ranges, we compared vegetation characteristics and dung counts between sage-grouse use locations and home range available locations using paired *t*-tests. We used two-sample *t*-tests to compare the means of microhabitat characteristics at used and home range available locations to those characteristics measured at population range available locations. We conducted all statistical analyses in R studio and set statistical significance at alpha = 0.05. We adjusted *P*-values using the Bonferroni correction to correct the experiment-wise error rate inherent in multiple *t*-tests (Dunn 1961).

RESULTS

We used 90 use locations from 24 GPS-marked sage-grouse, 90 “home range available,” and 90 “population available” locations (Figure 1). Six of 10 shrub characteristics differed between used and available locations within home ranges. Non-sagebrush shrub canopy cover (%), non-sagebrush height (cm), shrub species richness (no.), and sagebrush presence did not differ between used and available locations within the home range (Table 2). At grouse use locations, overall canopy cover (28.9% ± 1.0) and big sagebrush canopy cover (24.3% ± 1.1) were greater compared to available locations within the home range (20.8% ± 1.3 and 15.5% ± 1.2, respectively; Table 1). Sub-shrub canopy cover (0.9% ± 0.2) was lower at grouse use locations compared to available home range locations (1.5 ± 0.3; Table 1). Big sagebrush height (37.8 cm ± 0.6), overall shrub height (35.0 cm ± 0.5), and visual obstruction (1.8 dm ± 0.1) were higher at grouse use locations compared to available locations within the home range (30.6 cm ± 0.4, 26.0 cm ± 0.4, and 0.8 dm ± 0.1, respectively; Table 1).

There were 6/10 shrub characteristics that differed between grouse use and population-scale available locations (Table 2). Non-sagebrush height (cm), overall shrub height (cm), non-sagebrush shrub canopy cover (%), and species richness (no.) did not differ between grouse used and population-scale random locations (Table 2). Overall canopy cover (28.9% ± 1.0) and big sagebrush canopy cover (24.3% ± 1.1) were 2.3- and 1.2-times higher at grouse use locations compared to available population-scale locations (12.6% ± 1.1 and 20.6 ± 1.1, respectively; Table 1). Big sagebrush height (37.8 cm ± 0.6) and visual obstruction (1.8 dm ± 0.1) were higher at grouse use locations compared to available population-scale locations (33.5 cm ± 0.6 and 1.0 dm ± 0.1, respectively; Table 1). Species richness (2.7 ± 0.1) and sub-shrub canopy cover (0.9%

± 0.2) were lower at grouse use locations compared to available population-scale locations (3.4 ± 0.2 and 2.8% ± 0.5, respectively; Table 1).

We found no difference (0/10) in shrub characteristics or dung counts (piles/400m^2) between random locations within the home range compared to the population range (Table 2). We found no differences in dung counts for any ungulate between sage-grouse use locations and home range or population range available locations. Sage-grouse dung counts at use locations (14.8 ± 1.6) were 7.0-times greater compared to home range available locations (2.1 ± 0.5) and 9.9-times greater compared to population range available locations (1.5 ± 0.6; Tables 1 and 2).

DISCUSSION

We did not find support for our first prediction, with equal numbers of differences (6) in shrub characteristics between sage-grouse use and home range and population range random locations. Available home range and population range locations only varied in comparison to use locations in overall shrub height and sagebrush presence. We found strong support for our second prediction that available habitat was similar between scales, with no differences (0/10) in shrub characteristics or dung counts between random home range and population range locations. Wintering sage-grouse used areas of higher overall shrub canopy cover and big sagebrush canopy cover (*Artemisia* spp. Nutt.), taller big sagebrush, and greater visual obstruction compared to random locations within both home and population ranges. Canopy cover of sub-shrubs was higher at random locations within home range and population scales, further indicating sage-grouse selected microhabitat for big sagebrush and other taller shrubs. Our results indicate sage-grouse were highly selective for sagebrush cover at the microhabitat scale within home and population ranges and agree with large-scale (0.1–10.0 km radii for analysis windows) habitat selection models in the same population using remotely sensed data (Smith et al. 2014, 2021). Sage-grouse dung piles were also more abundant at used locations than random locations within home or population ranges, confirming higher use of these areas by grouse. Our microhabitat results were congruent with other research from the Red Desert that indicate wintering sage-grouse select taller sagebrush and greater sagebrush canopy cover (Dzaliak et al. 2013; Smith et al. 2021). Because surveys were conducted during the summer, we were unable to account for shrub height relative to snow depth. In some regions, sage-grouse were reported to prefer areas with shorter sagebrush species (low sagebrush [*A. arbuscula* Nutt.], Hagen et al. 2011; black [*A. nova* A. Nelson], Frye et al. 2013) if snow levels did not exceed vegetation height (Hanff et al. 1994.) The use of taller sagebrush during our study period could be the result of unusually high snow depths (91^{st} percentile compared to the 30-year average; Hupp and Braun 1989, Hanf et al. 1994, PRISM 2022). Similar to microhabitat selection during nesting and brood-rearing, sage-grouse selected winter habitat with greater canopy cover, visual obstruction, and shrub height (Kirol et al. 2012; Dinkins et al. 2016). These results indicate concealment cover is important to sage-grouse throughout their annual cycle. Our results support conservation of landscapes with continuous, mature stands of sagebrush for sage-grouse throughout all seasons.

