To the University of Wyoming:

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Lautenbach, Jonathan, D., *Subspecies Delineation, Habitat Ecology, and Population Demography of Sharp-tailed Grouse in Southcentral Wyoming*, Doctor of Philosophy, Program in Ecology and Evolution, May, 2025.

ABSTRACT

Prairie grouse (*Tympanuchus*) are a closely related group of upland game birds comprised of three species: lesser prairie-chicken (*T. pallidicinctus*), greater prairie-chicken (*T. cupido*), and sharp-tailed grouse (*T. phasianellus*). Across the ranges of prairie grouse species, many populations of prairie grouse are species of conservation concern. Across the range of sharp-tailed grouse, Columbian sharp-tailed grouse and sharp-tailed grouse in western Wyoming (west of the Continental Divide) are populations of conservation concern. Sharp-tailed grouse in western Wyoming are primarily found in south-central Wyoming, in Carbon County. This population of sharp-tailed grouse is relatively understudied, and the subspecies of the population is in question. The aim of my Dissertation was to evaluate overlap in the distributions of all prairie grouse populations and to evaluate the subspecies identity, evaluate lek locations in relation to seasonal habitat selection and mortality risk, and to evaluate the population demography of sharp-tailed grouse in southcentral Wyoming.

In Chapter 1, I examined the overlap and correlation of encounter rates of prairie grouse populations (greater prairie-chicken, lesser prairie-chicken, and sharp-tailed grouse) and sharp-tailed grouse populations (six extant subspecies and two populations where the subspecies is unknown or in question). Encounter rates are similar to occupancy models and are used for semi-structured datasets, such as eBird data. I found that the encounter rates of prairie grouse and sharp-tailed grouse populations were more correlated for populations that were more closely related. My results suggest that differences in habitat may have aided in the speciation for more

distantly related populations and that subspeciation of populations within prairie grouse species is complex.

In Chapter 2, I examined the subspecies of sharp-tailed grouse occurring in south-central Wyoming by evaluating differences in habitat, morphology, and genetic markers between my focal population in southcentral Wyoming and the two geographically closest subspecies of sharp-tailed grouse, Columbian sharp-tailed grouse (*T. p. columbianus*) and plains sharp-tailed grouse (*T. p. jamesi*). We found that the population of sharp-tailed grouse in south-central Wyoming is different from both Columbian and plains Sharp-tailed Grouse and we recommend that the subspecies identification of the population continue to be evaluated using more targeted phylogenetic studies. This chapter is *in press* in *Ecology and Evolution* with co-authors A. Gregory, S. Galla, A. Pratt, M. Schroeder, and J. Beck (Lautenbach et al. *In Press.* Using habitat, morphological, and genetic characteristics to delineate the subspecies of Sharp-tailed Grouse in southcentral Wyoming. *Ecology and Evolution*).

In Chapter 3, I evaluated sharp-tailed grouse lek-site selection and size in relation to seasonal habitat use, seasonal mortality risk, and landscape features. We found that sharp-tailed grouse lek-site selection was based on a combination of landscape features and seasonal female habitat. Specifically, leks were located in areas with less rugged terrain and lower nest, brood, and late nonbreeding season mortality risks. Lek size increase was related to landscape features. Consequently, we recommend that management of lekking species continue to be focused around leks. This chapter is *in revision* at *Ecosphere* with co-authors A. Pratt and J. Beck.

The objective of Chapter 4 was to evaluate the population demography of sharp-tailed grouse in southcentral Wyoming using a Bayesian integrated population model. We found that the sharp-tailed grouse in southcentral Wyoming were declining, population growth was correlated with adult and chick survival, and instantaneous risk of mortality was lowest for adults and highest for juveniles during the fall. Our results highlight that potential hunting seasons should consider the timing of harvest relative to biologically important seasons and try to minimize the impacts of hunting on population size and growth. This chapter is formatted for submission to *The Journal of Wildlife Management* with co-authors S. Mathews-Sanchez, A. Pratt, P. Coates, and J. Beck.

Subspecies Delineation, Habitat Ecology, and Population Demography of Sharp-tailed Grouse in Southcentral Wyoming

By

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CHAPTER ONE

Similarities and differences in the distributions of prairie grouse species: potential implications for range expansion and hybridization

ABSTRACT

By definition, different species occupy different habitats, however it has been suggested that some closer related species may occupy similar habitats. Prairie grouse (genus *Tympanuchus*) are a group of closely related upland game bird species that can be found throughout much of North America. Prairie grouse populations diverged from each other in the past 300-500,000 years and differentiation of these species has been linked to the glacial cycles of the past million years and varying refugia created during past glacial maximums. Prairie grouse species generally occupy different habitats; however, recent range expansion has led to a hybrid zone between the populations and areas of range overlap. I investigated if closer related populations of prairie grouse occupy similar habitats through evaluating differences and similarities in encounter rate models for each of the three prairie grouse species (greater prairie-chicken [*T. cupido*], lesser prairie-chickens [*T. pallidicinctus*], and sharp-tailed grouse [*T. phasianellus*]) and the seven sharp-tailed grouse subspecies. Encounter rate models are used as a proxy for occupancy models in semi-structured citizen science data such as eBird. I generated encounter rate models from eBird observations based on land cover data and current bioclimatic conditions and evaluated overlap and correlation between the encounter rates of the different populations. I found that the encounter rates of prairie grouse populations were more correlated for populations that were more related while encounter rate overlap was more related to time since known range overlap. For sharp-tailed grouse populations, I found that encounter rates for more closely related populations had more overlap and were more correlated, with northern populations all being similar to each other and southern populations generally differing from each other. My results support ecological niche conservatism, with the encounter rates of more closely related populations being more correlated. However, my results suggest that differences in habitat may have aided in the speciation and subspeciation of populations within the prairie grouse species is complex.

INTRODUCTION

Avian species and subspecies are typically defined by checklist committees (e.g., North American Classification Committee; Chesser et al. 2024) and are typically updated annually. By definition, different species occupy different habitats, requiring diverse resources to survive and reproduce (Hall et al. 1997). Differences in resource requirements and the availability of new resources has helped facilitate evolution in some sympatric species (Petren et al. 1999, Danley and Kocher 2001, Loses et al. 2003). However, some species that are closely related still require similar resources and occupy similar habitat conditions compared to more distantly related species (Harvey and Pagel 1991, Holt and Gaines 1992, Ricklefs and Latham 1992, Peterson et al. 1999, Pryon et al. 2015), which can lead to range overlap and hybridization.

Prairie grouse (*Tympanuchus*) are a closely related group of upland game birds comprised of three species: lesser prairie-chicken (*T. pallidicinctus*), greater prairie-chicken (*T. cupido*), and sharp-tailed grouse (*T. phasianellus*). Prairie grouse can be found throughout much of North America, ranging from coastal Texas to the south, western Quebec to the east, central Washington to the west, and Alaska to the north (Hagen and Giesen 2020, Johnson et al. 2020, Connelly et al. 2024). Prairie grouse are typically found in rangeland habitats such as shrublands and grasslands, with the different species generally occupying different habitat conditions (Hagen and Giesen 2020, Johnson et al. 2020, Connelly et al. 2024). Greater prairie-chickens typically inhabit grasslands that may include a shrub component (Johnson et al. 2020); lesser prairie-chickens typically inhabit grassland and shrubby grasslands with vegetation less than one meter in height (Hagen and Giesen 2020); and sharp-tailed grouse typically inhabit more shrubby areas than the other prairie grouse (DeYoung and Williford 2016, Connelly et al. 2024).

Recently, landscape changes and range shifts have led to prairie grouse populations coming in contact, and creating hybrid zones (Johnsgard and Wood 1968, Oyler-McCance et al. 2016), which has resulted in documented cases of hybridization between greater and lesser prairie-chickens (Bain and Farley 2002, Oyler-McCance et al. 2016) and between greater prairie-chicken and sharp-tailed grouse (Johnsgard and Wood 1968, Sparling 1980). These hybridization zones are likely caused by intersections in habitat needs and available habitat conditions being suitable for the populations that overlap. Additionally, recent genetic (Black et al. 2024) and morphological (Stein 2023) evidence suggests that greater and lesser prairie-chicken are very similar and may not be fully diverged from each other. Evidence also suggests that all three species of prairie grouse have recently diverged from each other, with sharp-tailed grouse diverging from greater and lesser prairie-chicken ~300,000 years before present (ybp; Spaulding et al. 2006, DeYoung and Williford 2016), and prairie-chickens diverging more recently from each other (~170,000 ybp; Galla and Johnson 2015, DeYoung and Williford 2016). The recent divergence of the three species has been attributed to sexual selection (Spaulding 2007, Oyler-McCance et al. 2010) and glacial cycles over the past million years (Drovetski 2003, DeYoung and Williford 2016). Prairie grouse populations are generally thought to have occupied different areas during the last glacial maximum (~21,000 ybp), with sharp-tailed grouse predicted to have a different refugia than both species of prairie-chickens (DeYoung and Williford 2016), suggesting that differing climatic conditions and resulting habitats helped differentiate these species.

Within the prairie grouse group, there are also multiple subspecies that are recognized, including three greater prairie-chicken subspecies and seven subspecies of sharp-tailed grouse (Johnson et al. 2020, Connelly et al. 2024). Of the three greater prairie-chicken subspecies, only two are extant (Attwater's [*T. c. attwateri*] and greater [*T. c. pinnatus*]) and one is extinct (heath hen [*T. c. cupido*]); *T. c. attwateri* only occur in a small portion of Texas, whereas *T. c. pinnatus* is found throughout the rest of their range in the Great Plains, and *T. c. cupido* was formerly found along the East Coast of the United States from Maine to Virginia (Johnson et al. 2020, 2023). Of the seven recognized subspecies of sharp-tailed grouse, one is extinct (New Mexico [*T. phasianellus hueyi*]) and six are extant (prairie [*T. p. campestris*], Alaskan [*T. p. caurus*], Columbian [*T. p. columbianus*], plains [*T. p. jamesi*], northwestern [*T. p. kennicotti*], *and* northern [*T. p. phasianellus*]; Connelly et al. 2024). Sharp-tailed grouse populations have historically been delineated using slight visual differences and differences in habitat (Johnsgard 2002, Connelly et al. 2024). With different species and subspecies complex of prairie-grouse occupying different habitats, this suggests that habitat may have played a role in speciation and subspeciation, respectively, and understanding current habitat differences might lead to a better understanding of where the different species and subspecies occur and why hybridization zones occur.

I sought to understand differences in habitat use, using both current environmental conditions (e.g., land cover and topographic conditions) and current and past (last glacial maximum) bioclimatic conditions, between the three species of prairie grouse (hereafter prairie grouse populations), and between the six extant subspecies of sharp-tailed grouse and two populations of sharp-tailed grouse with unknown subspecies (hereafter sharp-tailed grouse populations). Specifically, I evaluated differences between the encounter rates of the different populations using a species distribution modeling approach. The encounter rate of a species is the average rate at which an observer will encounter the species and reflects the product of occupancy and detectability (Johnson et al. 2021). Encounter rate models are a form of species distribution model that are used in place of occupancy models when the input data does not meet all the assumptions of occupancy models, such as absolute detectability, such as the semi-structured citizen science database, eBird (Johnson et al. 2021, Strimas-Mackey et al. 2023*c*). Encounter rate models are based on locations where the focal species is observed and locations where the focal species is not observed, a version of use versus availability study designs (Johnson et al. 2021). However, encounter rate models do account for some variability in detectability and therefore, are typically proportional to occupancy models (Strimas-Mackey et al. 2023*c*). Species distribution models have been used to quantify differences and potential overlap in habitat conditions suitable for different species (Warren et al. 2008).

I used eBird data to estimate the encounter rates of each prairie grouse and sharp-tailed grouse population relative to habitat features (e.g., land cover and topography) and bioclimatic conditions using Random Forests models (Breiman 2001). I then compared the individual encounter rates for prairie grouse populations and sharp-tailed grouse populations to understand if there was overlap and correlation in encounter rates between populations. Overlap in encounter rates represents the potential for populations to interact while correlation represents similar responses to the environmental conditions being evaluated. I hypothesize that populations of prairie grouse and sharp-tailed grouse that are genetically more related to each other will have greater overlap and correlation between their encounter rates (Harvey and Pagel 1991). I predict, of the prairie grouse populations, greater and lesser prairie-chickens will have the most overlap and correlation in encounter rates because these are the two more closely related species with sharp-tailed grouse being a sister group to the prairie-chickens (Galla and Johnson 2015, Johnson et al. 2023). For sharp-tailed grouse populations, I predict that the encounter rates of the northern populations (*T. p. caurus*, *T. p. kennicotti*, *T. p. phasianellus*, and a population with unknown subspecies in northern Canada) will have more overlap than with other populations, as the northern populations are more related based on mitochondrial DNA (Galla and Johnson 2015) and autosomal DNA (Johnson et al. 2023; but see Galla and Johnson 2015). Additionally, I predict that of the southern populations (*T. p. campestris*, *T. p. columbianus*, *T. p. jamesi*, and a population with unknown subspecies in southern Wyoming and northwestern Colorado), *T. p. columbianus* and *T. p. jamesi* will have the most overlap because they are more related based on mitochondrial DNA (Galla and Johnson 2015) and autosomal DNA (Johnson et al. 2023; but see Galla and Johnson 2015).

METHODS

Study area

For my analyses of prairie grouse populations, my study area was comprised of the middle northern portion of the United States and the majority of Canada and encompassed the ranges of all three prairie-grouse populations (Figure 1.1). For my analysis of sharp-tailed grouse populations, my study area encompassed the range of the sharp-tailed grouse in the United States and Canada (Figure 1.1). For each of my analyses, I obtained eBird checklists from across the ranges of the populations of interest between 1 January 2010 and 31 October 2023 (eBird 2023).

Environmental conditions

To understand available environmental conditions, I obtained remotely sensed land cover and topography data. I obtained available land cover data from two different sources: 1) the North American Land Change Monitoring System (NALCMS; 30-m grain size) from the Commissions for Environmental Cooperation (https://www.cec.org/; Table 1.1) and 2) International Geosphere-Biosphere Programme (IGBP; 463-m grain size) from MODIS data collection (Friedl and Sull-Menashe 2022; Table 1.1). I used these two different land cover databases because they estimate different land cover classes and are produced on different temporal scales (NALCMS is only available for 2010, 2015, and 2020; IGBP is available annually from 2010–2023). I converted land cover data to binary data for each classification value using the *classify* function within the *terra* package in Program R (Hijmans 2025, R Core Team 2024). To understand available topographic differences, I used a digital elevation model from the Commission for Environmental Cooperation (https://www.cec.org/; 250-m grain size). I calculated heat load index (McCune and Keon 2002, McCune 2007), terrain ruggedness index (Riley et al. 1999), and topographic position index (De Reu et al. 2013) using the *hli*, *tri*, and *tpi* functions in the *spatialEco* package in program R (Evans and Murphy 2023). Once I generated all of the land cover and topographic layers, I used the *project* function using the *bilinear* method from the *terra* package in Program R (Hijmans 2025) to re-sample all of the NALCMS and topographic layers to the same spatial resolution and coordinate reference system as the IGBP layers. I resampled to the IGBP layers because this dataset had the coarsest spatial resolution. To accommodate the imprecise locations from eBird, I used a 1,500-m moving window analysis using the *focalMat* and *focal* functions in the *terra* package (Hijmans 2025) in Program R version 4.4.1 (R Core Team 2024) to get average available conditions within 1,500-m of each cell and extracted the average within each cell at each observation location.

Bioclimatic conditions

I obtained current (1979–2013) and last glacial maximum (~21,000 ybp) bioclimatic conditions from Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA; Karger et al. 2017*a*, *b*). The bioclimatic conditions from the last glacial maximum were developed from the PMIP3 general circulation model using the NCAR-CCSM4 model (Karger et al. 2017*a*). I downloaded the current and last glacial maximum data sets using the *paleoclim* function within the *rpaleoclim* package in Program R (Brown et al. 2018).

Observation locations

To obtain locations where individuals of each population were observed and not observed across the occupied range of all populations, I used eBird checklists with confirmed observations of the population of interest. I removed duplicate observations from the database prior to analyzing eBird data. I categorized the population of interest based on whether the species was observed (prairie grouse populations; Figure 1.1) or based on the published ranges of each subspecies (sharp-tailed grouse populations; Spaulding et al. 2006, Galla and Johnson 2015; Figure 1.1). For sharp-tailed grouse populations, I separated the populations by subspecies range and in cases where the subspecies identity was in question (e.g., southcentral Wyoming and northern Canada, see Chapter 2 of this dissertation) by populations for a total of eight populations (Figure 1.1). The 8 sharp-tailed grouse populations I evaluated were *T. p. campestris*, *T. p. caurus*, *T. p. columbianus, T. p. jamesi, T. p. kennicotti*, *T. p. phasianellus*, a population with unknown subspecies in Canada population (unknown Canada), and a population with unknown subspecies in Wyoming/Colorado (unknown Wyoming/Colorado; Figure 1.1). I used checklists from January 2010–October 2023 and filtered checklist data according to data use recommendations (Johnson et al. 2021, Strimas-Mackey et al. 2023*c*); this included limiting checklists to complete checklists where all observed individuals were reported, checklists with distances less than 5 km, checklists less than 6 hours long, checklists with less than 10 observers, and checklists with speeds less than 100 kmph (Johnson et al. 2021, Strimas-Mackey et al. 2023*c*). To obtain non-detection data, I used the *auk_zerofill* function within *auk* package in program R (Johnson et al. 2021, Strimas-Mackey et al. 2023*a*). To account for spatial bias, temporal bias, and class imbalance (between checklists where the focal species was observed and not observed), I independently subsampled detection and non-detection locations within a 3-km grid by selecting one detection and one non-detection location per grid cell per week using the *grid_sample_stratified* function within the *ebirdst* package in program R (Johnson et al. 2021, Strimas-Machey et al. 2023*b*, *c*). Once I had filtered all the locations, I extracted the environmental covariates and bioclimatic variables, identified above, to each checklist. I aligned checklists with land cover data based on the year of the checklist. Because annual land cover data was not available from the NALCMS dataset, I used 2010 land cover data for points from 2010–2012, I used 2015 land cover data for points from 2013–2017, and I used 2020 land cover data for points from 2018–2023.

Statistical analysis

I used Random Forests models to generate encounter rates for each prairie grouse and sharp-tailed grouse population to compare overlap in encounter rates between populations (Breiman 2001). I calculated encounter rates because the nature of eBird data does not allow for calculations of true species distribution models, but they do approximate a species occupancy and can be considered “apparent distributions” of a species (Johnson et al. 2021). Encounter rates modeled using eBird data can be approximated as the probability that an eBirder encounters the species of interest on a standard eBird checklist and are similar to occupancy models (Strimas-

Mackey et al. 2023*c*). Once I identified my final presence and pseudo-absence locations, I used a down-sampled Random Forests model (Valavi et al. 2021) using the *ranger* function from the *ranger* package in program R (Wright and Ziegler 2017). I used the suite of environmental variables and several effort variables as predictors of encounter rate. I used effort variables to help account for differences in detectability; the effort variables that I used were time of day, day of year, year, duration of the checklist, length of the checklist, speed of the checklist, and number of observers.

I ran my Random Forests models using 80% of the data as training data so that I could use the remaining 20% of the data (test data set) to assess the fit of the model. I evaluated the fit of the Random Forests models using mean square error using the test data set (Johnson et al. 2021); all mean square error estimates were less than 0.01 indicating a good fit to the data. I standardized variable importance values so the top variable equaled 1 and the remaining variables were proportions derived by dividing by the top variable (Doherty et al. 2018). In addition, I generated partial dependency plots of the three most important variables that were in common between all (prairie grouse) or most (sharp-tailed grouse) of the populations. Once I ran the training model, I calibrated the model following Strimas-Mackey et al. (2023*c*). I used the calibrated model to generate a predictive surface for environmental conditions, current bioclimatic conditions, and last glacial maximum bioclimatic condition and I reclassified the encounter rate probability between zero and one for each predictive surface. This provided the ability to calculate overlap in encounter rates between populations.

To evaluate overlap in encounter rates, I calculated pairwise *I* statistics (a measure derived from Hellinger distance; Warren et al. 2008) and Spearman’s rank correlations (ρ) using the *raster.overlap* function in the *ENMTools* package in program R (Warren et al. 2008, Warren and Dinnage 2024). Specifically, *I* quantifies the potential for species to interact or compete with one another and measures shared suitable habitat, where 0 represents no overlap and 1 represents complete overlap (Warren et al. 2008). Spearman's rank correlation (ρ) evaluates the population responses to habitat conditions and identifies if the suitable habitat conditions are similar between populations. Spearman's rank correlation coefficients vary between -1 and 1, with negative 1 representing complete opposite encounter rates and positive 1 representing complete correlation in encounter rates. For each metric (*I* and ρ), I considered encounter rates to have minimal overlap/correlation for values between |0.0–0.5|, moderate overlap/correlation for values between |0.5–0.7|, and I considered them to have high overlap/correlation with values between |0.7–1.0|. For negative Spearman's rank correlation values, I used the same categories but considered the encounter rates to have minimal negative correlation, moderate negative correlation, and high negative correlation, respectively.

RESULTS

In total, there were 7,486 greater prairie-chicken, 1,569 lesser prairie-chicken, and 20,538 sharp-tailed grouse observations in the eBird dataset from January 2010–October 2023 that met my criteria to be included in my analyses. For sharp-tailed grouse subspecies, observation totals were 5,886 for *T. p. campestris*, 282 for *T. p. caurus*, 738 for *T. p. columbianus*, 11,787 for *T. p. jamesi*, 46 for *T. p. kennicotti*, 595 for *T. p. phasianellus*, 178 unknown sharp-tailed grouse subspecies in Canada, and 510 observations of unknown sharp-tailed grouse subspecies in Wyoming/Colorado. The total observations of sharp-tailed grouse subspecies/populations do not add up to the total sharp-tailed grouse observations because some of the eBird observations were outside the recognized subspecies/population ranges.

Environmental conditions encounter rate models

Prairie grouse encounter rate model overlap—I created predictive surfaces for each species of prairie grouse as predicted by the Random Forests models (Figure 1.2). When evaluating encounter rate overlap using *I*, all species of prairie grouse had moderate overlap with each other, with the overlap between greater prairie-chicken and sharp-tailed grouse being the highest (I = 0.65) followed by lesser prairie-chicken and sharp-tailed grouse and the species pair with the least overlap being greater and lesser prairie-chicken (Table 1.3). I found that the encounter rates of greater and lesser prairie-chicken were highly correlated (ρ = 0.73) while sharp-tailed grouse were moderately correlated with both greater (ρ = 0.53) and lesser prairie-chicken (ρ = 0.57; Table 1.2).