Declaration of Competing Interest

None.

Acknowledgments

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TABLES AND FIGURES

Table A.1 Mean (± SE) of winter microhabitat characteristics at locations used by sage-grouse, random locations within home ranges, and random locations within the population range. Vegetation characteristics and dung counts (piles/400 m^2) at winter 2019/2020 plots were recorded in summer 2020, northwest Colorado and southcentral, Wyoming, USA.

Microhabitat characteristics	Grouse use	Randomly available	
		Home range	Population range
Canopy cover (%)			
Big sagebrush	24.3 ± 1.1	15.5 ± 1.2	12.6 ± 1.1
Non-sagebrush shrub	3.7 ± 0.6	3.9 ± 0.9	5.7 ± 0.8
Sub-shrub	0.9 ± 0.2	1.5 ± 0.3	2.8 ± 0.5
Overall (shrub + sub-shrub)	28.9 ± 1.0	20.8 ± 1.3	20.6 ± 1.1
Height (cm)			
Big sagebrush	37.8 ± 0.6	30.6 ± 0.4	33.5 ± 0.6
Non-sagebrush	25.7 ± 1.0	18.8 ± 0.8	20.8 ± 0.8
Other Shrub Attributes			
Sagebrush presence (0/1)	1.0 ± 0.0	0.9 ± 0.02	0.9 ± 0.03
Shrub species richness (no.)	2.7 ± 0.1	2.8 ± 0.1	3.4 ± 0.2
Visual obstruction (dm)	1.8 ± 0.1	0.8 ± 0.1	1.0 ± 0.1
Dung counts (piles/400m^2)			
Cattle	7.6 ± 0.8	4.9 ± 0.7	6.5 ± 1.2
Horse	3.3 ± 0.6	3.4 ± 0.7	3.9 ± 0.9
Native ungulate[1]	52.1 ± 4.3	51.7 ± 5.8	46.1 ± 4.5
Sage-grouse	14.8 ± 1.6	2.1 ± 0.5	1.5 ± 0.6

[1]Native ungulates included elk, mule deer, and pronghorn

Table A.2 Paired *t*-tests for microhabitat characteristics and dung counts (piles/400m^2) between grouse-use locations and paired home range randomly available plots. Student's *t*-tests comparisons between population range available plots and the home range available and use plots. We recorded vegetation characteristics and dung counts (piles/400 m^2) at winter 2019/2020 habitat plots in summer 2020, northwest Colorado and southcentral, Wyoming, USA.

	Use versus random home range		Use versus random population range			Random home range versus random population range		
Microhabitat characteristics	t^1	P^2	t	DF	P^2	t	DF	P^2
Canopy cover (%)								
Big sagebrush	5.92	**<0.001**	-7.99	178.0	**<0.001**	-2.04	175.3	0.640
Non-sagebrush shrub	-0.11	1.000	2.00	168.9	0.710	1.58	175.1	1.000
Sub-shrub	-2.00	**0.049**	4.03	112.9	**0.002**	2.38	154.7	0.278
Overall (shrub + sub-shrub)	5.31	**<0.001**	-5.35	176.0	**<0.001**	-0.11	176.2	1.000
Height (cm)								
Big sagebrush	4.79	**<0.001**	-3.42	170.7	**0.011**	0.61	175.2	1.000
Non-sagebrush	1.40	1.000	0.01	150.9	1.000	1.11	173.8	1.000
Overall (shrub + sub-shrub)	4.99	**<0.001**	-2.26	135.5	0.380	0.94	131.1	1.000
Other shrub attributes								
Sagebrush presence (0/1)	2.29	0.368	-3.34	89.0	**0.018**	-1.35	162.7	1.000
Species richness	-0.49	1.000	2.71	168.3	0.111	2.37	166.4	0.285
Visual obstruction (dm)	6.12	**<0.001**	-4.55	176.1	**<0.001**	0.87	159.0	1.000
Dung counts (piles/400m^2)								
Cattle	2.78	0.099	-0.77	156.9	1.000	1.18	151.1	1.000
Horse	-0.21	1.000	0.57	160.0	1.000	0.42	170.3	1.000
Native ungulate[3]	0.05	1.000	-0.98	177.6	1.000	-0.77	167.5	1.000
Sage-grouse	7.49	**<0.001**	-7.72	111.2	**<0.001**	-0.81	171.9	1.000