Prairie grouse variable importance—For greater prairie-chicken encounter rate modeling, the most important land cover and topographic variables for predicting encounter rates were shrublands, grasslands, croplands, conifer forest, and terrain ruggedness index (Table 1.3). For lesser prairie-chicken, the most important land cover and topographic variables predicting lesser prairie-chicken encounter rate were wetlands, grasslands, conifer forests, mixed forests, and terrain ruggedness index (Table 1.3). For sharp-tailed grouse, the most important land cover and topographic variables predicting sharp-tailed grouse encounter rate were grasslands, terrain ruggedness index, croplands, topographic position index, and shrublands (Table 1.3). Partial dependency plots showed that encounter rates were highest in areas with a greater proportion of grasslands within 1,500 m for all species (Figure 1.3), encounter rates were highest in areas with less rugged terrain for all species (Figure 1.4), and encounter rates were highest for greater prairie-chicken in areas with a lower proportion of shrublands within 1,500 m while encounter rates were highest for lesser prairie-chicken and sharp-tailed grouse in areas with a greater proportion of shrublands within 1,500 m (Figure 1.5).

Sharp-tailed grouse encounter rate model overlap—I created a predictive surface for each subspecies/population of sharp-tailed grouse as predicted by the Random Forests models (Figure 1.6). When evaluating overlap (I) in encounter rate, *T. p. caurus*, *T. p. phasianellus*, *T. p. kennicotti*, and the unknown Canada populations, all moderate or high overlap with each other (Table 1.4). The encounter rate of *T. p. columbianus* had moderate overlap with *T. p. caurus*, *T. p. jamesi*, *T. p. phasianellus*, and the unknown Canada population (Table 1.4). When evaluating correlation (ρ) in encounter rates between sharp-tailed grouse populations, I found that *T. p. caurus*, *T. p. kennicotti*, *T. p. phasianellus*, and the unknown Canada population were highly correlated with each other (range of $\rho = 0.77$–0.88; Table 1.4). I found that the encounter rate of *T. p. jamesi* was negatively correlated with *T. p. caurus*, *T. p. kennicotti*, *T. p. phasianellus*, and the unknown Canada population and *T. p. jamesi* was moderately correlated with *T. p. columbianus* (Table 1.4). For complete results evaluating overlap (I) and Spearman's rank correlation (ρ) between sharp-tailed grouse populations see Table 1.4.

Sharp-tailed grouse variable importance—For encounter rate models of sharp-tailed grouse subspecies, the most important land cover and topographic variables as predicted by the Gini index for predicting encounter rate of *T. p. campestris* were terrain ruggedness index, deciduous forest, topographic position index, heat load index, and croplands (Table 1.4). For *T. p. caurus*, the most important land cover and topographic variables predicting encounter rate were conifer forests, woody savannas, mixed forest, wetlands, and barren lands (Table 1.4). For *T. p. columbianus*, the most important land cover and topographic variables predicting encounter rate were shrublands, heat load index, croplands, mixed forest, and terrain ruggedness index (Table 1.4). The most important land cover and topographic variables predicting the encounter rate of *T. p. jamesi* were grasslands, woody savanna, conifer forests, croplands, and terrain ruggedness index (Table 1.4). The most important land cover and topographic variables predicting the encounter rate of *T. p. kennicotti* were savanna, croplands, conifer forest, topographic position index, and terrain ruggedness index (Table 1.4). The most important land cover and topographic variables predicting the encounter rate of *T. p. phasianellus* were conifer forests, terrain ruggedness index, woody savanna, mixed forests, and topographic position index (Table 1.4). The most important land cover and topographic variables predicting the encounter rate of unknown sharp-tailed grouse in Canada were croplands, woody savanna, wetlands, conifer forests, and mixed forest (Table 1.4). For unknown sharp-tailed grouse in Wyoming/Colorado, the most important land cover and topographic variables predicting encounter rate were shrublands, terrain ruggedness index, deciduous forest, grasslands, and barren lands (Table 1.4). Partial dependency plots for conifer forest demonstrated that more northern populations of sharp-tailed grouse (e.g., *T. p. caurus*, *T. p. kennicotti*, *T. p. phasianellus*, and unknown Canada population) had higher encounter rates when there was more conifer forest cover (Figure 1.7 B, E, F, G) while the more southern populations (e.g., *T. p. campestris*, *T. p. jamesi*, *T. p. columbianus*, and unknown Wyoming/Colorado population) generally had lower encounter rates when there was more conifer forest (Figure 1.7 A, C, D, H). Partial dependency plots for terrain ruggedness index demonstrated that in general, sharp-tailed grouse populations had higher encounter rates when terrain was less rugged (Figure 1.8), while the encounter rates for *T. p. columbianus* and unknown Wyoming/Colorado were highest in slightly more rugged terrain (Figure 1.8 C and H). Partial dependency plots for croplands did not follow a trend for all populations, but the encounter rates for *T. p. campestris*, *T. p. columbianus*, and *T. p. jamesi* increased as the proportion of croplands increased (Figure 1.9 A, C, D) while the encounter rates for *T. p. caurus*, *T. p. kennicotti*, and unknown Canada were highest when the proportion of grasslands was low (Figure 1.9 B, E, G).

Bioclimatic encounter rate models

Prairie grouse encounter rate model overlap—I created predictive surfaces for each species of prairie grouse as predicted by the Random Forests models for current bioclimatic conditions (Figure 1.10) and bioclimatic conditions during the last glacial maximum (Figure 1.11). Using current bioclimatic conditions, there was little overlap (*I*) between prairie grouse encounter rates, while the encounter rates between greater and lesser prairie-chicken were the most correlated ($\rho = 0.47$; Table 1.6). Using bioclimatic conditions during the last glacial maximum, there was significant overlap in encounter rates between all populations and encounter rates of greater and lesser prairie-chicken were moderately correlated ($\rho = 0.65$; Table 1.7).

Sharp-tailed grouse encounter rate model overlap—I created predictive surfaces for each species of prairie grouse as predicted by the Random Forests models for current bioclimatic conditions (Figure 1.12) and bioclimatic conditions during the last glacial maximum (Figure 1.13). Under current bioclimatic conditions, I found that there was moderate overlap (*I*) between the three northern most populations (*T. p. caurus*, *T. p. kennicotti*, and unknown Canada) and moderate overlap between *T. p. kennicotti* and unknown Wyoming/Colorado (Table 1.8). Under current bioclimatic conditions, there was moderate to high correlation between the four most northern populations (*T. p. caurus, T. p. kennicotti*, *T. p. phasianellus*, and unknown Canada; $\rho = 0.61–0.88$; Table 1.8). Additionally, *T. p. campestris*, *T. p. phasianellus*, and unknown Canada populations were all correlated ($\rho = 0.71–0.79$) and *T. p. columbianus* and unknown Wyoming/Colorado were moderately correlated ($\rho = 0.63$). Under bioclimatic conditions during the last glacial maximum, I found that there was high overlap (*I*) between all populations of sharp-tailed grouse (Table 1.9). Under bioclimatic conditions during the last glacial maximum, there was high correlation (ρ) between the three most northern populations (*T. p. caurus*, *T. p. kennicotti*, and unknown Canada; Table 1.9) and moderate to low correlation between the rest of the populations (Table 1.8). For complete results evaluating overlap (*I*) and Spearman's rank correlation (ρ) between sharp-tailed grouse populations based on bioclimatic conditions see Tables 1.8 and 1.9.

DISCUSSION

Prairie grouse are found through much of the rangelands in the Great Plains and Intermountain West of North America and are known to hybridize in portions of their ranges (Hagen and Giesen 2020, Johnson et al. 2020, Connelly et al. 2024). I evaluated the overlap and correlation of the encounter rates of the different species of prairie grouse and the different subspecies of sharp-tailed grouse based on land cover and topography and bioclimatic condition. Among prairie grouse species, I found that the encounter rates of the more closely related species were more correlated with each other (greater and lesser prairie-chicken) indicating more similarity in required habitat conditions, while the species with the larger projected hybridization zone (greater prairie-chicken and sharp-tailed grouse) had the most overlap in encounter rates which indicates a greater potential to interact. Within the populations of sharp-tailed grouse, the encounter rates of more closely related populations generally had more overlap and were generally more correlated with each other, forming a more northerly group (*T. p. caurus*, *T. p. kennicotti*, *T. p. phasianellus*, and unknown Canada), with the southern populations having limited overlap or correlation with each other except for moderate overlap and correlation in encounter rates between *T. p. jamesi* and *T. p. columbianus* based on current land cover and topographic conditions. The trends of overlap and correlation of encounter rates during the last glacial maximum were generally similar to those based on current conditions. My results suggest that more closely related populations within the prairie grouse species and subspecies complex generally have more similar land cover and bioclimatic habitat requirements.

The ranges of prairie grouse are thought to have shifted over the past 200 years as a result of land use change (Johnsgard and Wood 1968, Bain and Farley 2002), likely resulting in currently observed areas of range overlap between the populations. The ranges of the greater and lesser prairie-chicken are thought to have come in contact during the past 30 to 40 years (Bain and Farley 2002, Hagen and Giesen 2020) with known hybrids occurring since at least 2001 (Bain and Farley 2002). My results demonstrate that the encounter rates of greater and lesser prairie-chicken were most correlated between the three prairie grouse populations, suggesting that these species occupy similar environmental conditions. While I did not evaluate future conditions, similar habitat use in areas of overlap (Dahlgren et al. 2016), coupled with my results demonstrating correlation in encounter rates using both land cover and bioclimatic conditions suggest that there is potential for more range overlap in the future. My results indicate that there is more overlap between greater prairie-chicken and sharp-tailed grouse encounter rates then there is correlation suggesting that there is more potential for these species to interact, likely as a result of these species co-occurring since the late 1800's (Gurney 1884, Johnsgard and Wood 1968), with hybrids documented as early as 1877 (Gurney 1884). The areas where greater prairie-chicken and sharp-tailed grouse co-occur are thought to have expanded during the late 1800s as a result of land-use changes associated with expansion of agriculture (Johnsgard and Wood 1968).

Prairie grouse speciation is predicted to have occurred because of periodic glaciation during the late Pleistocene and prairie grouse are generally thought to have been geographically separated from each other prior to European settlement (DeYoung and Williford 2016). Similar to my results, a previous study evaluating habitat suitability of prairie grouse based on museum specimens suggests that there was more correlation in habitat conditions between greater and lesser prairie-chicken with limited correlation between sharp-tailed grouse and both prairie-chicken species during the last glacial maximum (DeYoung and Williford 2016). Greater and lesser prairie-chicken are closely related, and thought to have diverged around 170,000 ybp (Galla and Johnson 2015, DeYoung and Williford 2016), whereas prairie-chickens are thought to have diverged from sharp-tailed grouse around 300,000 ybp (Spaulding et al. 2006, DeYoung and Williford 2016). While I did not evaluate genetic relationships, the correlation in suitable habitat during the last glacial maximum aligns with the expected genetic relationships between these populations with more closely related species having more correlation between suitable habitats. Similar to prairie-grouse populations, I found that the suitable habitat of more closely related sharp-tailed grouse populations were generally more correlated with each other during the last glacial maximum. The greater correlation in suitable habitat during the last glacial maximum for closer related populations suggests that differences in habitat requirements may have aided in the divergence of prairie grouse species and populations, generally following the patterns of phylogenetic niche conservatism, where closely related populations retain some ancestral ecological characteristics over time (Harvey and Pagel 1991, Ricklefs and Latham 1992, Peterson et al. 1999, Pryon et al. 2015). To better understand the connection between habitat conditions and genetic relationships among prairie grouse populations, I recommend a phylogeographic and landscape genetic study that includes samples from across the range of each population of prairie grouse.

When evaluating sharp-tailed grouse subspecies, I observed the encounter rates of the northern populations (*T. p. caurus*, *T. p. kennicotte*, *T. p. phasianellus*, and unknown Canada) generally overlapped, were generally correlated, and had similar variables important for predicting encounter rates. The northern populations of sharp-tailed grouse are more closely related genetically to each other then they are to the southern populations (*T. p. campestris*, *T. p. columbianus*, *T. p. jamesi*, and unknown Wyoming/Colorado; Galla and Johnson 2015, Johnson et al. 2023) and the northern populations share similar morphology with these populations appearing darker-colored overall and smaller than the southern populations (Connelly et al. 2024). In contrast, a phylogeographic study of sharp-tailed grouse populations suggests that there is limited genetic connectivity between the northern populations (Perktaş and Elverici 2019), though the sample size was small and represent a small fraction of the northern populations. The two southern populations I observed with the most overlap based on land cover and topography were *T. p. columbianus* and *T. p. jamesi*, which are also two of the more related southern populations (Galla and Johnson 2015, Johnson et al. 2023); however, based on bioclimatic conditions, the encounter rates of these two populations did not overlap. The encounter rates of *T. p. columbianus* and the unknown Wyoming/Colorado population had limited overlap and correlation based on land cover and topography, despite the unknown Wyoming/Colorado population historically classified as *T. p. columbianus* (Spaulding et al. 2006, Connelly et al. 2024). When using more detailed data on vegetation cover, a Random Forests classification model was able to identify differences in habitat between *T. p. columbianus*, *T. p. jamesi*, and unknown Wyoming/Colorado populations (Chapter 2, this Dissertation). In contrast, encounter rates based on bioclimatic condition had moderate overlap and correlation between *T. p. columbianus* and unknown Wyoming/Colorado populations. Land use changes have resulted in increased grasslands across portions of the range of *T. p. columbianus* (Hoffman et al. 2015, Stevens et al. 2023), likely altering the land cover types occupied by *T. p. columbianus* despite similarities in bioclimatic conditions.

My results suggest that the encounter rates of more closely related populations are more correlated, suggesting these populations have similar habitat requirements. The populations of prairie grouse with more overlap (greater prairie-chicken and sharp-tailed grouse) have a longer history of known range overlap and hybridization (Gurney 1884, Johnsgard and Wood 1968, Johnson et al. 2020). Similarly, the populations of prairie-grouse with more correlated encounter rates (greater and lesser prairie-chicken) are more closely related to each other (Galla and Johnson 2015, Johnson et al. 2023), with some suggesting that they may not be fully diverged from each other (Black et al. 2024). The relationships between sharp-tailed grouse populations were similar, with more closely related populations typically having more overlap and correlation between populations. My results support ecological niche conservatism, with the encounter rates of more closely related populations being more correlated; however, my results also suggest that differences in habitat requirements may have aided in the speciation and subspeciation of populations within the prairie grouse species complex by helping to maintain spatial and ecological separation of populations.

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TABLES

Table 1.1. Names, description, the original values from the original datasets used to derive the variable, the initial spatial resolution of the variables, and a description of why and references supporting the inclusion the variables in the models that were used to understand differences in habitat use between populations of prairie grouse (lesser prairie-chicken, greater prairie-chicken, and sharp-tailed grouse) and between populations of sharp-tailed grouse (sharp-tailed grouse subspecies).

Environmental Condition	**Layer description**	**Layer value(s)[a]**	**Initial Spatial Resolution**	**Reason for inclusion in analysis**	**References**
Barren lands[b]	Combination of barren lands and sub-polar and polar barren lands	13, 16	30 m[e]	Bare ground is avoided by prairie grouse and barren lands might represent unimproved roads or small developments avoided by prairie grouse	Lawrence et al. 2022, Burr et al. 2017, McNew et al. 2015
Cropland[b]	All croplands	15	30 m[e]	Used by some prairie grouse populations during the nonbreeding season	Roy and Chen 2023
Deciduous forests[b]	Temperate or sub-polar broadleaf deciduous forests	5	30 m[e]	Avoided and used by different prairie grouse populations	Lawrence et al. 2022, Raymond 2001, Connelly et al. 2024
Mixed forests[b]	Mixed deciduous and coniferous forests	6	30 m[e]	Potentially avoided by prairie grouse populations, but some evidence for use by sharp-tailed grouse	Raymond 2001, Connelly et al. 2024
Conifer forests[b]	Temperate and sub-polar coniferous forest	1, 2	30 m[e]	Avoided by some prairie grouse populations	Lautenbach et al. 2017

Grasslands[b]	All grasslands including temperate, tropical, and sub-polar grasslands	9, 10, 12	30 m[e]	Important habitat component for all prairie grouse populations and most sharp-tailed grouse populations	Hagen and Giesen 2020, Johnson et al. 2020, Connelly et al. 2024
Shrublands[b]	All shrublands including temperate, tropical, and sub-polar shrublands	7, 8, 11	30 m[e]	Important component for some lesser prairie-chicken and sharp-tailed grouse populations	Hagen and Giesen 2020, Connelly et al. 2024
Wetlands[b]	All wetland cover	14	30 m[e]	Avoidance and selection by prairie grouse populations	Hiller et al. 2019
Savannas[c]	Savannas with 10–30% tree cover	8	465 m[e]	Open conifer and deciduous woodlands used by some populations	Connelly et al. 2024
Woody savannas[c]	Savannas with 30–60% tree cover	9	465 m[e]	Open conifer and deciduous woodlands used by some populations	Connelly et al. 2024
Heat load index[d]	Calculated from digital elevation model (McCune and Keon 2002)	—	250 m[e]	Southern populations of prairie grouse use areas that minimize exposure to temperature extremes	Hovick et al. 2014, Raynor et al. 2018
Terrain ruggedness index[d]	Calculated from digital elevation model (Riley et al. 1999)	—	250 m[e]	Prairie grouse typically occupy less rugged terrain	Jarnevich et al. 2016, Burda et al. 2022
Topographic position index[d]	Calculated from digital elevation model (De Reu et al. 2014)	—	250 m[e]	Prairie grouse leks are typically located on hill tops	Hagen and Giesen 2020, Johnson et al. 2020, Connelly et al. 2024

[a] Layer values are the values used from the respective land cover database to derive the layer used

[b] Derived from the North American Land Monitoring System dataset from: http://www.cec.org/north-american-land-change-monitoring-system/

[c] Derived from the International Geosphere-Biosphere Programme land cover classification from MODIS available from: https://lpdaac.usgs.gov/products/mcd12q1v061/

[d] Derived from a digital elevation model downloaded from http://www.cec.org/north-american-environmental-atlas/elevation-2023/

[e] Final spatial resolution used for all layers was 465 m to ensure that all layers used were in the same spatial resolution for projection. For layers that were not originally in this spatial resolution, I reprojected them to the same spatial resolution as the International Geosphere-Biosphere Programme raster layer using the ‘bilinear’ method within the *project* function in the *terra* package in Program R (Hijmans 2025).

Table 1.2. Pairwise metrics for *I* statistic (above diagonal line) and Spearman's rank correlation (ρ; below diagonal line) comparing the overlap (*I*) and correlation (ρ) in Random Forests models predicting encounter rates for greater prairie-chicken, lesser prairie-chicken, and sharp-tailed grouse across North America using land cover and topographic features. Because the encounter rate models include effort and date variables, the encounter rate is predicted for 15 April 2020. Overlap (*I*) represents two populations' potential to interact with each other while correlation (ρ) identifies if the two populations' responses to habitat conditions are similar between populations.

	Greater prairie-chicken	**Lesser prairie-chicken**	**Sharp-tailed grouse**
Greater prairie-chicken		0.57	0.65
Lesser prairie-chicken	0.73		0.64
Sharp-tailed grouse	0.52	0.57	

Table 1.3. Scaled variable importance (Gini index) for the top five most important land cover and topographic variables from Random Forests models predicting the encounter rate of greater prairie-chicken, lesser prairie-chicken, and sharp-tailed grouse in North America using land cover and topographic features (Jan 2010–Oct 2023).

Species	**Predictor**	**Scaled variable importance**
Greater prairie-chicken	Shrublands	1.00
	Grasslands	0.68
	Croplands	0.57
	Conifer forests	0.39
	Terrain ruggedness index	0.36
Lesser prairie-chicken	Wetlands	0.75
	Grasslands	0.66
	Conifer forests	0.64
	Mixed forests	0.33
	Terrain ruggedness index	0.32
Sharp-tailed grouse	Grasslands	1.00
	Terrain ruggedness index	0.83
	Croplands	0.58
	Topographic position index	0.45
	Shrublands	0.45

Table 1.4. Pairwise metrics for *I* statistic (above diagonal line) and Spearman's rank correlation (ρ; below diagonal line) comparing the overlap (*I*) and correlation (ρ) in Random Forests models predicting encounter rates based on eBird data for subspecies of sharp-tailed grouse (*Tympanuchus phasianellus*) and populations where the subspecies is unknown or in question (Unknown) across the sharp-tailed grouse range in North America using land cover and topographic features. Because the encounter rate models include effort and date variables, the encounter rate is predicted for 15 April 2020. Overlap (*I*) represents two populations' potential to interact with each other while correlation (ρ) identifies if the two populations' responses to habitat conditions are similar between populations.

	T. p. campestris	***T. p. caurus***	***T. p. columbianus***	***T. p. jamesi***	***T. p. kennicotti***	***T. p. phasianellus***	**Unknown Canada**	**Unknown WY/CO**
T. p. campestris		0.58	0.45	0.30	0.37	0.65	0.63	0.09
T. p. caurus	0.34		0.56	0.21	0.59	0.81	0.88	0.17
T. p. columbianus	-0.54	-0.49		0.63	0.48	0.54	0.63	0.41
T. p. jamesi	-0.13	-0.72	0.55		0.20	0.22	0.28	0.11
T. p. kennicotti	0.11	0.77	-0.27	-0.50		0.68	0.70	0.12
T. p. phasianellus	0.56	0.78	-0.48	-0.53	0.76		0.91	0.12
Unknown Canada	0.38	0.88	-0.42	-0.52	0.84	0.86		0.16
Unknown WY/CO	-0.55	-0.01	0.41	-0.12	0.05	-0.28	-0.14	

Table 1.5. Scaled variable importance (Gini index) for the top five most important land cover and topographic variables from Random Forests models predicting the encounter rate of sharp-tailed grouse subspecies (*Tympanuchus phasianellus*) and populations where the subspecies is in question or unknown (Unknown) as predicted using eBird observations from across the range of sharp-tailed grouse in North America using land cover and topographic features (Jan 2010–Oct 2023).

Subspecies	**Predictor**	**Scaled Importance**
T. p. campestris	Terrain ruggedness index	1.00
	Deciduous forest	0.48
	Topographic position index	0.34
	Heat load index	0.30
	Cropland	0.27
T. p. caurus	Conifer forest	1.00
	Woody savanna	0.74
	Mixed Forest	0.54
	Wetlands	0.48
	Barren lands	0.47
T. p. columbianus	Shrublands	1.00
	Heat load index	0.29
	Cropland	0.25
	Mixed Forest	0.25
	Terrain ruggedness index	0.25
T. p. jamesi	Grasslands	1.00
	Woody savanna	0.43
	Conifer forest	0.41
	Cropland	0.40
	Terrain ruggedness index	0.38
T. p. kennicotti	Savanna	1.00
	Cropland	0.86
	Conifer forest	0.79
	Topographic position index	0.21
	Terrain ruggedness index	0.19
T. p. phasianellus	Conifer forest	1.00
	Terrain ruggedness index	0.71
	Woody savanna	0.69

	Mixed Forest	0.39
	Topographic position index	0.31
Unknown Canada	Cropland	1.00
	Woody savanna	0.55
	Wetlands	0.53
	Conifer forest	0.46
	Mixed Forest	0.40
Unknown Wyoming/Colorado	Shrublands	1.00
	Terrain ruggedness index	0.52
	Deciduous forest	0.31
	Grasslands	0.20
	Barren lands	0.18

Table 1.6. Pairwise metrics for *I* statistic (above diagonal line) and Spearman's rank correlation (ρ; below diagonal line) comparing the overlap (*I*) and correlation (ρ) in Random Forests models predicting encounter rates for greater prairie-chicken, lesser prairie-chicken, and sharp-tailed grouse across North America using current (1979–2013) bioclimatic conditions. Because the encounter rate models include effort and date variables, the encounter rate is predicted for 15 April 2020. Overlap (*I*) represents two populations' potential to interact with each other while correlation (ρ) identifies if the two populations' responses to habitat conditions are similar between populations.

	Greater prairie-chicken	**Lesser prairie-chicken**	**Sharp-tailed Grouse**
Greater prairie-chicken		0.13	0.20
Lesser prairie-chicken	0.47		0.01
Sharp-tailed Grouse	0.08	-0.21	

Table 1.7. Pairwise metrics for *I* statistic (above diagonal line) and Spearman's rank correlation (ρ; below diagonal line) comparing the overlap (*I*) and correlation (ρ) in Random Forests models predicting encounter rates for greater prairie-chicken, lesser prairie-chicken, and sharp-tailed grouse across North America using bioclimatic conditions during the last glacial maximum (~21,000 ybp). Because the encounter rate models include effort and date variables, the encounter rate is predicted for 15 April 2020. Overlap (*I*) represents two populations' potential to interact with each other while correlation (ρ) identifies if the two populations' responses to habitat conditions are similar between populations.

	Greater prairie-chicken	**Lesser prairie-chicken**	**Sharp-tailed Grouse**
Greater prairie-chicken		0.83	0.74
Lesser prairie-chicken	0.65		0.67
Sharp-tailed Grouse	-0.10	-0.32	

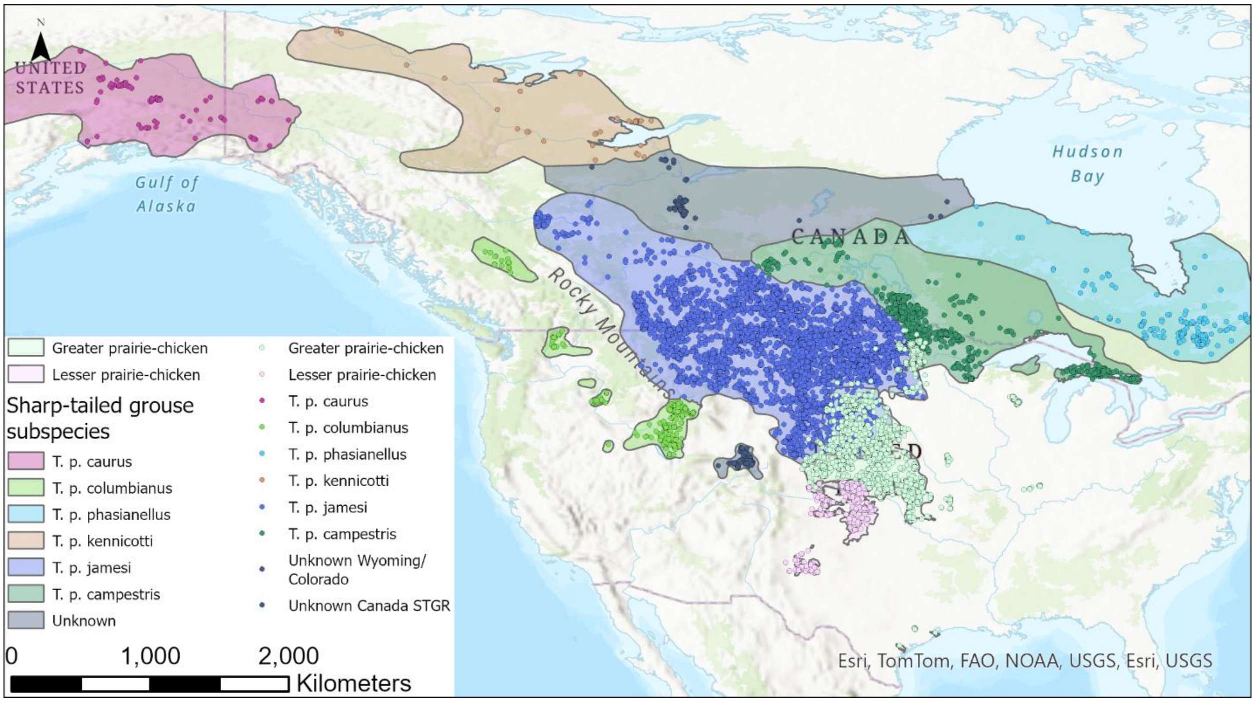
Table 1.8. Pairwise metrics for *I* statistic (above diagonal line) and Spearman's rank correlation (ρ; below diagonal line) comparing the overlap (*I*) and correlation (ρ) in Random Forests models predicting encounter rates based on eBird data for subspecies of sharp-tailed grouse (*Tympanuchus phasianellus*) and populations where the subspecies is unknown or in question (Unknown) across the sharp-tailed grouse range in North America using current (1979–2013) bioclimatic conditions. Because the encounter rate models include effort and date variables, the encounter rate is predicted for 15 April 2020. Overlap (*I*) represents two populations' potential to interact with each other while correlation (ρ) identifies if the two populations' responses to habitat conditions are similar between populations.

	T. p. campestris	**T. p. caurus**	**T. p. columbianus**	**T. p. jamesi**	**T. p. kennicotti**	**T. p. phasianellus**	**Unknown Canada**	**Unknown WY/CO**
T. p. campestris		0.15	0.04	0.08	0.18	0.20	0.30	0.14
T. p. caurus	0.33		0.20	0.15	0.76	0.36	0.54	0.47
T. p. columbianus	-0.53	0.01		0.11	0.21	0.10	0.12	0.43
T. p. jamesi	-0.13	-0.11	-0.34		0.13	0.09	0.17	0.26
T. p. kennicotti	0.47	0.88	-0.03	-0.21		0.45	0.68	0.53
T. p. phasianellus	0.71	0.61	-0.33	-0.23	0.75		0.50	0.29
Unknown Canada	0.74	0.67	-0.43	0.00	0.77	0.79		0.36
Unknown WY/CO	-0.39	0.26	0.63	-0.17	0.23	-0.09	-0.20	

Table 1.9. Pairwise metrics for *I* statistic (above diagonal line) and Spearman's rank correlation (ρ; below diagonal line) comparing the overlap (*I*) and correlation (ρ) in Random Forests models predicting encounter rates based on eBird data for subspecies of sharp-tailed grouse (*Tympanuchus phasianellus*) and populations where the subspecies is unknown or in question (Unknown) across the sharp-tailed grouse range in North America using bioclimatic conditions during the last glacial maximum (~21,000ybp). Because the encounter rate models include effort and date variables, the encounter rate is predicted for 15 April 2020. Overlap (*I*) represents two populations' potential to interact with each other while correlation (ρ) identifies if the two populations' responses to habitat conditions are similar between populations.

	T. p. campestris	**T. p. caurus**	**T. p. columbianus**	**T. p. jamesi**	**T. p. kennicotti**	**T. p. phasianellus**	**Unknown Canada**	**Unknown WY/CO**
T. p. campestris		0.87	0.69	0.85	0.92	0.95	0.95	0.87
T. p. caurus	0.52		0.73	0.80	0.88	0.84	0.92	0.83
T. p. columbianus	-0.56	-0.45		0.84	0.59	0.64	0.64	0.79
T. p. jamesi	0.24	-0.05	-0.43		0.73	0.78	0.80	0.83
T. p. kennicotti	0.81	0.78	-0.50	0.06		0.89	0.94	0.81
T. p. phasianellus	0.86	0.56	-0.45	0.05	0.80		0.94	0.83
Unknown Canada	0.82	0.74	-0.58	0.13	0.89	0.84		0.83
Unknown WY/CO	0.53	0.35	-0.18	-0.09	0.55	0.53	0.43	

FIGURES



Esri, TomTom, FAO, NOAA, USGS, Esri, USGS

Figure 1.1. Range maps of greater prairie-chicken, lesser prairie-chicken, and sharp-tailed grouse in North America and locations of eBird observations (colored points) of each species. Sharp-tailed grouse range and observation are split into the different subspecies/populations. The range boundary for greater prairie-chicken was created by an interstate working group of state wildlife agency personnel (ArcGIS ID: 4ddf4b84148e4994a69c9e221d9108f8); the range boundary for lesser prairie-chicken was obtained from WAFWA Lesser Prairie-Chicken Interstate Working Group (2022); and the range boundary for sharp-tailed grouse and the different subspecies of sharp-tailed grouse was derived from Spaulding et al. (2006) and Galla and Johnson (2015).

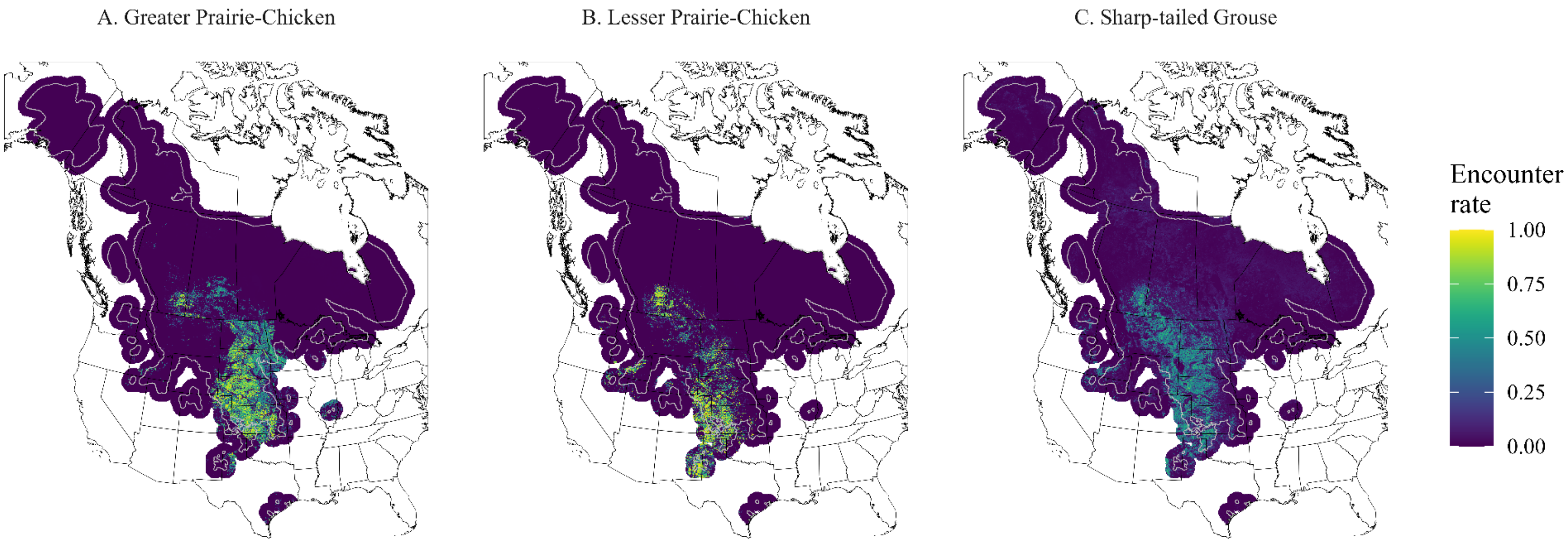


Figure 1.2. Predicted encounter rate based on eBird observations generated using Random Forests models based on land cover and topographic features for three species of grouse: greater prairie-chicken (**A**), lesser prairie-chicken (**B**), and sharp-tailed grouse (**C**) across the combined range of the three species in North America. Cooler colors represent lower probability of encountering the species and warmer colors represent greater probability of encountering the species; white border represents the combined described ranges of the three species.

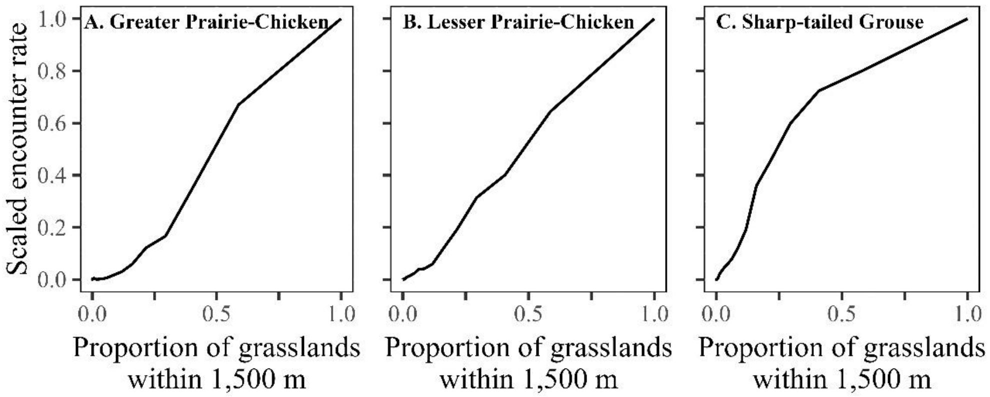


Figure 1.3. Partial dependence plots for the proportion of grasslands within 1,500 m as predicted by Random Forests models predicting the encounter rates of three species of prairie grouse using eBird observations: greater prairie-chicken (**A**), lesser prairie-chicken (**B**), and sharp-tailed grouse (**C**) in North America (2010–2023).

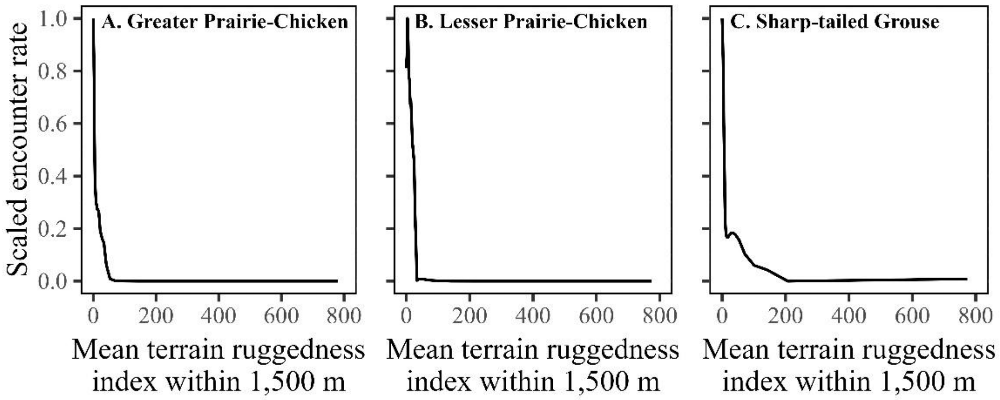


Figure 1.4. Partial dependence plots for the mean terrain ruggedness index within 1,500 m as predicted by Random Forests models predicting the encounter rates of three species of prairie grouse using eBird observations: greater prairie-chicken (**A**), lesser prairie-chicken (**B**), and sharp-tailed grouse (**C**) in North America (2010–2023).

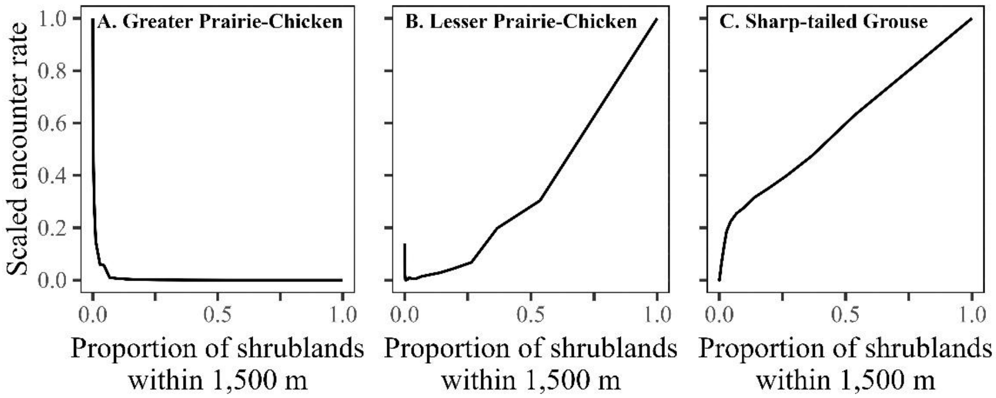


Figure 1.5. Partial dependence plots for the proportion of shrublands within 1,500 m as predicted by Random Forests models predicting the encounter rates of three species of prairie grouse using eBird observations: greater prairie-chicken (**A**), lesser prairie-chicken (**B**), and sharp-tailed grouse (**C**) in North America (2010–2023).

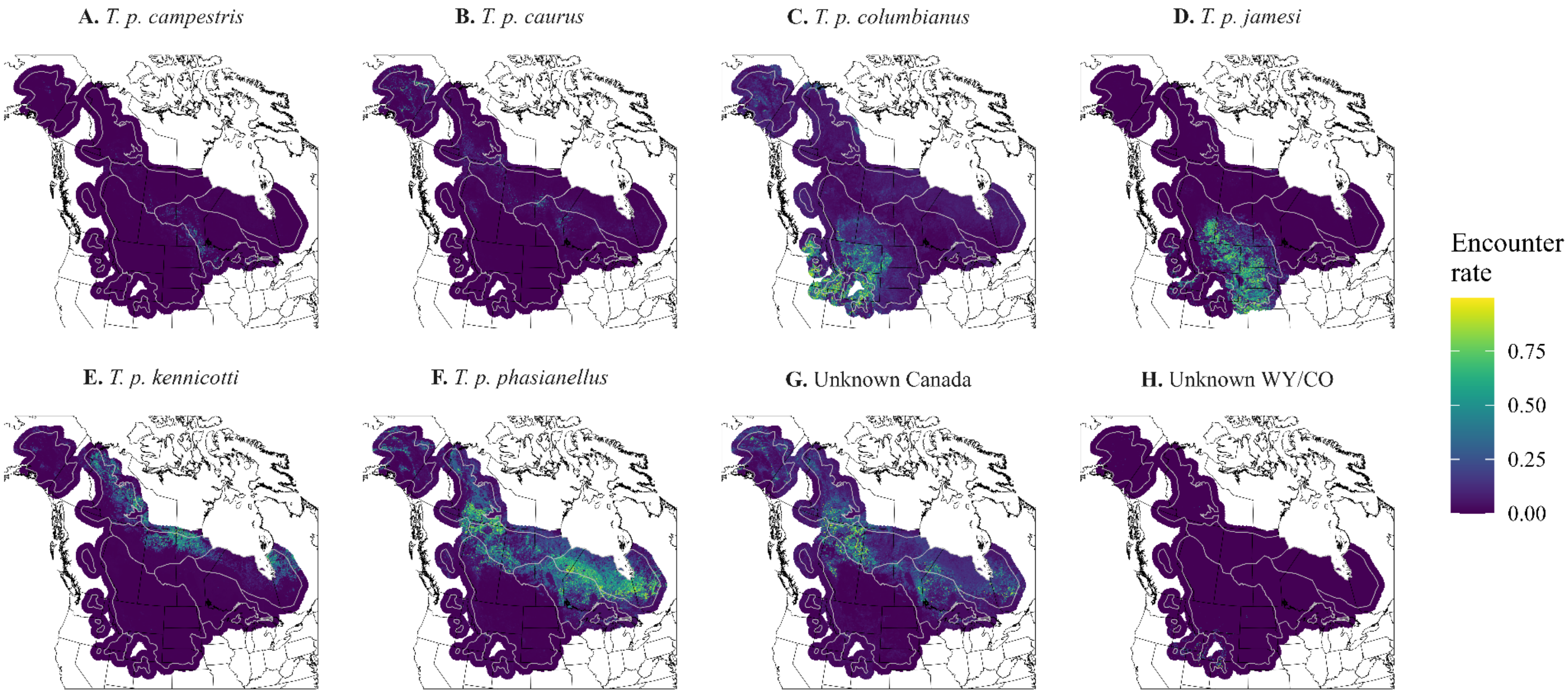


Figure 1.6. Predicted encounter rate based on eBird observations generated using Random Forests models based on land cover and topographic features for eight populations/subspecies of sharp-tailed grouse: *Tympanuchus phasianellus campestris* (**A**), *T. p. caurus* (**B**), *T. p. columbianus* (**C**), *T. p. jamesi* (**D**), *T. p. kennicotti* (**E**), *T. p. phasianellus* (**F**), a population with unknown subspecies in Canada (**G**), and a population with unknown subspecies in Wyoming/Colorado (**H**) across the range of sharp-tailed grouse in North America. Cooler colors represent lower probability of encountering the species and warmer colors represent greater probability of encountering the species; white border represents the published ranges of the different populations.