[1]All degrees of freedom were 89 for paired t-tests

[2]*P*-values were adjusted using the Bonferroni correction

[3]Native ungulates included elk, mule deer, and pronghorn

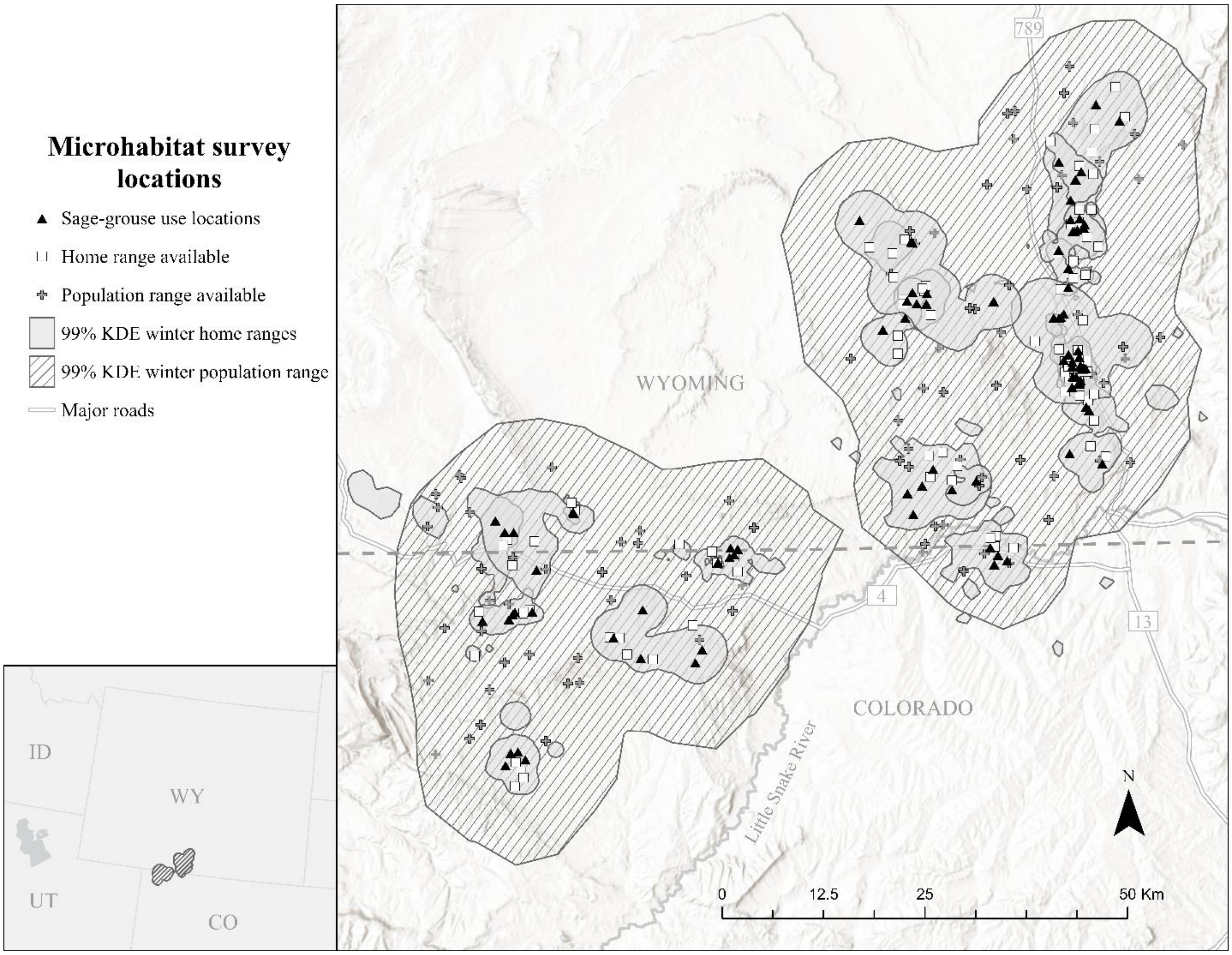

Figure A.1 Study area location map depicting locations of used grouse and random locations within home ranges and at the population scale, southwestern Wyoming and northwestern Colorado, winter 2019/2020.