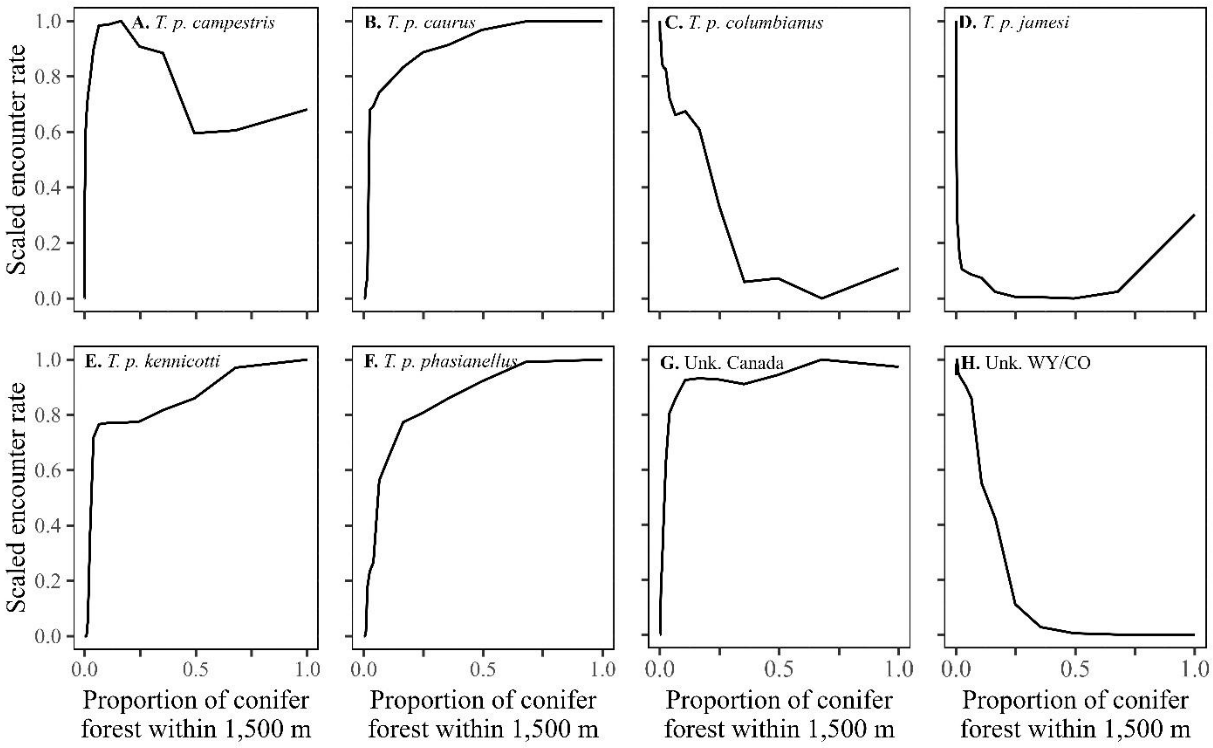


Figure 1.7. Partial dependence plots for the proportion of conifer forest within 1,500 m as predicted by Random Forests models predicting the encounter rates of eight populations of sharp-tailed grouse (*Tympanuchus phasianellus*) using eBird observations: *T. p. campestris* (**A**), *T. p. caurus* (**B**), *T. p. columbianus* (**C**), *T. p. jamesi* (**D**), *T. p. kennicotti* (**E**), *T. p. phasianellus* (**F**), a population with unknown subspecies in Canada (**G**), and a population with unknown subspecies in Wyoming/Colorado (**H**) across the sharp-tailed grouse range in North America (2010–2023).

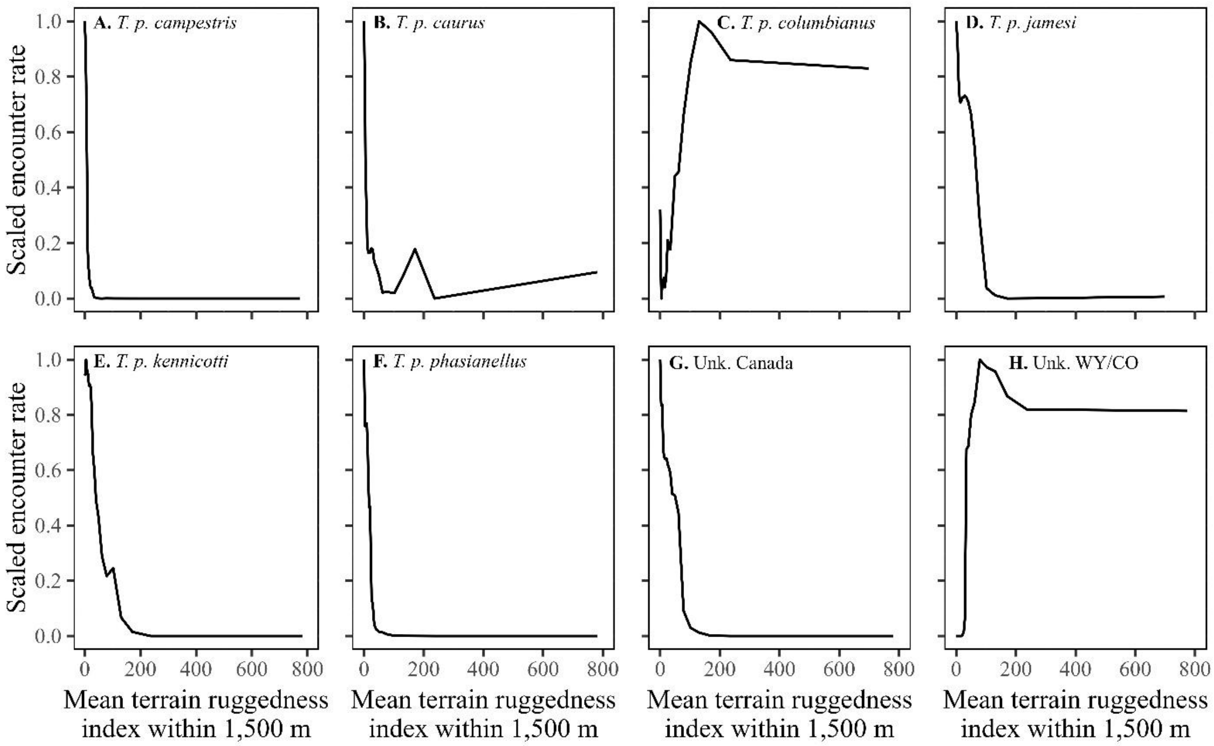


Figure 1.8. Partial dependence plots for the mean terrain ruggedness index within 1,500 m as predicted by Random Forests models predicting the encounter rates of eight populations of sharp-tailed grouse (*Tympanuchus phasianellus*) using eBird observations: *T. p. campestris* (**A**), *T. p. caurus* (**B**), *T. p. columbianus* (**C**), *T. p. jamesi* (**D**), *T. p. kennicotti* (**E**), *T. p. phasianellus* (**F**), a population with unknown subspecies in Canada (**G**), and a population with unknown subspecies in Wyoming/Colorado (**H**) across the sharp-tailed grouse range in North America (2010–2023).

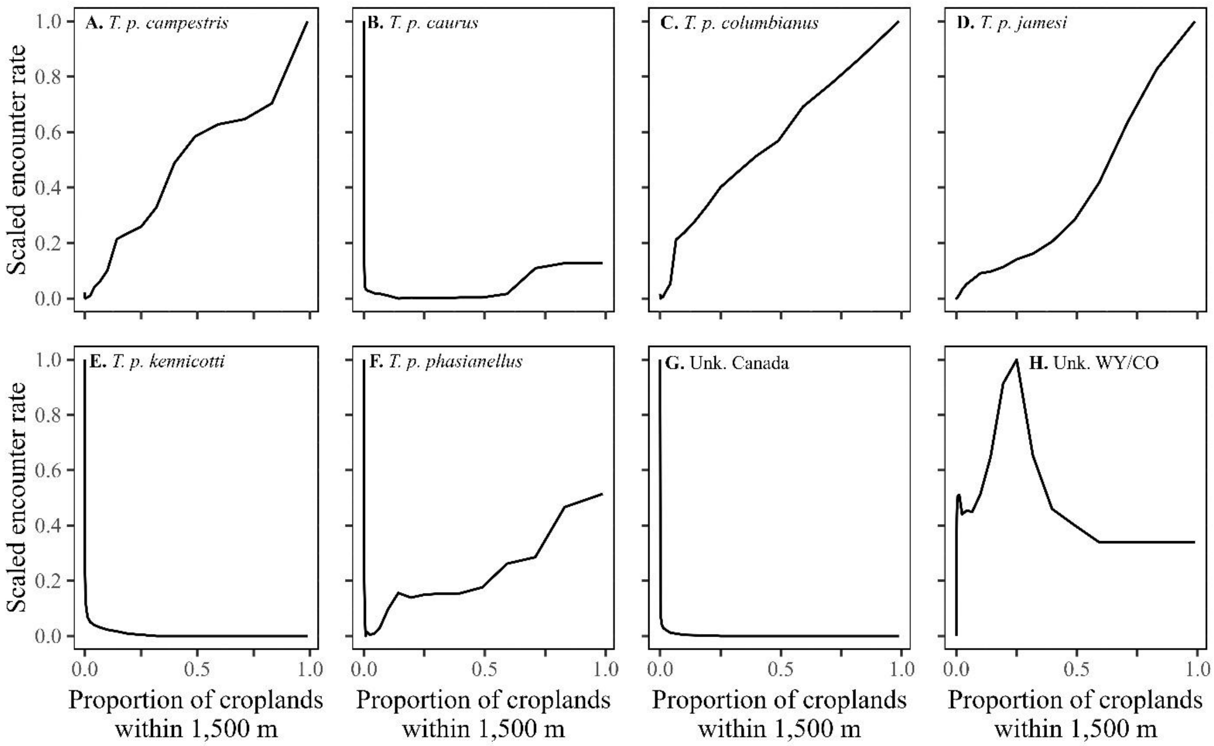


Figure 1.9. Partial dependence plots for the proportion of croplands within 1,500 m as predicted by Random Forests models predicting the encounter rates of eight populations of sharp-tailed grouse (*Tympanuchus phasianellus*) using eBird observations: *T. p. campestris* (**A**), *T. p. caurus* (**B**), *T. p. columbianus* (**C**), *T. p. jamesi* (**D**), *T. p. kennicotti* (**E**), *T. p. phasianellus* (**F**), a population with unknown subspecies in Canada (**G**), and a population with unknown subspecies in Wyoming/Colorado (**H**) across the sharp-tailed grouse range in North America (2010–2023).

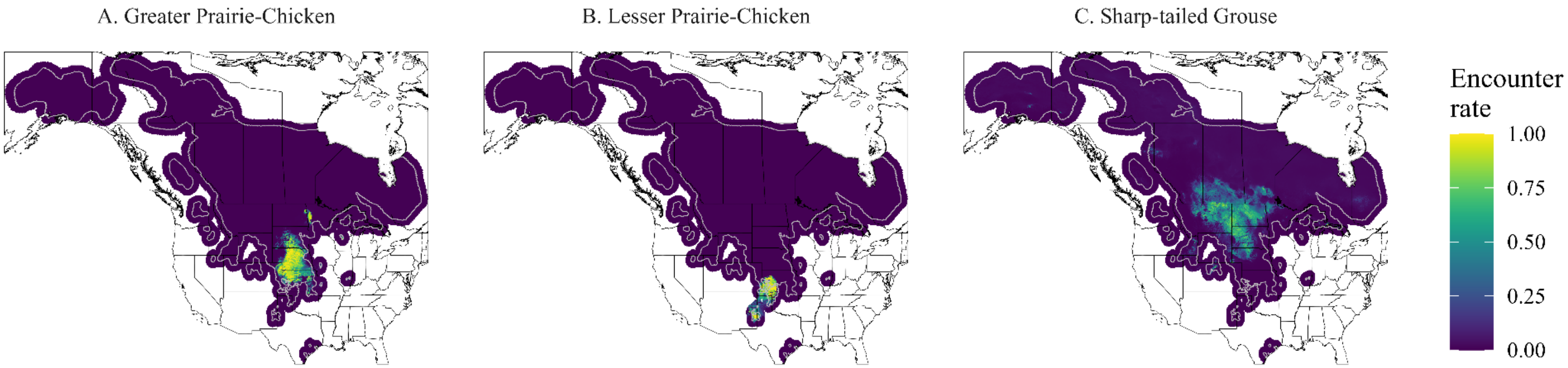


Figure 1.10. Predicted encounter rate based on eBird observations generated using Random Forests models based on current bioclimatic conditions for three species of grouse: greater prairie-chicken (**A**), lesser prairie-chicken (**B**), and sharp-tailed grouse (**C**) across the combined range of the three species in North America. Cooler colors represent lower probability of encountering the species and warmer colors represent greater probability of encountering the species; white border represents the combined described ranges of the three species.

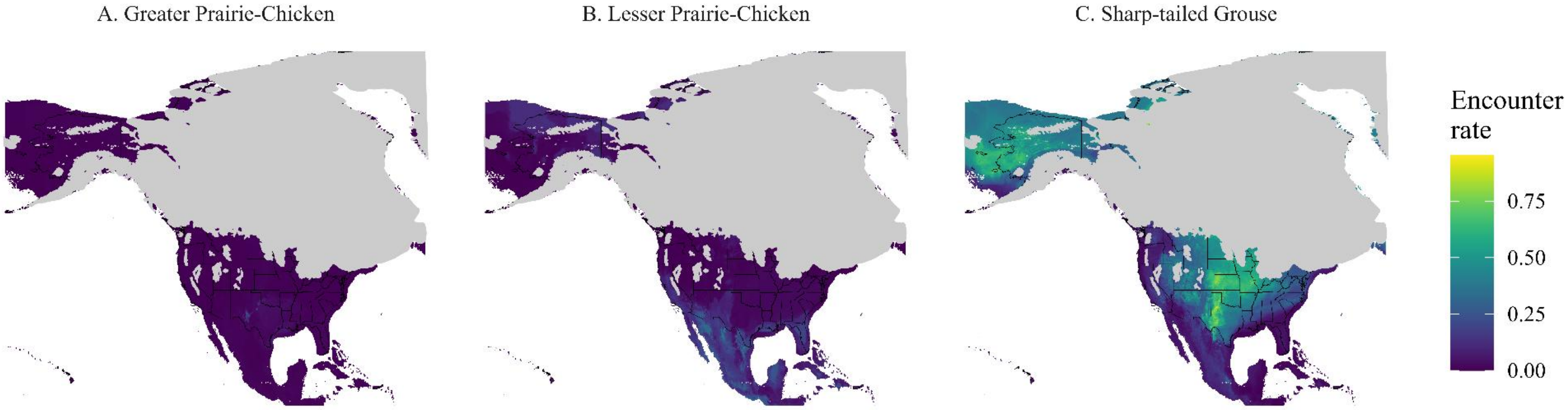


Figure 1.11. Predicted encounter rate based on eBird observations generated using Random Forests models based on bioclimatic conditions during the last glacial maximum (~21,000 ybp) for three species of grouse: greater prairie-chicken (**A**), lesser prairie-chicken (**B**), and sharp-tailed grouse (**C**) across the combined range of the three species in North America. Cooler colors represent lower probability of encountering the species and warmer colors represent greater probability of encountering the species; white border represents the combined described ranges of the three species.

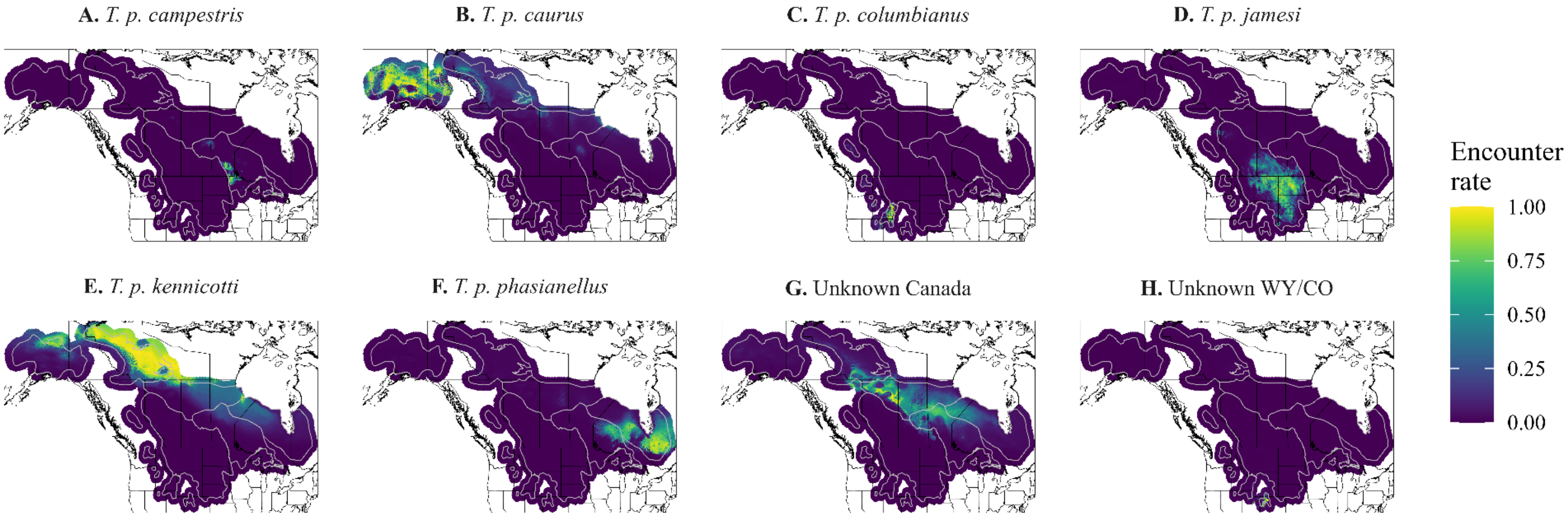


Figure 1.12. Predicted encounter rate based on eBird observations generated using Random Forests models based on current bioclimatic conditions for eight populations/subspecies of sharp-tailed grouse: *Tympanuchus phasianellus campestris* (**A**), *T. p. caurus* (**B**), *T. p. columbianus* (**C**), *T. p. jamesi* (**D**), *T. p. kennicotti* (**E**), *T. p. phasianellus* (**F**), a population with unknown subspecies in Canada (**G**), and a population with unknown subspecies in Wyoming/Colorado (**H**) across the range of sharp-tailed grouse in North America. Cooler colors represent lower probability of encountering the species and warmer colors represent greater probability of encountering the species; white border represents the published ranges of the different populations.

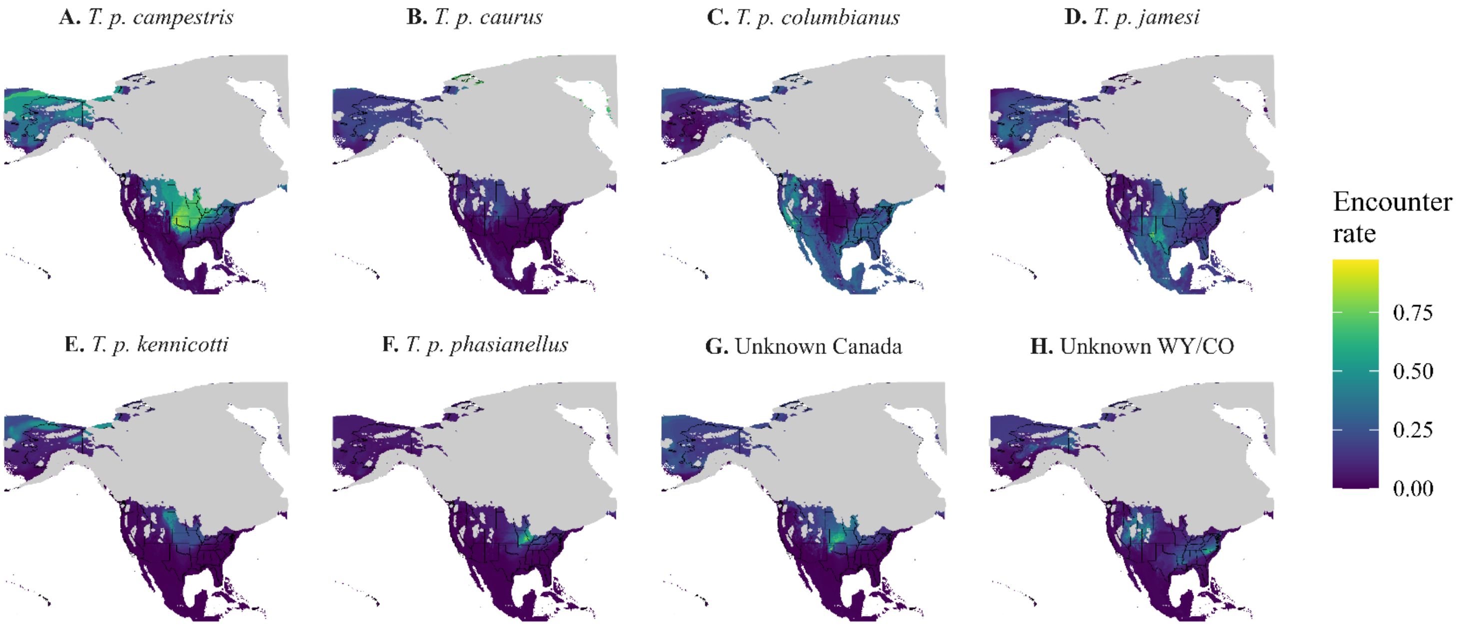


Figure 1.13. Predicted encounter rate based on eBird observations generated using Random Forests models based on bioclimatic conditions during the last glacial maximum (~21,000ybp) for eight populations/subspecies of sharp-tailed grouse: *Tympanuchus phasianellus campestris* (**A**), *T. p. caurus* (**B**), *T. p. columbianus* (**C**), *T. p. jamesi* (**D**), *T. p. kennicotti* (**E**), *T. p. phasianellus* (**F**), a population with unknown subspecies in Canada (**G**), and a population with unknown subspecies in Wyoming/Colorado (**H**) across the range of sharp-tailed grouse in North America. Cooler colors represent lower probability of encountering the species and warmer colors represent greater probability of encountering the species; white border represents the published ranges of the different populations.

CHAPTER TWO

Using habitat, morphological, and genetic characteristics to delineate the subspecies of Sharp-tailed Grouse in southcentral Wyoming

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ABSTRACT

Identifying species and subspecies is the foundation for focusing conservation efforts and studying evolutionary ecology. Subspecies delineation has occurred using multiple data types, including ecological, morphological, and genetic data. There are currently seven recognized Sharp-tailed Grouse (*Tympanuchus phasianellus*, Linnaeus, 1758) subspecies, with two of these subspecies occurring in Wyoming: Columbian Sharp-tailed Grouse (*T. p. columbianus*) and plains Sharp-tailed Grouse (*T. p. jamesi*). There is a third population of Sharp-tailed Grouse in south-central Wyoming with an unknown subspecific identification. Historically this population has been classified as Columbian Sharp-tailed Grouse, however previous genetic evidence questioned this classification. To better understand the subspecific status of this south-central Wyoming population, our study used habitat characteristics, morphological characteristics, and genetic data (microsatellite loci and single nucleotide variants) collected from known Columbian Sharp-tailed Grouse, known plains Sharp-tailed Grouse, and the south-central Wyoming population of Sharp-tailed Grouse. We modeled differences among the populations using discriminant analysis of principal components and Random Forests classification models. Across all four datasets and both modeling techniques, we found that each population (Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, and south-central Wyoming population of Sharp-tailed Grouse) generally represented its own cluster. Our results suggests that the population of Sharp-tailed Grouse in south-central Wyoming is different from both Columbian and plains Sharp-tailed Grouse. We recommend further evaluation of the subspecies of Sharp-tailed Grouse using more targeted phylogenomic studies to identify if Sharp-tailed Grouse in south-central Wyoming represent a separate subspecies or are a distinct population of another subspecies. Our results potentially change our understanding of Columbian Sharp-tailed Grouse distribution and management and highlight the importance of using a more comprehensive approach to identifying subspecies.

Key words: genetics, genomics, morphology, habitat, subspecies, Sharp-tailed Grouse, *Tympanuchus*

INTRODUCTION

Taxonomic classifications assist ecologists in measuring the distribution of biodiversity on a changing planet and enacting conservation actions. Infraspecific taxonomic classifications, or those below the rank of species (e.g., subspecies), are important in providing designations to conserve biodiversity into the future (Haig et al. 2006, Haig and D'Elia 2010, Winker 2010, Taylor et al. 2017b). Subspecies and other infraspecific classifications (e.g., ecotypes, varieties, distinct population segments, and evolutionary significant units) represent the diversity of functional traits—and therefore evolutionary potential—within a species (Haig et al. 2006) and conservation of subspecific taxa may help ensure species persistence in a changing environment (Winker 2010). This has been explicitly recognized by the Endangered Species Act as amended in 1978 (16 U.S.C. §§ 1532[16]) allowing listing of not just entire species but also subspecies, Distinct Population Segments, and Evolutionary Significant Units (NOAA 1991, USFWS 1996). Despite this recognition of the importance of infraspecific classification of organisms, there is still debate about what methods best describe significant intraspecific variation (Zink 2004, Haig et al. 2006, Remsen 2010, Winker 2010, Patten 2015).

Different approaches have been used to conceptualize and describe subspecies (Haig et al. 2006, Winker 2010). Some of the primary approaches used to describe subspecies have been based on ecology (e.g., the ecological and biological species concepts), morphology (e.g., the morphological species concept), and phylogeny (e.g., the phylogenetic species concept). Each of these species concepts have limitations associated with the application to define subspecies. For example, within the ecological species concept, populations may inhabit different habitats, but may not be distinguishable in terms of genetics or morphology; within the morphological species concept, morphological differences in subspecies may not represent genetic differences (Zink 1989, Ball and Avise 1992, Zink 2004, Haig et al. 2006); and the phylogenetic species concept recognizes species as the smallest supported monophyletic unit, but groupings within species (e.g., subspecies) do not exist (Haig et al. 2006). Because of these issues, some authors suggest using multiple species concepts to define and assess the validity of subspecies (Helbig et al. 2002, Haig et al. 2006, Wallin et al. 2017), though some recent studies have used or suggested the use of phylogenetics (Archer et al. 2017, Taylor et al. 2017a, Nevard et al. 2020, Ferrante et al. 2022, Black et al. 2024). One generally accepted rule for demarcating subspecies is the “75%

rule," where 75% of individuals in a population are identifiable from ≥99% of overlapping populations (Amadon 1947, Patten and Unitt 2002, Patten 2010, Winker 2010, Taylor et al. 2017b), however there are multiple different methods to identify which individuals are different from overlapping populations. Utilizing multiple subspecies concepts and having a unified approach to identifying individuals that differ from overlapping populations across different subspecies concepts might lead to a more unified understanding of subspecies delineations.

North American prairie grouse (genus *Tympanuchus*) are a recently diverged group of three species of Galliformes (Greater Prairie-Chicken [*T. cupido*, Linnaeus, 1758], Lesser Prairie-Chicken [*T. pallidicinctus*, Ridgway, 1873], and Sharp-tailed Grouse [*T. phasianellus*, Linnaeus, 1758]) found throughout portions of the grasslands and shrublands of Canada and the United States (Galla and Johnson 2015, DeYoung and Williford 2016). This group represents a unique opportunity to study species and subspecies classifications given their recent diversification (Galla and Johnson 2015, Black et al. 2024). Sharp-tailed Grouse are of special interest, given the recognition of six extant subspecies and one extinct subspecies (Spaulding et al. 2006, Oyler-McCance et al. 2010, Connelly et al. 2024). The six extant subspecies of Sharp-tailed Grouse are primarily differentiated geographically (e.g., Continental Divide and the Red River in Minnesota, North Dakota, and Manitoba), with slight differences in morphology and habitat use (Johnsgard 2016, Connelly et al. 2024). Some populations having no clear definition for their subspecies status (Spaulding et al. 2006). One population of Sharp-tailed Grouse in south-central Wyoming and northwestern Colorado has mixed support (genetic and morphological) for it belonging to two different subspecies of Sharp-tailed Grouse: Columbian (*T. phasianellus columbianus*, Ord, 1815) and plains (*T. p. jamesi*, Lincoln, 1917; Spaulding et al. 2006, Connelly et al. 2024). Columbian Sharp-tailed Grouse are of conservation interest, given they now occupy <10% of their historical range (Miller and Graul 1980, Hoffman et al. 2015) and they have been petitioned for listing under the Endangered Species Act of 1973 on two occasions (USDI 2000, 2006). Identifying the subspecies of Sharp-tailed Grouse for the population in south-central Wyoming will provide a map for future identification of populations to subspecies and important information to practitioners for conservation.

The goal of our research was to apply ecological (i.e., habitat association), morphological, and genetic conceptual approaches to identify the subspecies of Sharp-tailed Grouse inhabiting south-central Wyoming (hereafter, unknown Sharp-tailed Grouse). Through using multiple lines of evidence, we aimed to provide a robust assessment of which subspecies the unknown Sharp-tailed Grouse population assigns to. We used ecological (i.e., habitat) characteristics, morphological variation, and genetic differentiation to test three hypotheses regarding the unknown Sharp-tailed Grouse population: 1) the population assigns to Columbian Sharp-tailed Grouse, 2) the population assigns to plains Sharp-tailed Grouse, and 3) the population does not assign to either Columbian or plains Sharp-tailed Grouse. We compared habitat characteristics, morphological characteristics, nuclear DNA microsatellite loci, and single nucleotide variants (SNVs, including insertions and deletions) derived from low-resolution whole genome resequencing data between three groups of Sharp-tailed Grouse namely: known Columbian Sharp-tailed Grouse from the nearest population in southeastern Idaho, known plains Sharp-tailed Grouse from the nearest population in eastern Wyoming, and unknown Sharp-tailed Grouse in south-central Wyoming. We included Lesser Prairie-Chicken, a closely related species within the genus *Tympanuchus*, as an outgroup to help provide discriminatory power for our analyses. Outgroups serve as a reference group for the groups that are being evaluated and are less related to the groups being evaluated than the groups being evaluated are to each other.

Using Lesser Prairie-Chicken as an outgroup allowed us to compare Sharp-tailed Grouse populations to a related organism to better understand the differences in habitat characteristics, morphological characteristics, and single nucleotide variant data; we were not able to collect microsatellite data from Lesser Prairie-Chickens and we did not include an outgroup in our microsatellite analyses.

METHODS

To evaluate the subspecies of Sharp-tailed Grouse in south-central Wyoming, we used four different datasets: habitat data, morphological data, and two genetic datasets (microsatellite genotype data and low-resolution genome-wide single nucleotide variants [SNVs, including insertion and deletions] data). We collected data on four populations of grouse: Lesser Prairie-Chicken, Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse. To evaluate differences in habitat associations, we used occurrence locations from eBird, a citizen-science database (Sullivan et al. 2009, eBird 2023). Morphological data and genetic samples for Lesser Prairie-Chickens were collected at four different study areas in western Kansas and southeastern Colorado from 2013–2017; detailed descriptions of these study areas can be found in Lautenbach et al. (2019; Figure 1). We attempted to collect morphological and genetic samples from the populations of Columbian and plains Sharp-tailed Grouse closest to our focal population in south-central Wyoming because these are the areas that unknown Sharp-tailed Grouse potentially interacted with in the past. Morphological data for Columbian Sharp-tailed Grouse were collected from areas throughout Idaho and Washington in 2005–2012 (Figure 1). Genetic samples for Columbian Sharp-tailed Grouse were collected in eastern Idaho in 2019 as well three samples from western Wyoming in Grand Teton National Park in 2013, 2016, and 2021. Morphological and genetic data for Columbian Sharp-tailed Grouse were collected during different years and from different locations because we were not able to collect morphological data for Columbian Sharp-tailed Grouse and we were only able to obtain morphological data from a previous study (Schroeder et al. 2023). We obtained genetic samples for Columbian Sharp-tailed Grouse from hunter harvested wings (eastern Idaho) or road killed specimens (Grand Teton National Park). We collected morphological data and genetic samples for plains Sharp-tailed Grouse in eastern Wyoming in Laramie and Goshen counties in 2019. We collected morphological data and genetic samples for unknown Sharp-tailed Grouse in western Carbon County, Wyoming from 2017–2019.

Genetic and Morphological Field Data Collection

DNA collection techniques varied depending on the population. We captured Lesser Prairie-Chicken, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse and collected blood samples from captured birds and stored these samples for latter DNA extraction. We captured Lesser Prairie-Chickens and plains and unknown Sharp-tailed Grouse at leks using walk-in funnel traps (Haukos et al. 1990; Schroeder and Braun 1991) and drop nets (Lesser Prairie-Chickens only; Silvy et al. 1992). Upon capture, we collected blood via syringe from the ulnar vein or clipped the toenail of the helix toe to obtain a small sample of blood (10–30 µL). Blood samples for Lesser Prairie-Chickens were stored in 700 µL lysis buffer (Longmire et al. 1997) and then frozen at -20 °C. Blood samples for plains and unknown Sharp-tailed Grouse were stored on Whatman FTA Micro Cards (GE Healthcare, Chicago, IL, USA) at room temperature. We collected morphological measurements from the birds we captured on leks including culmen length (mm), head length (mm), mass (g), tail (mm), tarsus + longest toe (mm), and wing cord (mm). For Columbian Sharp-tailed Grouse, we collected DNA samples from tissue from hunter harvested wings (eastern Idaho) or breast tissue from road-killed birds (Grand Teton Nation

Park, Wyoming). We obtained morphological measurements from Columbian Sharp-tailed Grouse captured during spring for another project (Schroeder et al. 2023); morphological measurements from Columbian Sharp-tailed Grouse included mass (g), tail (mm), tarsus + longest toe (mm), and wing cord (mm). Capturing and handling techniques for Lesser Prairie-Chickens were approved by the Kansas State University Institutional Animal Care and Use Committee (protocol numbers 3241 and 3703), Kansas Department of Wildlife, Parks, and Tourism (scientific collection permit numbers SC-042-2013, SC-079-2014, SC-001-2015, and SC-014-2016), and Colorado Parks and Wildlife (scientific collection license numbers 13TRb2053, 14TRb2053, and 15TRb2053). Capture and handling techniques for plains and unknown Sharp-tailed Grouse were approved by the University of Wyoming Institutional Animal Care and Use Committee (protocol 20170324AP00266 [versions -01, -02, and -03]) and by the Wyoming Game and Fish Department (Chapter 33 permits 1098 and 1214).

Genetic Methods

We extracted DNA from blood and muscle samples using the Omega E.Z.N.A. Tissue DNA extraction kit (D3396; Omega Bio-Tek, Norcross, GA, USA). For muscle tissue, we finely chopped up ~30 g of muscle tissue and followed the manufactures protocol. For blood samples stored on FTA micro cards, we used approximately 0.25–0.50 cm^2 of blood on the Whatman card, finely chopped the card and let it soak in Longmire's lysis buffer (Longmire et al. 1997) for ≥ 4 hours. Following lysis, we followed the manufactures protocol for the remainder of the extraction process.

Microsatellite genotyping—Once DNA was extracted, we amplified nine microsatellite loci using polymerase chain reaction (PCR). The nine microsatellite loci we amplified were ADL230 (Cheng and Crittenden 1994), BG16 (Piertney and Höglund 2001), LLSD7 (Piertney and Dallas

1997), LLST1 (Piertney and Dallas 1997), SG MS6.6 (Oyler-McCance and St. John 2010), SG MS6.8 (Oyler-McCance and St. John 2010), SG28 (Fike et al. 2015), TTD6 (Caizergues et al. 2001), and TUT4 (Segelbacher et al. 2000). We conducted PCR in a 12.5 μL solution, including 0.0025 nmoles forward primer, 0.0025 nmoles reverse primer, 0.0015 nmoles M13 primer, 10ng of DNA template, and 6.25 μL of GoTaq G2 Master Mix (Promega, Madison, WI, USA). We used the published PCR amplification protocols for each primer.

Whole genome resequencing—We used low resolution whole genome resequencing using single strand sequencing technologies from the third-generation sequencing platform MinION (Oxford Nanopore Technologies, Oxford, UK). We used the native barcoding kit SQK-LSK109 with barcoding expansions EXP-NBD104 and EXP-NBD114 for ligation sequencing on genomic DNA. We followed the manufactures protocols for library preparation and MinION platform sequencing. We sequenced the libraries on R9.4.1 FlowCells and Flongles. We conducted base calling using *dorado* v0.3.3 within the MinKNOW software set to *super accurate* base calling. We aligned sequence reads to the Lesser Prairie-Chicken genome (Black et al. 2023) using *minimap2* (Li 2018), indexed sequence reads using *samtools* version 1.17 (Danecek et al. 2021), and used *clair3* (Zheng et al. 2022) to call single nucleotide variants (i.e., SNVs, including insertions and deletions) at a read depth of ≥2X coverage. We used the *merge* tool within the *bcftools* version 1.13 (Danecek et al. 2021) to merge single nucleotide variants across all individuals and exported as a VCF file. After we merged all single nucleotide variants, we imported the VCF file into Program R version 4.4.1 (R Core Team 2024) and converted the VCF file to a GDS file using the *SNPRelate* package (Zheng et al. 2012). We then used the *snpgdsLDpruning* function within the *SNPRelate* package in Program R (Zheng et al. 2012, R Core Team 2024) to prune markers based on linkage disequilibrium, percent missingness, and minor allele frequency. We used the *composite* method built into the *snpgdsLDpruning* function and set the missing rate to 33.33%, minor allele frequency to 0.5%, a pruning window of 50 KB, and the *ld.threshold* set to 0.4 resulting in 453 single nucleotide variants used in our analyses.

Statistical Analysis

General statistical methods—To evaluate if there were differences between our three focal populations of Sharp-tailed Grouse and an out group for our ecological characteristics (i.e., habitat), morphological characteristics, microsatellite loci, and SNVs datasets we conducted two main analyses: 1) discriminant analysis of principal components (DAPC; Jombart et al. 2010) and 2) a Random Forests classification model (Breiman 2001). The DAPC facilitated comparing different characteristics (e.g., environmental conditions, morphological measurements, microsatellite loci, or SNVs) among populations and to assign a probability of each individual bird or observation to each population based on those characteristics. We used the *xvalDapc* and *dapc* functions in the *adegenet* package in Program R (Jombart 2008, Jombart and Ahmed 2011, R Core Team 2024). Random Forests models have been used to classify subspecies using genetic data (Archer et al. 2017) but Random Forests models can also be used to classify other similar datasets. We used the *randomForest* package (Liaw and Weiner 2002) in Program R (R Core Team 2024) to run our Random Forests models. We ran Random Forests models with 10,000 trees for each forest built and models were run with replacement. To understand the importance of variables (e.g., environmental conditions and morphological measurements) contributing to the habitat association and morphological Random Forests models, we standardized variable importance values so the top variable equaled 1 and the remaining variables were proportions derived by dividing by the top variable (Doherty et al. 2018).

Habitat association analyses—To compare ecological (habitat use) differences between populations, we used DAPC and Random Forests classification models to compare environmental conditions at eBird observation locations of focal populations. To obtain eBird observation locations across the occupied ranges Sharp-tailed Grouse and Lesser Prairie-Chickens in the United States, we used eBird checklists (eBird 2023) with confirmed observations for each species. We removed duplicate observations from the database prior to analyzing eBird data. For Sharp-tailed Grouse observations, we categorized each location to a subspecies or population (Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse) based on the published ranges of each subspecies (Spaulding et al. 2006, Galla and Johnson 2015) and we used all locations for Lesser Prairie-Chickens as our outgroup. We only used observations on checklists from January 2010–October 2023. We filtered checklist data according to data use recommendations for using eBird data (Johnson et al. 2021, Strimas-Mackey et al. 2023a); this included limiting checklists to complete checklists, checklists with distances < 5 km, < 6 hours long, < 10 observers, and checklist speeds < 100 kmph (Johnson et al. 2021, Strimas-Mackey et al. 2023a; see Figure 1 for map of observation locations for each population). To obtain environmental data at use locations, we used readily available remotely sensed environmental data. We obtained annual data (30-m resolution) for annual herbaceous vegetation (biomass and cover), perennial herbaceous vegetation (biomass and cover), bare ground, litter, coniferous forest canopy cover, deciduous forest canopy cover, mixed forest canopy cover, unclassified forest canopy cover, and shrub cover from the Rangeland Analysis Platform (RAP; Robinson et al. 2019, Allred et al. 2021, Jones et al. 2021). We obtained National Land Cover Database layers (NLCD; 30-m resolution; Jin et al. 2019) from 2011, 2013, 2016, 2019, and 2021; from each of these layers, we created multiple binary landcover layers including croplands, developed lands, emergent wetland, pasture, and water. We obtained general climate data including 30-year average maximum temperature and 30-year average precipitation from PRISM data (800-m resolution; PRISM Climate Group 2014). We obtained topographic data from a 30-m resolution digital elevation model (DEM, USGS 2011). From the DEM, we calculated heat load index, terrain ruggedness index, and topographic position index using the *hli*, *tri*, and *tpi* functions in the *spatialEco* package in Program R (Riley et al. 1999, McCune and Keon 2002, McCune 2007, De Reu et al. 2013, Evans and Murphy 2023, R Core Team 2024). We resampled all 30-m grain data to 800 m using the *aggregate* and *project* functions in the package *terra* (Hijmans 2024) in Program R version 4.4.1 (R Core Team 2024) to enable comparison across all ecological covariates. Because eBird locations are not precise, we followed recommendations to use environmental variables averaged over a 1,500-m radius surrounding locations (Strimas-Mackey et al. 2023a). To accommodate the imprecise locations from eBird, we used a 1,600-m moving window analysis using the *focalMat* and *focal* functions in the *terra* package (Hijmans 2024) in Program R version 4.4.1 (R Core Team 2024) to get average available conditions within 1,600 m of each cell and extracted the average within each cell at each observation location. Once we extracted the environmental covariates to the eBird checklist locations, we ensured that the year for the environmental data was aligned with the year of the checklist (Jan–Dec) by aligning checklists year with year of environmental data (e.g., for checklists from Jan–Dec 2020 we used 2020 RAP). Because NLCD data was not available annually, we aligned checklists from 2010–2011 to 2011 NLCD data, checklists from 2012–2014 to 2013 NLCD data, checklists from 2015–2017 to 2016 NLCD data, checklists from 2018–2020 to 2019 NLCD data, and checklists from 2021–2023 to 2021 NLCD data. We then used a DAPC and a Random Forests model to compare environmental conditions between populations and assign a probability of each individual to each population based on habitat characteristics. To understand the differences in general habitat characteristics between populations, we used a Kruskal-Wallis test ($\alpha = 0.05$) and a pairwise Wilcox test ($\alpha = 0.05$) on the six most important environmental characteristics identified in the Random Forests model.

Morphological analyses—To evaluate if there were differences in morphological characteristics between Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, unknown Sharp-tailed Grouse, and Lesser Prairie-Chicken we used a Kruskal-Wallis test ($\alpha = 0.05$) and a pairwise Wilcox test ($\alpha = 0.05$) to evaluate which populations differed from each other. When evaluating morphological differences, we only used males from all populations because males and females differ in size. To evaluate if there were any differences between the four populations in the morphological spaces they occupied, we ran three different DAPCs models and three different Random Forests models. For both the DAPC analyses and the Random Forests models, the three models we ran were 1) an analysis on all four groups including mass, 2) an analysis on all four groups excluding mass, as mass can fluctuate during a season and between seasons, and 3) an analysis on only plains Sharp-tailed Grouse, unknown Sharp-tailed Grouse, and Lesser Prairie-Chicken excluding mass. We included mass in one of our analyses because, generally, Columbian Sharp-tailed Grouse are generally described as being smaller while plains Sharp-tailed Grouse are generally described as being larger (Connelly et al. 2024) and including mass would help evaluate this. We ran the final analysis on only these three populations because we could include more morphological characteristics that were collected on all three of those populations. Specifically, for the first model including mass (all four populations), we included tail length, wing cord length, tarsus + longest toe length, mass, and all pairwise comparisons for a total of ten covariates. For the second model excluding mass (all four populations) we included tail length, wing cord length, tarsus + longest toe length, and all pairwise comparisons for a total of six covariates. For the final model (three populations: Lesser Prairie-Chicken, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse), we included wing cord length, culmen length, total head length, tarsus + longest toe length, tail length, and all pairwise combinations for a total of 15 covariates.

Microsatellite analyses—We scored microsatellite fragments using Geneious Prime 2022.2.2 software (https://www.geneious.com) to create an individual genetic profile for each individual. We conducted a standard assessment of microsatellite marker suitability for genetic analyses that included tests for Hardy-Weinberg Equilibrium (HWE) calculated using the *hw.test* function from the *pegas* package in Program R (Paradis 2010, R Core Team 2024), allelic richness for each population calculated using the *allel.rich* function in the *PopGenReport* package in Program R (Adamack and Gruber 2014, Gruber and Adamack 2015, R Core Team 2024), F_{ST} and F_{IS} using the *basic.stats* function from the *hierfstat* package in Program R (Goudet and Jombart 2022, R Core Team 2024), and expected heterozygosity (H_E) and observed heterozygosity (H_O) using the *summary* function in the *adegenet* package in Program R (Jombart 2008, Jombart and Ahmed 2011, R Core Team 2024). We checked for null alleles using the program MICRO-CHECKER (Van Oosterhout et al. 2004) and evaluated linkage disequilibrium using the *test_LD* function in the *genepop* package in Program R (Rousset 2008, R Core Team 2024).

Following the assessments of microsatellite suitability, we used a DAPC (Jombart et al. 2010) and a Random Forests model to evaluate if there was differentiation between the populations based on microsatellite loci. We included all loci that fit the criteria that we outlined above. We only included genotype data for our in-group populations (i.e., Sharp-tailed Grouse, not Lesser Prairie-Chicken).

Whole genome resequencing analyses—We calculated observed heterozygosity (H_E), subpopulation heterozygosity (H_S), and inbreeding coefficient (F_{IS}) for each population using the *gl.basic.stats* function in the *dartR* package in Program R (Gruber et al. 2018, Mijangos et al. 2022, R Core Team 2024). We calculated pairwise proportional genetic variance (F_{ST}) using the *stamppFst* function in the *StAMPP* package in Program R (Pembleton et al. 2013, R Core Team 2024). To evaluate the subspecies classification of our populations using SNVs identified above, we used a DAPC analysis and a Random Forests classification model. We used these models to compare SNVs across individuals and assign the probability of identification of each individual to each population. Once common SNVs were identified across sequenced individuals, we removed duplicate SNVs from the dataset. We obtained sequencing data from individuals in all in-group populations (Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, unknown Sharp-tailed Grouse) and our outgroup (Lesser Prairie-Chickens). We ran the DAPC and Random Forests model with SNVs identified to fit the criterion after pruning. For the Random Forests model, because there were missing values in the data set, we used the *rfImpute* function from within the *randomForest* package in Program R (Liaw and Weiner 2002, R Core Team 2024) to impute missing values. We conducted the DAPC and Random Forests analyses on all of the populations and only the Sharp-tailed Grouse populations because our sample size for Lesser Prairie-Chickens was small ($n = 2$).

RESULTS

We obtained 812 eBird checklist locations with Columbian Sharp-tailed Grouse observations, 7,951 eBird checklist locations with plains Sharp-tailed Grouse observations, 509 eBird checklist locations with unknown Sharp-tailed Grouse observations, and 1,628 eBird checklist locations with Lesser Prairie-Chicken observations (

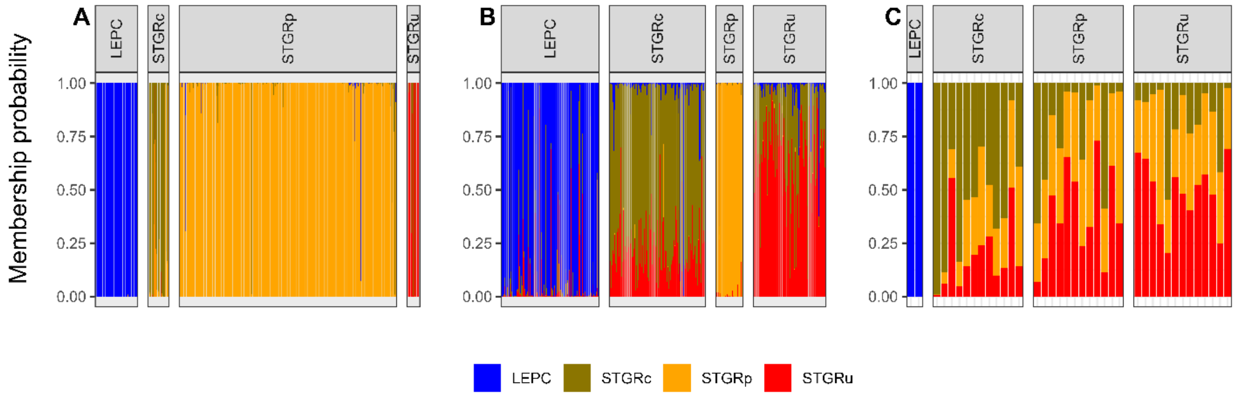

Figure A1 Figure A1). We obtained morphological measurements from males for 219 Columbian Sharp-tailed Grouse, 64 plains Sharp-tailed Grouse, 165 unknown Sharp-tailed Grouse, and 223 Lesser Prairie-Chicken. We obtained genotype results from nine microsatellite loci from 53 Columbian Sharp-tailed Grouse, 32 plains Sharp-tailed Grouse, and 175 unknown Sharp-tailed Grouse. We identified 1,750 single nucleotide variants (SNVs) with <33.3% missing data; after pruning, we obtained 453 SNVs from 12 Columbian Sharp-tailed Grouse, 12 plains Sharp-tailed Grouse, 13 unknown Sharp-tailed Grouse, and 2 Lesser Prairie-Chickens to use for analysis. While Lesser Prairie-chicken provided discriminatory power as our outgroup (see Appendix A), here we only present results for our in-group populations of Sharp-tailed Grouse.

Habitat associations—Using a DAPC analysis on environmental conditions surrounding observed locations, we found that the model was able to correctly predict 65.6% of Columbian Sharp-tailed Grouse, 98.8% of plains Sharp-tailed Grouse, and 87.2% of unknown Sharp-tailed Grouse (Table 2.1, Figure 2.2A). The largest proportion of the average membership probability for each population was identified as the original population of the observation (Table 2.2). The population with the lowest average membership probability for the population of origin was

Columbian Sharp-tailed Grouse, with an average membership probability of individuals of 65.5% Columbian Sharp-tailed Grouse, 24.9% plains Sharp-tailed Grouse, and 9.5% unknown Sharp-tailed Grouse (Table 2.2). In general, Columbian Sharp-tailed Grouse occupied a principal component space that overlapped both plains and unknown Sharp-tailed Grouse; unknown and plains Sharp-tailed Grouse did not overlap in principal component space (Figure 2.3A). Our Random Forests model evaluating habitat characteristics for three Sharp-tailed Grouse populations was able to correctly classify 93.6% of Columbian Sharp-tailed Grouse, 100% of plains Sharp-tailed Grouse, and 98.0% of unknown Sharp-tailed Grouse (Table 2.5). The three habitat characteristics with the highest importance in the Random Forests model were percent cover of shrubs (1.00), terrain ruggedness index (0.27), and heat load index (0.22; Table 2.6 and Figure 2.6).

Morphology—Using morphological measurements from the three Sharp-tailed Grouse populations, we found that there was a difference in average tail length between populations (χ^2_2 = 23.37, $P \leq 0.001$). Columbian (mean = 109.59 mm, SD = 4.55 mm) and unknown Sharp-tailed Grouse (mean = 110.58 mm, SD = 5.92 mm) had the shortest tail lengths that did not differ from each other (P = 0.09) and plains Sharp-tailed Grouse had the longest tails (mean = 112.87 mm, SD = 7.05 mm; Figure 2.4A). Wing cord length differed between populations (χ^2_2 = 98.31, $P \leq 0.001$). Unknown Sharp-tailed Grouse had the shortest wing cord length (mean = 209.58 mm, SD = 4.02 mm), Columbian Sharp-tailed Grouse (mean = 211.53 mm, SD = 3.82 mm) had intermediate wing cord lengths, and plains Sharp-tailed Grouse had the longest wing cord lengths (mean = 216.59 mm, SD = 5.11 mm; Figure 2.4B). We found that tarsus + longest toe length differed between the populations (χ^2_2 = 274.68, $P \leq 0.001$). Columbian Sharp-tailed Grouse had the shortest tarsus + longest toe length (mean = 90.95 mm, SD = 2.41 mm), unknown Sharp-tailed Grouse (mean = 96.74 mm, SD = 2.91 mm) had intermediate tarsus + longest toe length, and plains Sharp-tailed Grouse had the longest tarsus + longest toe length (mean = 98.00 mm, SD = 2.74 mm; Figure 2.4C). We found that mass differed between the three populations (χ^2_2 = 180.15, $P \leq 0.001$) with Columbian Sharp-tailed Grouse having the lowest mass (mean = 741.80 g, SD = 35.03 g), unknown Sharp-tailed Grouse having intermediate mass (mean = 758.92 g, SD = 34.91 g), and plains Sharp-tailed Grouse had the greatest mass (mean = 930.05 g, SD = 40.77 g; Figure 2.4D).

Using a discriminant analysis of principal components (DAPC) on morphological characteristics including mass on all populations, we found that this model correctly predicted the population in 79.9% of all instances for Columbian Sharp-tailed Grouse, 96.8% of all instances for plains Sharp-tailed Grouse, and 60.0% of all instances for unknown Sharp-tailed Grouse (Table 2.1, Figure 2.2B). The largest proportion of the average membership probability for individuals in each population was identified as the original population of each individual (Table 2.2). The population with the lowest average membership probability for the population of origin was unknown Sharp-tailed Grouse, with an average membership probability of individuals of 42.6% Columbian Sharp-tailed Grouse, 0.2% plains Sharp-tailed Grouse, and 57.2% unknown Sharp-tailed Grouse (Table 2.2). In general, the morphological spaces of Columbian Sharp-tailed Grouse and unknown Sharp-tailed Grouse occupied similar spaces while plains Sharp-tailed Grouse occupied their own principal components space (Figure 2.3B). Our Random Forests model evaluating four populations including mass was able to correctly classify 93.6% of Columbian Sharp-tailed Grouse, 98.5% of plains Sharp-tailed Grouse, and 89.1% of unknown Sharp-tailed Grouse (Table 2.5). The three morphological characteristics of the highest importance in the Random Forests model were tarsus + longest toe length (1.00), wing cord length to tarsus + longest toe length ratio (0.84), and mass (0.50; Table 2.7).

When excluding mass from the DAPC analysis on all populations, we found that the model was able to correctly predict the population in 94.1% of all instances for Columbian Sharp-tailed Grouse, 58.7% of all instances for plains Sharp-tailed Grouse, and 80.6% of all instances for unknown Sharp-tailed Grouse (Table 2.1, Figure 2.5A). The largest proportion of the average membership probability for individuals in each population was identified as the original population of each individual (Table 2.2). The population with the lowest average membership probability for the population of origin was plains Sharp-tailed Grouse, with an average membership probability for individuals of 14.2% Columbian Sharp-tailed Grouse, 50.7% plains Sharp-tailed Grouse, and 35.0% unknown Sharp-tailed Grouse (Table 2.2). In general, in this model excluding mass, plains Sharp-tailed Grouse and unknown Sharp-tailed Grouse occupied similar morphological spaces, while Columbian Sharp-tailed Grouse occupied a mostly unique morphological space (Figure 2.5B). Our Random Forests model evaluating four populations including mass correctly classified 91.3% of Columbian Sharp-tailed Grouse, 58.7% of plains Sharp-tailed Grouse, and 82.4% of unknown Sharp-tailed Grouse (Table 2.5). The three morphological characteristics of the highest importance in the Random Forests model were tarsus + longest toe length (1.00), the wing cord length to tarsus + longest toe length ratio (0.78), and wing cord length (0.40; Table 2.8).

Microsatellite Genotyping—The number of alleles at each loci varied (7–23; Table 2.3). Allelic richness in each population varied, with the highest average allelic richness occurring in the plains Sharp-tailed Grouse population (mean = 8.43), followed by Columbian Sharp-tailed Grouse (mean = 8.13), and unknown Sharp-tailed Grouse had the average lowest allelic richness (mean = 7.02; Table 2.3). Hardy-Weinberg exact tests indicated significant deviations from Hardy-Weinberg equilibrium expectations for several markers (Table 2.3). Deviations from Hardy-Weinberg equilibrium were expected given that our dataset includes individuals from multiple subspecies and populations that were separated by significant distances. Tests for linkage disequilibrium indicated linkage between several markers, however these markers were only significant in one population. In our Columbian Sharp-tailed Grouse population ADL230 and LLSD7 showed linkage ($P = 0.035$) and ADL230 and SGMS06.8 showed linkage ($P = 0.006$). For unknown Sharp-tailed Grouse, LLST1 and TUT4 showed linkage ($P = 0.017$). The markers LLST1 and TUT4 showed weak evidence of having null alleles present due to excess homozygotes for most allele classes as indicated by MICRO-CHECKER in our unknown Sharp-tailed Grouse population, likely due to latent population structure and likely to not influence our results (Van Oosterhout et al. 2006). In exploratory analyses removing either LLST1 or TUT4, our results did not change.

Using a DAPC analysis on genotype data from microsatellites, we found that the model was able to correctly predict the population 90.5% of the time for Columbian Sharp-tailed Grouse, 78.1% of the time for plains Sharp-tailed Grouse, and 98.3% of the time for unknown Sharp-tailed Grouse (Table 2.1; Figure 2.2C). The largest proportion of the average membership probability for individuals in each population was identified as the original population of each individual (Table 2.2). The population with the lowest average membership probability for the population of origin was plains Sharp-tailed Grouse, with an average membership probability for individuals of 5.5% Columbian Sharp-tailed Grouse, 77.6% plains Sharp-tailed Grouse, and 16.9% unknown Sharp-tailed Grouse (Table 2.2). In general, the principal components space of Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse were unique, with each species occupying their own spaces (Figure 2.3C). Our Random Forests model evaluating 9 microsatellites across all individuals genotyped was able to correctly classify 73.6% of Columbian Sharp-tailed Grouse, 31.2% of plains Sharp-tailed Grouse, and 98.3% of unknown Sharp-tailed Grouse (Table 2.5).

Whole Genome Resequencing— Diversity (H_O, H_S, F_{IS}) across our in-group (Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse) populations was low, but consistent across populations, with our out-group (Lesser Prairie-Chicken) showing lower diversity (Table 2.4). Pairwise genetic differentiation (F_{ST}) was low among our in-group populations, with greater differentiation between our in-group population and our out-group population (Table 2.4). Using a DAPC on low-resolution whole genome resequencing single nucleotide variant data, the model was able to correctly predict 91.7% of Columbian Sharp-tailed Grouse, 83.3% of plains Sharp-tailed Grouse, and 92.3% of unknown Sharp-tailed Grouse (Table 2.1, Figure 2.2D). All populations had a high proportion of the average membership probability (>85.0%) for individuals in each population identified as the original population of each individual (Table 2.2). In general, all three populations of Sharp-tailed Grouse occupied a unique principal component space (Figure 2.4D). Our Random Forests model evaluating 453 SNVs across all Sharp-tailed Grouse populations was able to correctly classify 41.7% of Columbian Sharp-tailed Grouse, 41.7% of plains Sharp-tailed Grouse, and 46.2% of unknown Sharp-tailed Grouse (Table 2.5).

DISCUSSION

Historically, Sharp-tailed Grouse subspecies have been demarcated using geographic boundaries (e.g., Continental Divide or the Red River in Minnesota, North Dakota, and Manitoba), differences in habitat, and slight differences in morphology and plumage (Aldrich and Duvall 1955, Connelly et al. 2024). We evaluated the subspecific status of a population of Sharp-tailed Grouse in south-central Wyoming using habitat, morphological, and genetic (microsatellite and genome-wide SNVs) characteristics. Our results suggest that the three populations of Sharp-tailed Grouse that we evaluated form three unique groups. This pattern is most evident when using habitat associations, microsatellite markers, and single nucleotide variants across the three Sharp-tailed Grouse populations. Differences between populations were less pronounced when evaluating morphological characteristics, however there were still differences between the populations when both including and excluding mass in the comparisons. Including Lesser Prairie-Chicken as an outgroup in our analysis (see Appendix A for results including outgroup) provided a strong discriminatory power and showed similar results, with our three populations of Sharp-tailed Grouse generally forming their own groups and Lesser Prairie-Chicken forming their own group as well. Overall, our results suggest that the Sharp-tailed Grouse population in south-central Wyoming is different from both the plains and Columbian Sharp-tailed Grouse subspecies and might represent a different subspecies.

Typically, subspecies have been described using a single approach, ranging from ecological differences (Philips 1948, Wilson et al. 2010, Khimoun et al. 2013), morphological differences (Pivnička 1970, Owen and Webster 1983, Marantz and Patten 2010), and genetic differences (Funk et al. 2007, Archer et al. 2017, Ferrante et al. 2022). While many studies use a single approach, there are some that use multiple approaches to evaluate subspecies (e.g., Zink 2015, Meiri et al. 2017, Walsh et al. 2017). We used multiple data types (e.g., habitat, morphology, and genetic) and analytical approaches (e.g., DAPC and Random Forests) to evaluate the Sharp-tailed Grouse population in south-central Wyoming with the results from the different data types and analytical approaches generally aligning. However, there were some discrepancies depending on which analytical approach was used. The two analytical approaches (DAPC and Random Forests models) for morphological, microsatellite, and SNVs did not always agree, with the Random Forests models typically having poorer performances than DAPC models. Specifically, the Random Forests classification models had poorer performances when we used smaller sample sizes or included fewer variables in the analysis and the poorer performance is likely a result of not having adequate sample sizes or including enough predictor variables (Archer et al. 2017, Brieuc et al. 2018, Luan et al. 2020). For example, the Random Forests model evaluating SNVs performed poorly and we only had 12-13 samples per population. Conversely, with more information to discern differences among sample groups, our morphological Random Forest analysis was able to better discriminate among the three populations when we included mass as a covariate (note, all variables that included mass had intermediate importance in the Random Forest model; Table S2) had lower classification error than when we excluded mass from the model.

The majority of the DAPC models correctly differentiated and identified the population of origin of >75% of all the individuals evaluated, except for morphology characteristics and habitat associations models. Morphological differences between the populations were less pronounced and differentiation depended on what variables were included in the analysis. When mass was included in the analysis, unknown Sharp-tailed Grouse were similar to Columbian Sharp-tailed Grouse; however, when mass was excluded from the analysis, unknown Sharp-tailed Grouse were similar to plains Sharp-tailed Grouse. Further, when we included more morphological measurements, unknown Sharp-tailed Grouse were different from plains Sharp-tailed Grouse (see Appendix A for results). This suggests that the number of morphological measurements is important and a study that includes more morphological characteristics for all populations will provide better insight into morphological differentiation. For the habitat associations model, the DAPC was able to correctly differentiate habitat use for the unknown subspecific population in south-central Wyoming from Columbian and plains Sharp-tailed Grouse habitat, however it did a poor job of differentiating Columbian Sharp-tailed Grouse from plains Sharp-tailed Grouse habitat. The inability of the DAPC model to differentiate Columbian Sharp-tailed Grouse habitat characteristics from plains Sharp-tailed Grouse habitat characteristics likely stems from Columbian Sharp-tailed Grouse occupying Conservation Reserve Program grasslands in portions of their range (Hoffman et al. 2015, Stevens et al. 2023); Conservation Reserve Program grasslands found within the Columbian Sharp-tailed Grouse range share characteristics with grasslands found throughout much of the plains Sharp-tailed Grouse range.

Across their range, Sharp-tailed Grouse populations inhabit a variety of different habitats ranging from grasslands with no shrubs or trees to open clearings surrounded by predominately closed canopy forests, with occupied habitats generally differing among subspecies (Johnsgard 2016, Connelly et al. 2024). Our results help confirm that there are differences in habitat use between some populations of Sharp-tailed Grouse, with Sharp-tailed Grouse in south-central Wyoming generally occupying different habitat conditions then Columbian and plains Sharp-tailed grouse. The habitats that Sharp-tailed Grouse typically inhabit do not include continuous conifer forests, alpine areas, or high deserts, which are the predominate habitats found surrounding the area occupied by the unknown Sharp-tailed Grouse population. This large expanse of uninhabited areas surrounding the unknown Sharp-tailed Grouse population has resulted in the population being isolated from other populations of Sharp-tailed Grouse (Columbian and plains subspecies). Evidence suggests that *Tympanuchus* grouse can disperse over large distances, with potential dispersal distances up to 120 km in some areas (Earl et al. 2016, Roy and Gregory 2019), with these dispersal events occurring in human fragmented landscapes with patches of suitable habitat between them. The ranges of both the Columbian and plains Sharp-tailed Grouse are located farther from the maximum distance a *Tympanuchus* grouse has been observed to disperse (175 km and 130 km, respectively) with most of the distance between them representing unsuitable habitat, though a potential dispersal event cannot be ruled out. The isolation of the unknown Sharp-tailed Grouse population was likely not human-caused, unlike the fragmentation of Columbian Sharp-tailed Grouse in Idaho, Utah and Oregon (Miller and Graul 1980, Hoffman et al. 2015). Additional research is needed to evaluate the timeframe that the unknown Sharp-tailed Grouse population were isolated from other Sharp-tailed Grouse populations.

In our study, we used two different genetic approaches to discriminate populations: microsatellite loci and single nucleotide variants generated from low resolution whole genome resequencing. Results from both datasets analyzed using a DAPC indicated that the three populations of Sharp-tailed Grouse were different from each other, with few differences in discriminatory power between the two approaches. In other non-model systems, SNVs have shown more resolution to discriminate among populations than microsatellites, especially when populations are genetically depauperate (Galla et al. 2020, Zimmerman et al. 2020, Hauser et al. 2021; but see also Forsdick et al. 2021); this power often comes from the quantity of data obtained from high throughput sequencing approaches. We did not see strong differences between microsatellites and SNVs here and we have considered two explanations for this pattern. First, the SNVs called here were produced at 2x read depth using low resolution resequencing Nanopore data on relatively few individuals, which may have resulted in fewer SNVs and discriminatory power compared to microsatellites. Second, the microsatellite dataset here is robust, with a high number of possible alleles per locus, which may have allowed for substantial discriminatory power. We contend that both approaches were capable of discriminating populations in our analyses and therefore may be useful to others exploring this approach.

Our results indicate that the population of Sharp-tailed Grouse in south-central Wyoming differs from Columbian and plains Sharp-tailed Grouse using ecological, morphological, and genetic approaches. To fully evaluate the subspecific status, analyses including evolutionary relationships will provide a better understanding of which populations of Sharp-tailed Grouse belong to which subspecies. A recent phylogenetic study indicated high nodal support for branching between many Sharp-tailed Grouse subspecies, including plains and Columbian, depending on the genomic markers used (e.g., autosomal, Z-linked, intergenic, and genic sites; Johnson et al. 2023). While the sample size was small for Sharp-tailed Grouse from south-central Wyoming (n = 2), there is support for differentiation from plains and Columbian Sharp-tailed Grouse in some—but not all—species trees. This complexity may be due to the recent evolutionary history of North American prairie grouse (i.e., incomplete lineage sorting), hybridization between taxa, and pre-zygotic barriers of sexual selection (Galla and Johnson 2015). We recommend a more targeted phylogenomic study across Sharp-tailed Grouse, including adding samples from northwest Colorado (which is connected to the population in south-central Wyoming) and increased sample sizes for plain and Columbian Sharp-tailed Grouse from across their distributions to elucidate this complicated history. Finally, it should be noted that there was a historic population of Sharp-tailed Grouse in New Mexico that was classified as a separate subspecies (*Tympanuchus phasianellus hueyi*, Dickerman and Hubbard 1994). The plumage description of these birds by Dickerman and Hubbard (1994) is similar to what we observed in the population in south-central Wyoming (Lautenbach and Pratt, personal observation). The evolutionary history of this population remains unknown and could be assessed in relationship to historic and contemporary Sharp-tailed Grouse populations in the western United States, using museum specimens.

Conservation Implications

Our results may potentially change the current understanding of Sharp-tailed Grouse subspecies in western North America, which can impact how to manage them. Our results have particularly important implications for Columbian Sharp-tailed Grouse, a subspecies that has been petitioned for listing under the Endangered Species Act (USDI 2000, 2006). Historically the population in south-central Wyoming extending into northwestern Colorado was thought to be the Columbian subspecies. Excluding the estimated population size of Sharp-tailed Grouse in northwest Colorado and south-central Wyoming (approximately 8,000–10,000 birds; Hoffman 2001, Mong et al. 2017) reduces the estimated population of Columbian Sharp-tailed Grouse by about 10–20% (Columbian Sharp-tailed Grouse population is estimated to be between 41,000–62,000; Gillette 2014, Chutter 2015, Schoeder et al. 2023). Not only do our results potentially change our understanding of population sizes, it also could change how we manage these populations, including habitat management and translocations. To maintain the genetic integrity of Columbian Sharp-tailed Grouse populations, our results indicate managers should not use the population in south-central Wyoming (and likely northwest Colorado) as a source population for reintroduction and population augmentation efforts of Columbian Sharp-tailed Grouse in places with small or extirpated populations (e.g., Nevada, Oregon, and Washington). Our analyses of habitat conditions suggest that there are some habitat differences between south-central Wyoming/northwestern Colorado and Columbian Sharp-tailed Grouse populations. Currently, habitat management actions are applied uniformly between Columbian Sharp-tailed Grouse and populations of Sharp-tailed grouse in south-central Wyoming and northwest Colorado (Hoffman et al. 2015). Our results suggest a need to reevaluate habitat management approaches for Sharp-tailed Grouse across the range of these species/sub-species in Wyoming, Idaho, and northwest Colorado.

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AUTHOR CONTRIBUTIONS

JDL, ACP, AJG, and JLB conceived this project. JDL, ACP, and MAS collected field data. JDL and AJG designed and conducted laboratory work. JDL analyzed data. JDL drafted the manuscript, with assistance from JLB, AJG, and SG. All authors reviewed and approved this manuscript before submission.

DATA ACCESSIBILITY STATEMENT

Data accessibility: Habitat association, morphology, microsatellite, and single nucleotide variant data are available on Dryad (http://datadryad.org/stash/share/UopZzHUJC8MlMLGBIHsFQxbOHVNFTeWA7I8qbYz93ms). Raw eBird observations and records are archived and freely and publicly accessible through eBird. Spatial data used in the habitat associations analyses are available for download from the source (see Methods for where these data were obtained from). All code (R code and Linux code) used to generate, process, and analyze data are available on Dryad (http://datadryad.org/stash/share/UopZzHUJC8MlMLGBIHsFQxbOHVNFTeWA7I8qbYz93ms). Raw sequence reads and sequence sample metadata are deposited in the SRA (BioProject PRJNA1196947).

TABLES

Table 2.1. Number of variables, sample sizes, and assignment probabilities of discriminant analysis of principal components for populations of Columbian Sharp-tailed Grouse (STGRc; Idaho and Washington, 2005–2013), plains Sharp-tailed Grouse (STGRp; eastern Wyoming, 2019), and unknown Sharp-tailed Grouse (STGRu; south-central Wyoming, 2017–2019). Analyses were run on habitat characteristics, morphological characteristics, 9 microsatellite loci, and single nucleotide variants (SNVs).

		Sample size			Assignment probability		
Analyses	No. of variables	STGRc	STGRp	STGRu	STGRc	STGRp	STGRu
Habitat	22	812	7,951	509	0.66	0.99	0.87
Morphology	6[a]	219	63	165	0.80	0.97	0.60
	10[b]	219	63	165	0.94	0.59	0.81
Microsatellite	118[c]	53	32	175	0.88	0.78	0.98
SNVs	453	12	12	13	0.92	0.83	0.92

[a] Morphological analysis using tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons.

[b] Morphological analysis using mass (g), tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons

[c] Total number of alleles across nine microsatellite loci.

Table 2.2. Mean and median average membership probability of each individual assigned to each population of prairie-grouse evaluated using a discriminant analysis of principal components based on habitat characteristics, morphological characteristics, and single nucleotide variants for three populations of Sharp-tailed Grouse: Columbian Sharp-tailed Grouse (STGRc; Idaho and Washington, 2005–2013), plains Sharp-tailed Grouse (STGRp; eastern Wyoming, 2019), and a population of Sharp-tailed Grouse with unknown subspecific status (STGRu, south-central Wyoming, 2017–2019) in south-central Wyoming.

		Mean (median) average membership probability of each individual		
Analyses	**Population**	**STGRc**	**STGRp**	**STGRu**
Habitat	STGRc	0.66 (0.96)	0.25 (0.01)	0.10 (0.00)
	STGRp	0.01 (0.00)	0.99 (1.00)	0.00 (0.00)
	STGRu	0.13 (0.00)	0.00 (0.00)	0.87 (1.00)
Morphological[a]	STGRc	0.87 (0.95)	0.03 (0.01)	0.10 (0.04)
	STGRp	0.14 (0.02)	0.51 (0.52)	0.35 (0.32)
	STGRu	0.15 (0.04)	0.13 (0.06)	0.72 (0.84)
Morphological[b]	STGRc	0.69 (0.72)	0.00 (0.00)	0.31 (0.28)
	STGRp	0.01 (0.00)	0.97 (1.00)	0.02 (0.00)
	STGRu	0.43 (0.38)	0.00 (0.00)	0.57 (0.62)
Microsatellite	STGRc	0.91 (1.00)	0.02 (0.00)	0.07 (0.00)
	STGRp	0.04 (0.00)	0.79 (0.96)	0.17 (0.01)
	STGRu	0.01 (0.00)	0.02 (0.00)	0.97 (1.00)
Single nucleotide variants	STGRc	0.92 (1.00)	0.08 (0.00)	0.00 (0.00)
	STGRp	0.04 (0.00)	0.89 (1.00)	0.07 (0.00)
	STGRu	0.01 (0.00)	0.06 (0.00)	0.93 (1.00)

[a] Morphological analysis using tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons.

[b] Morphological analysis using mass (g), tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons

Table 2.3. Population genetic summary statistics for 9 microsatellite loci from 53 Columbian Sharp-tailed Grouse (STGRc, Idaho, 2018), 32 plains Sharp-tailed Grouse (STGRp, eastern Wyoming, 2019), and 175 unknown Sharp-tailed Grouse (STGRu, south-central Wyoming, 2017–2019). We report the number of alleles (N_A), allelic richness (*AR*) by populations, **inbreeding coefficient (F_{IS}),** proportional genetic variance (F_{ST}), expected heterozygosity (H_E), observed heterozygosity (H_O), and Hardy-Weinberg Equilibrium p-value (*HWE*).

Loci	N_A	AR_{STGRc}	AR_{STGRp}	AR_{STGRu}	F_{IS}	F_{ST}	H_O	H_E	***HWE***
ADL230	11	7.74	8.98	3.63	0.00	0.08	0.63	0.66	<0.001
BG16	11	7.48	7.62	7.65	-0.03	0.06	0.81	0.82	0.107
LLSD7	13	8.62	9.85	8.78	-0.04	0.01	0.85	0.81	0.022
LLST1	7	5.69	4.00	4.11	0.21	0.06	0.45	0.66	<0.001
SGMS06.6	23	13.00	13.52	12.42	-0.02	0.03	0.87	0.87	<0.001
SGMS06.8	11	7.51	8.23	5.58	-0.06	0.03	0.81	0.75	0.247
SG28	17	7.03	5.95	3.98	-0.02	0.02	0.22	0.22	1.000
TUT4	15	10.17	9.99	10.95	0.13	0.03	0.67	0.89	<0.001
TTD6	10	5.97	7.75	6.09	0.07	0.06	0.59	0.67	<0.001

Table 2.4. Sample size (*n*), proportional genetic variance (F_{ST}), observed heterozygosity (H_O), subpopulation heterozygosity (H_S), and inbreeding coefficient (F_{IS}) for 453 single nucleotide polymorphisms and insertions and deletions loci from 39 *Tympanuchus* samples (Lesser Prairie-Chicken [LEPC; Kansas, 2013], Columbian Sharp-tailed Grouse [STGRc; Idaho, 2018], plains Sharp-tailed Grouse [STGRp; eastern Wyoming, 2019], and unknown Sharp-tailed Grouse [STGRu; south-central Wyoming, 2017–2019]).

Subspecies	***n***	**F_{ST} LEPC**	**F_{ST} STGRc**	**F_{ST} STGRp**	**H_O**	**H_S**	**F_{IS}**
LEPC	2	–	–	–	0.19	0.11	-0.74
STGRc	12	0.06	–	–	0.22	0.16	-0.39
STGRp	12	0.00	0.02	–	0.22	0.17	-0.35
STGRu	13	0.16	0.06	0.04	0.23	0.17	-0.38

Table 2.5. Pairwise comparisons and classification error of Random Forests classification for three populations of Sharp-tailed Grouse based on habitat characteristics, morphological characteristics, microsatellite loci, and single nucleotide variants (SNVs). Sharp-tailed Grouse populations evaluated are Columbian Sharp-tailed Grouse (STGRc; Idaho and Washington, 2005–2013, 2018), plains Sharp-tailed Grouse (STGRp; eastern Wyoming, 2019), and unknown Sharp-tailed Grouse (STGRu; south-central Wyoming, 2017–2019).

Analysis	**Population**	**STGRc**	**STGRp**	**STGRu**	**Classification error (%)**
Habitat	STGRc	761	50	1	6.3
	STGRp	4	7947	0	0.1
	STGRu	8	1	500	1.8
Morphological[a]	STGRc	206	1	12	5.9
	STGRp	0	62	1	1.6
	STGRu	17	1	147	10.9
Morphological[b]	STGRc	200	4	15	8.7
	STGRp	6	36	21	42.9
	STGRu	16	13	136	17.6
Microsatellite loci	STGRc	39	3	11	26.4
	STGRp	3	10	19	68.8
	STGRu	2	1	172	1.7
SNVs	STGRc	6	2	4	50.0
	STGRp	3	5	4	58.3
	STGRu	4	2	7	46.2

[a] Morphological analysis using tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons.

[b] Morphological analysis using mass (g), tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons

Table 2.6. (S1) Standardized variable importance for Random Forests model predicting prairie-grouse populations based on habitat characteristics at observed locations (eBird), 2010–2023. Prairie-grouse populations evaluated were Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, and a population of Sharp-tailed Grouse with unknown subspecific status. Variable importance values were standardized so the top variable equals 1 and the remaining variables are proportions derived by dividing by the top variable (Doherty et al. 2018). PRISM represents 30-year average annual climate data (PRISM Climate Group 2014); RAP represents annual Rangeland Analysis Platform data (Robinson et al. 2019, Alred et al. 2021, Jones et al. 2021); NLCD represents the National Land Cover Database from 2011, 2013, 2016, 2019, and 2021 (Jin et al. 2019); canopy cover of different forest types was derived from both NLCD and RAP data layers.

Variable	**Importance value**
Percent cover of shrubs (RAP)	1.00
Terrain ruggedness index	0.27
Heat load index	0.22
Topographic position index	0.17
Percent cover of perennial herbaceous vegetation (RAP)	0.16
Canopy cover of deciduous forest (NLCD and RAP)	0.15
Mean annual precipitation (PRISM)	0.13
Percent cover of annual herbaceous vegetation (RAP)	0.12
Annual herbaceous vegetation biomass (RAP)	0.11
Croplands (NLCD)	0.11
Mean annual maximum temperature (PRISM)	0.10
Biomass of perennial herbaceous vegetation (RAP)	0.10
Canopy cover of unclassified forest (NLCD and RAP)	0.09
Canopy cover of all forest types (NLCD and RAP)	0.09
Canopy cover of coniferous forest (NLCD and RAP)	0.09
Percent cover of litter (RAP)	0.09
Anthropogenic development (NLCD)	0.06
Water (NLCD)	0.06
Pasture lands (NLCD)	0.05
Emergent wetlands (NLCD)	0.05
Percent bare ground (RAP)	0.04
Canopy cover of mixed forests (RAP)	0.03

Table 2.7. (S2) Standardized variable importance for Random Forests model predicting prairie-grouse populations based on morphological characteristics (mass (g), tail length (mm), wing cord length (mm), tarsus + longest toe length (mm) [tarsus + toe length], and all pairwise comparisons). Prairie-grouse populations evaluated were Columbian Sharp-tailed Grouse (2005–2013; Idaho and Washington), plains Sharp-tailed Grouse (2019; Wyoming), and a population of Sharp-tailed Grouse with unknown subspecific status (2017–2019; Wyoming). Variable importance values were standardized so the top variable equals 1 and the remaining variables are proportions derived by dividing by the top variable (Doherty et al. 2018).

Variable	**Importance value**
Tarsus + toe length	1.00
Wing cord length to tarsus + toe length ratio	0.84
Mass	0.50
Tarsus + toe length to mass ratio	0.42
Wing cord length to mass ratio	0.39
Tail length to mass ratio	0.21
Tail length to tarsus + toe length ratio	0.14
Wing cord length to tail length ratio	0.11
Wing cord length	0.11
Tail length	0.07

Table 2.8. (S3) Standardized variable importance for Random Forests model predicting prairie-grouse populations based on morphological characteristics (tail length (mm), wing cord length (mm), tarsus + longest toe length (mm) [tarsus + toe length], and all pairwise comparisons). Prairie-grouse populations evaluated were Columbian Sharp-tailed Grouse (2005–2013; Idaho and Washington), plains Sharp-tailed Grouse (2019; Wyoming), and a population of Sharp-tailed Grouse with unknown subspecific status (2017–2019; Wyoming). Variable importance values were standardized so the top variable equals 1 and the remaining variables are proportions derived by dividing by the top variable (Doherty et al. 2018).

Variable	**Importance value**
Tarsus + toe length	1.00
Wing cord length to tarsus + toe length ratio	0.78
Wing cord length	0.40
Tail length to tarsus + toe length ratio	0.33
Wing cord length to tail length ratio	0.24
Tail length	0.20

FIGURES

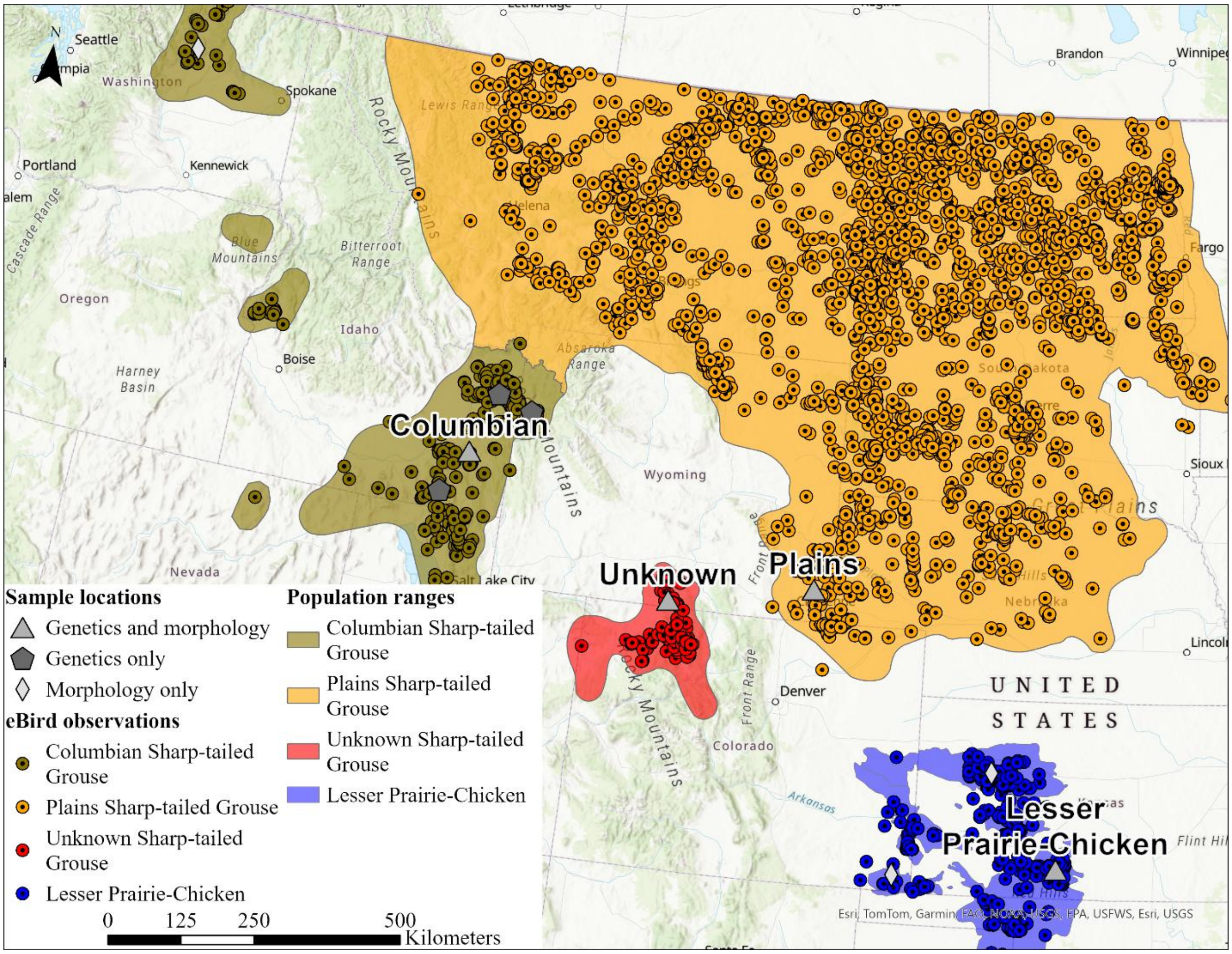

Figure 2.1. Sample locations for habitat association analysis (eBird checklist locations, 2010–2023; colored circles) and genetic and morphological data (gray triangles). The polygons represent the estimated range for the Lesser Prairie-Chicken (WAFWA Lesser Prairie-Chicken Interstate Working Group 2022) and the estimated ranges for subspecies of Sharp-tailed Grouse (Columbian, plains, and a population with an unknown subspecies) in the United States of America (Spaulding et al. 2006, Galla and Johnson 2015).

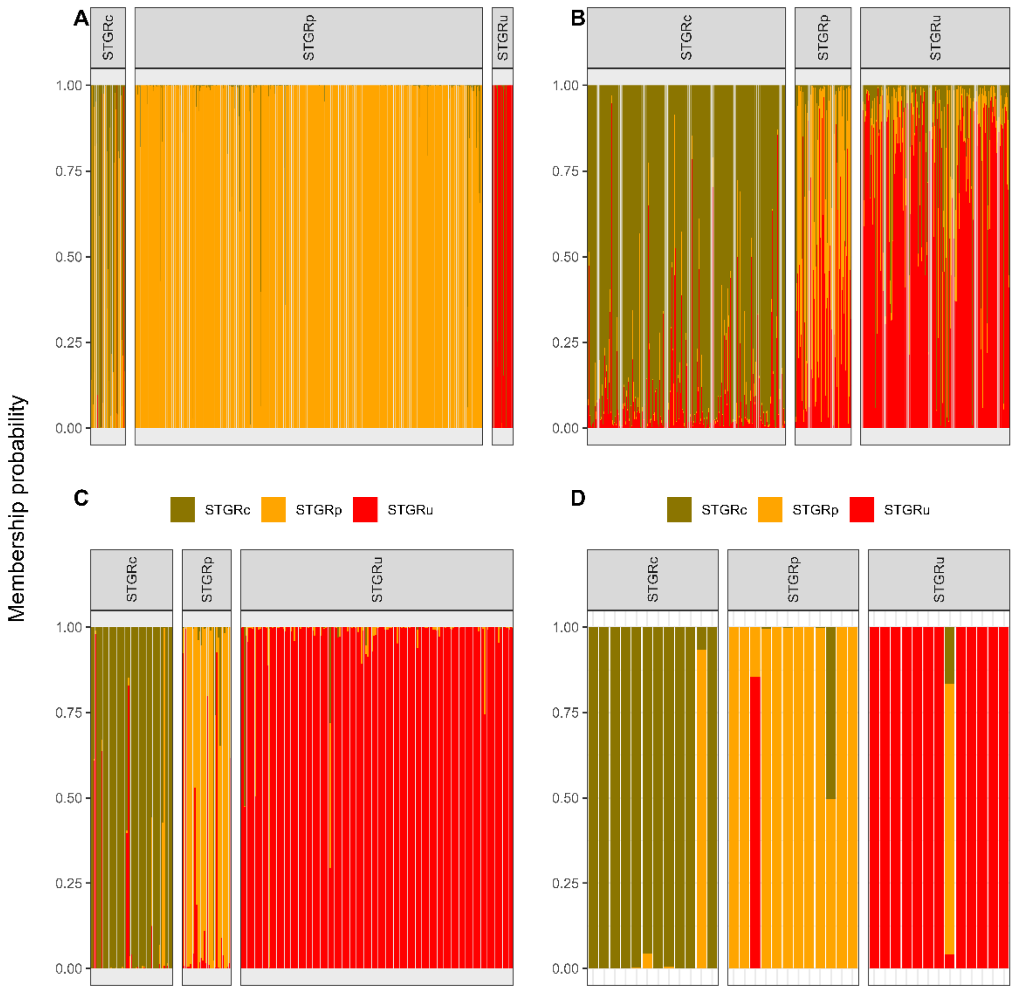

Figure 2.2. Membership probability (admixture) plots for discriminant analysis of principal components for habitat characteristics (A), morphological characteristics of males including mass (B), microsatellite loci analysis (C), and single nucleotide variants (SNVs; D) for Columbian Sharp-tailed Grouse (STGRc; Idaho and Washington, 2005–2013, 2018), plains Sharp-tailed Grouse (STGRp; eastern Wyoming, 2019), and unknown Sharp-tailed Grouse subspecies (STGRu; south-central Wyoming, 2017–2019). Membership probability plot depicts the proportion of assignment to each population, with different colors representing the proportion of each population in each individual. Facets represent the original population of each observation (habitat) or individual (morphology, microsatellite loci, and SNVs).

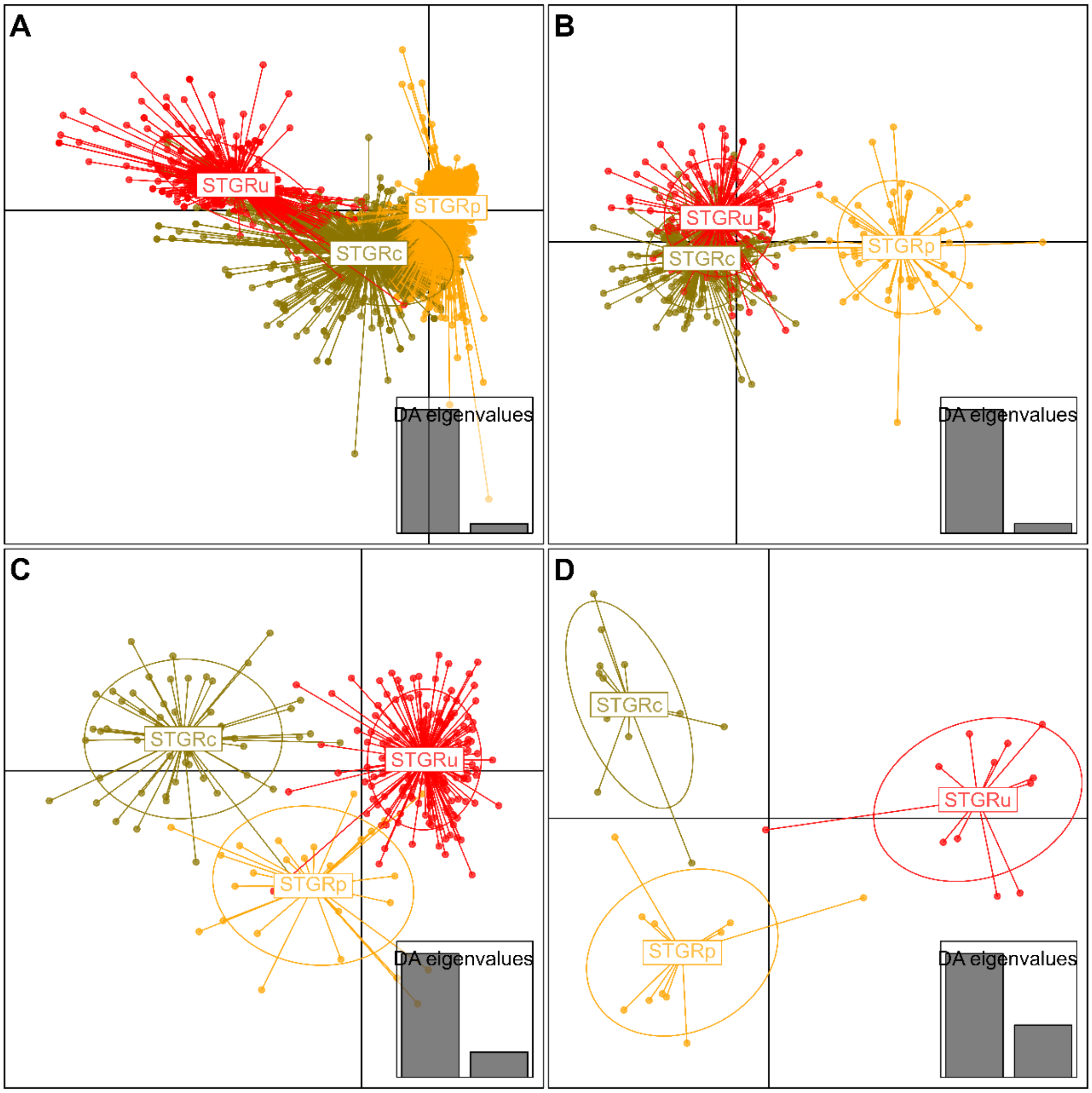

Figure 2.3. Principal component plot from discriminant analysis of principal components for habitat characteristics (A), morphological characteristics of males including mass (B), 9 microsatellite loci (C), and 453 single nucleotide variants (SNVs; D) for Columbian Sharp-tailed Grouse (STGRc; Idaho and Washington, 2005–2013, 2018), plains Sharp-tailed Grouse (STGRp; eastern Wyoming, 2019), and unknown Sharp-tailed Grouse subspecies (STGRu; south-central Wyoming, 2017–2019). Points represent individual observations (habitat) or individuals (morphology, microsatellite loci, and SNVs).

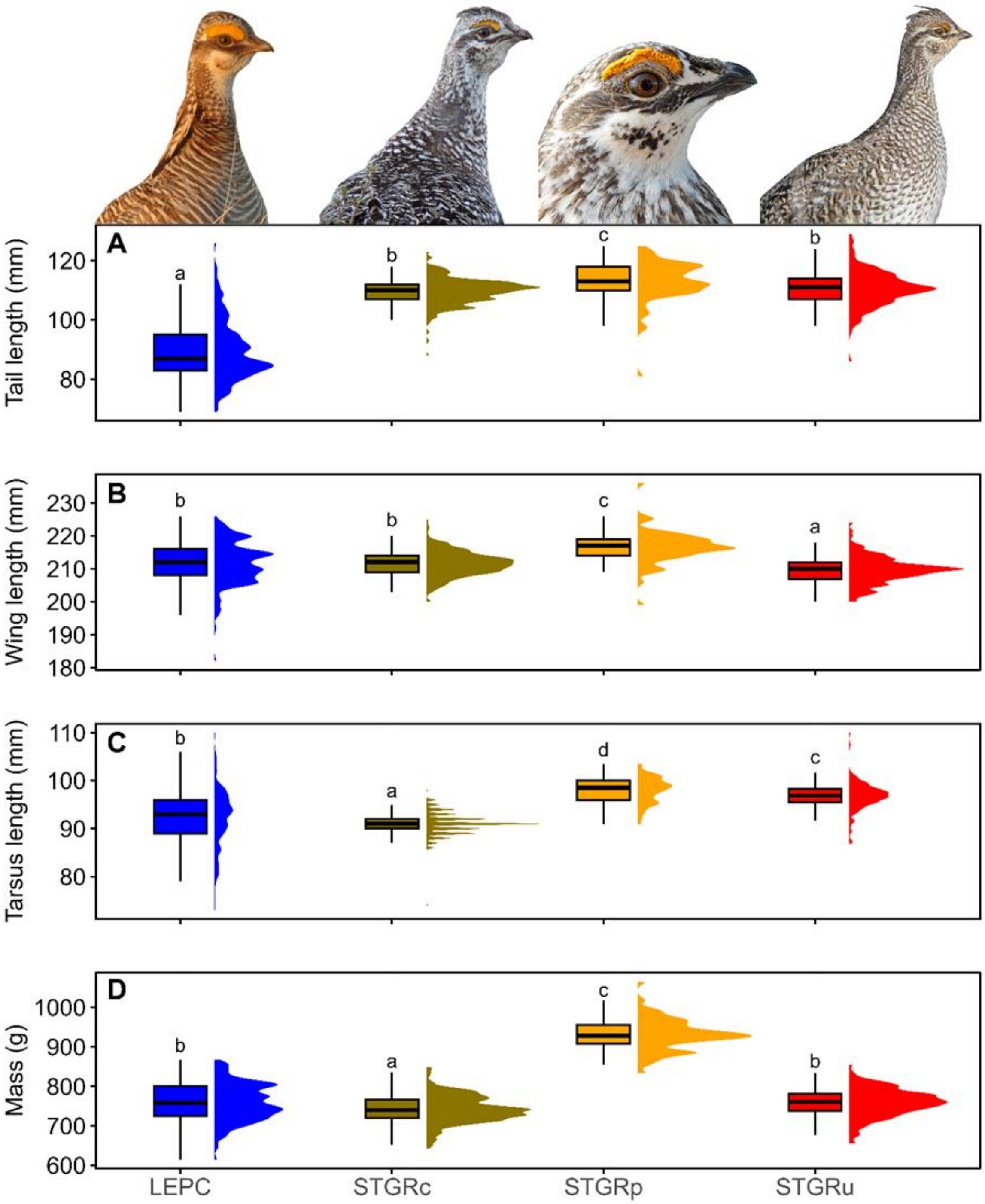

Figure 2.4. Comparison of raw morphometric measurements of males across four population of grouse: Lesser Prairie-Chicken (LEPC; Kansas and Colorado, 2013–2017), Columbian Sharp-tailed Grouse (STGRc; Idaho and Washington, 2005–2013), plains Sharp-tailed Grouse (STGRp;

eastern Wyoming, 2019), and a Sharp-tailed Grouse with an unknown subspecific status (STGRu; south-central Wyoming, 2017–2019). Morphometric measurements include tail length (mm), wing cord length (wing length; mm), tarsus + longest toe length (tarsus length; mm), and mass (g). Superscript letters above each boxplot represent statistical differences calculated using a Kruskal-Wallis rank sum test, where populations with the same letter did not differ from each other. All photos © Jonathan Lautenbach.

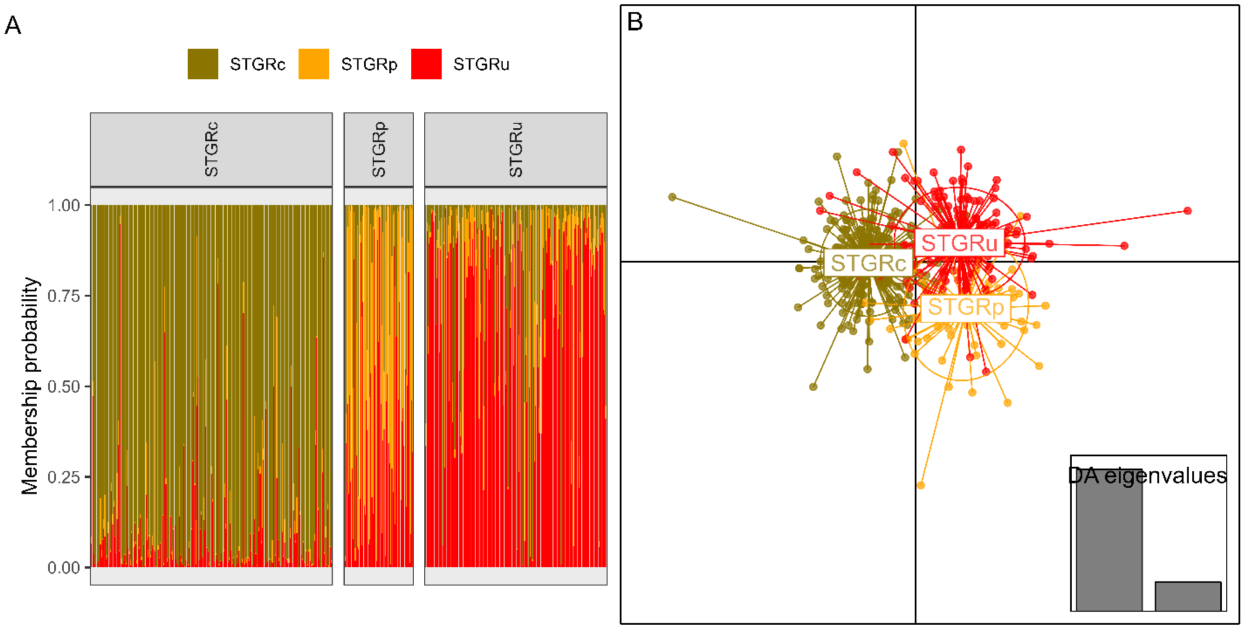

Figure 2.5. Membership probability (admixture) plot (A) and principal component plot (B) for discriminant analysis of principal components (DAPC) for three morphometric measurements of males and all pairwise comparisons for Columbian Sharp-tailed Grouse (STGRc; Idaho and Washington, 2005–2013), plains Sharp-tailed Grouse (STGRp; eastern Wyoming, 2019), and a Sharp-tailed Grouse population of unknown subspecies (STGRu; south-central Wyoming, 2017–2019).

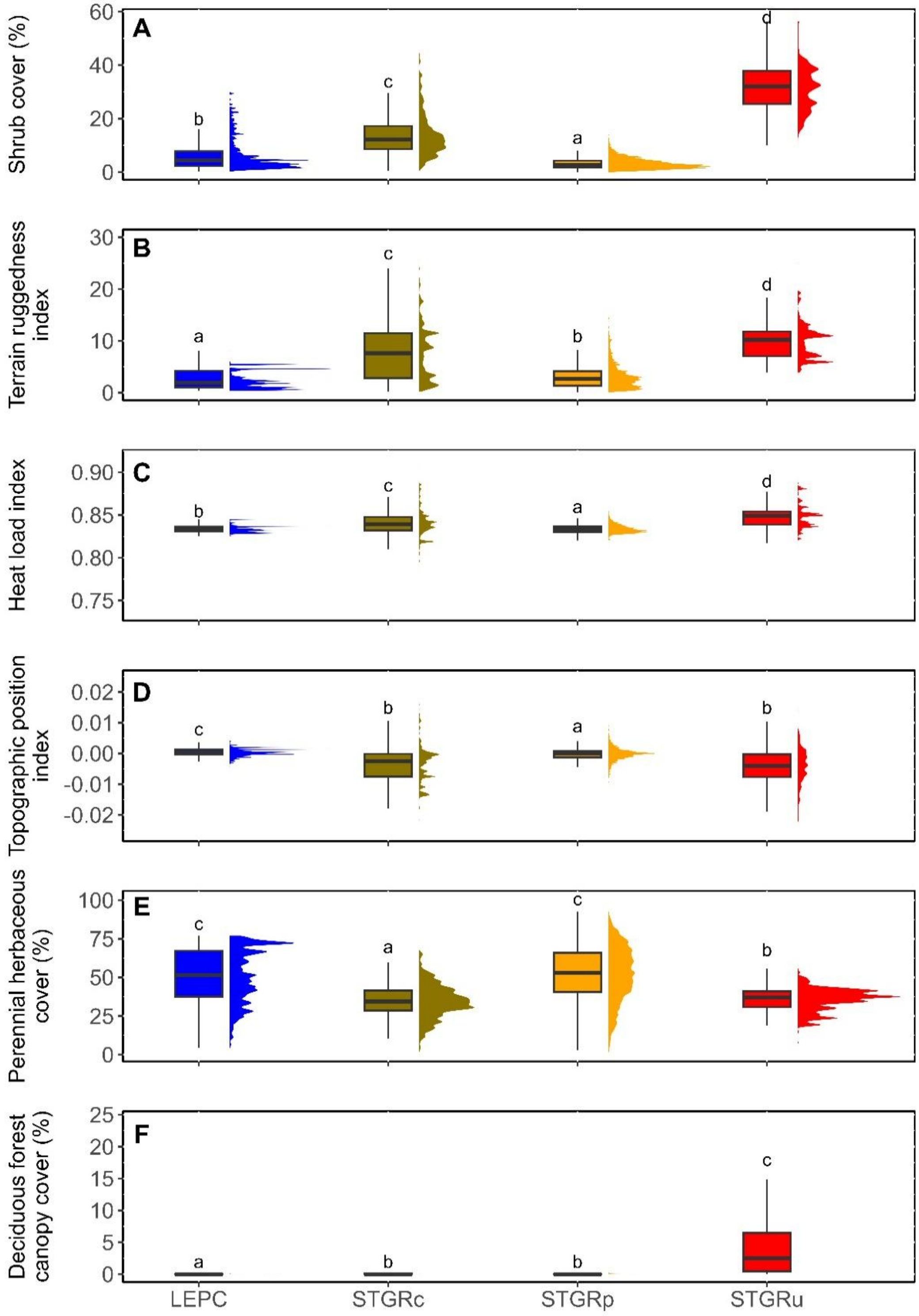

Figure 2.6. Comparison of raw habitat characteristics at eBird checklist locations across four populations of grouse: Lesser Prairie-Chicken (LEPC), Columbian Sharp-tailed Grouse (STGRc), plains Sharp-tailed Grouse (STGRp), and a Sharp-tailed Grouse with unknown

subspecific status (STGRu) in south-central Wyoming (2010–2023). Habitat characteristics include the top six most important variables from a Random Forests classification model (see Table 2.6). Habitat characteristics include percent cover of shrubs (**A**), terrain ruggedness index (**B**), heat load index (**C**), topographic position index (**D**), percent cover of perennial herbaceous vegetation (**E**), and percent canopy cover of deciduous forests (**F**). Superscript letters above each boxplot represent statistical differences calculated using a Kruskal-Wallis rank sum test, where populations with the same letter did not differ from each other.

CHAPTER THREE

Landscape features and seasonal female habitat predicts lek-site selection, but not lek size of a *Tympanuchus* grouse

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***Keywords**:* Andersen-Gill models; habitat management; lek hotspot hypothesis; nest, brood, and non-breeding habitat; resource selection; *Tympanuchus phasianellus*.

ABSTRACT

The lek hotspot hypothesis predicts that leks will form in areas where males are more likely to encounter females, providing wildlife managers with a framework supporting the use of leks as the focus for prairie and shrubland grouse conservation and monitoring. The lek hotspot hypothesis also implies that the number of males attending leks (lek size) will be higher in areas where there are more females. We used sharp-tailed grouse (*Tympanuchus phasianellus*) to evaluate if lek locations and lek size were more influenced by lek-specific habitat features or by female habitat requirements during different life-history stages. First, we evaluated which landscape features influenced female habitat selection and mortality risk during different seasons: nesting (Apr–Jun), brood-rearing (Jun–Aug), early nonbreeding (Sep–Nov), and late nonbreeding (Dec–Mar) seasons in south-central Wyoming (*n* = 213 VHF-marked females; 2017–2020). We found that habitat selection and mortality risk varied by season. Subsequently, we modeled lek locations and lek size relative to seasonal female habitat requirements (selection and mortality risk) and landscape features to identify key variables explaining lek-site selection and lek size. Lek-site selection was based on a combination of landscape features and seasonal female habitat. Specifically, leks were located in areas with less rugged terrain and lower nest, brood, and late nonbreeding season mortality risks. We found that lek size was primarily influenced by landscape features, specifically lek sizes were larger in areas with less bare ground. Our findings suggest that leks were located in areas more frequented by females at a broad spatial scale (≥800 m), consistent with the lek hotspot hypothesis, however, at a finer scale (≤400 m), leks are selected based on landscape features. Our research supports continuing to use lek locations as focal points for habitat management for lekking grouse.

INTRODUCTION

Lek mating is a breeding system where males gather at communal display grounds, known as a lekking arena, to attract and mate with females (Wiley 1978). In North America, this system is commonly associated with prairie and shrubland grouse (family Phasianidae; Johnsgard 2002); however, lek-mating systems occur across multiple taxa including mammals, insects, and other birds (Höglund and Alatalo 1995). There are several hypotheses that seek to explain lek formation, including hotspot hypothesis (Bradbury and Gibson 1983, Beehler and Foster 1988, Bradbury et al. 1989a), the hotshot hypothesis (Beehler and Foster 1988), female preference hypothesis (Bradbury 1981), the kin selection hypothesis (Kokko and Lindström 1996, Höglund 2003), the predation protection hypothesis (Wiley 1973, Gibson et al. 2002), and the blackhole hypothesis (Stillman et al. 1993). Of these hypotheses, the hotspot and predation protection hypotheses may help predict where leks form (Davies 1991, Gibson et al. 2002, Ryder et al. 2006), while the other hypotheses focus more on why leks form. The lek hotspot hypothesis states that males will form lekking arenas in areas with the highest probability of encountering females (Bradbury and Gibson 1983, Davies 1991, Ryder et al. 2006), suggesting that habitats used by females may play an important role in the locations of lekking arenas. Additionally, the hotspot hypothesis suggests that lekking arenas will be located in areas that increase detectability of the lek by females (sexual advertisement; Alonso et al. 2012). The predation avoidance hypothesis suggests that males form leks to reduce predation risk and suggests that leks will be located in areas that reduce predation risk (Wiley 1973, Gibson et al. 2002, Aspbury and Gibson 2004). Portions of the hotspot and predation avoidance hypotheses are not mutually exclusive, as landscape attributes that allow females to detect lekking arenas might also facilitate detection of lekking arenas by predators (Alonso et al. 2012).

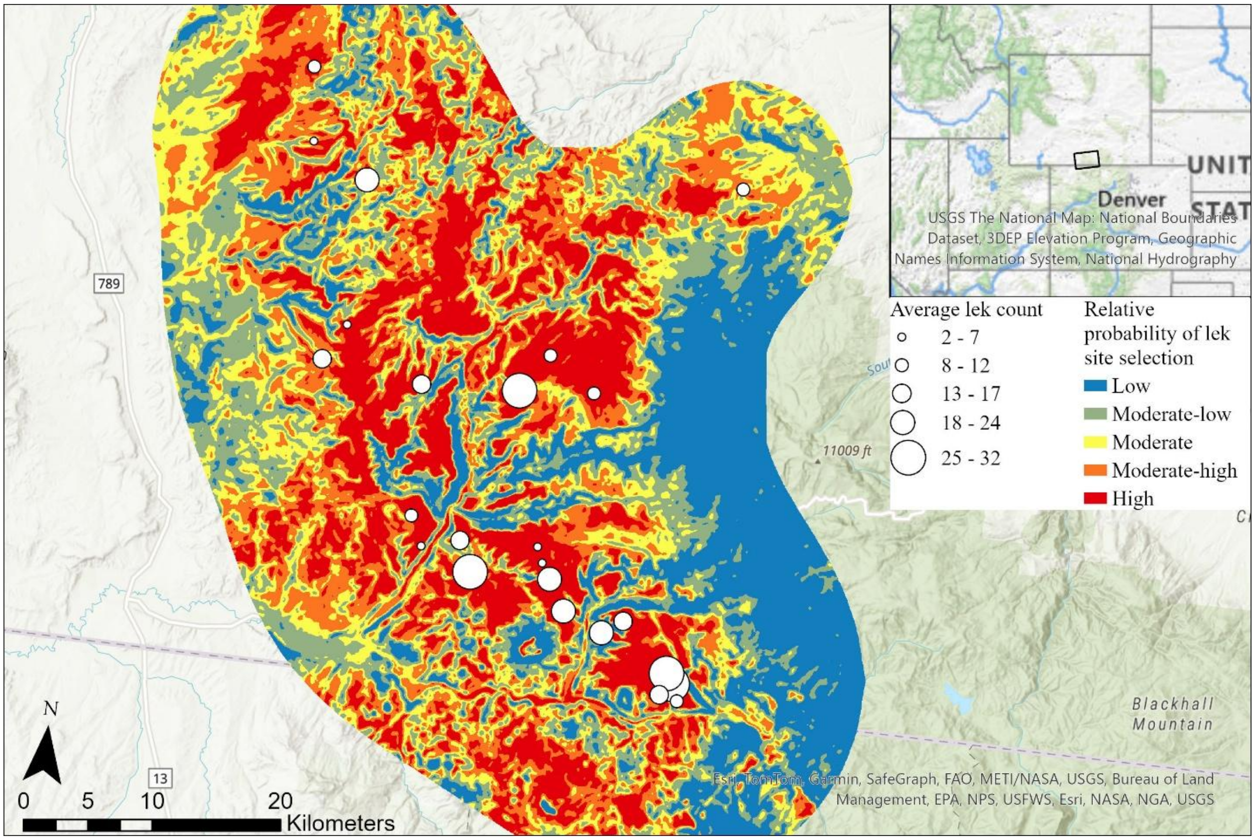
Prairie and shrubland grouse (*Tympanuchus* and *Centrocercus*; hereafter prairie grouse) are a group of lekking grouse found throughout much of northern North America. The locations of prairie grouse lekking arenas have been linked to the hotspot (Schroeder and White 1993, Gibson 1996, Gehrt et al. 2020) and predation avoidance hypotheses (Gibson et al. 2002, Ashbury and Gibson 2004), however there are few studies that evaluate both. Studies have associated the locations of prairie grouse lekking arenas with female migration patterns during the spring (Gibson 1996), nest-site locations and nesting habitat (Schroeder and White 1993, Gehrt et al. 2020), brood-rearing habitat (Gehrt et al. 2020), reduced predation risk by golden eagles (*Aquila chrysaetos*; Ashbury and Gibson 2004), and in relation to topographic features (Hovick et al. 2015*b*) that presumably increase detectability by females and decrease predation risk. In addition to breeding season habitat (e.g., lekking, nesting, and brood-rearing seasons), nonbreeding season habitats (fall and winter) might also play a role in how males determine where lekking arenas are located. Some species of prairie grouse (*Tympanuchus* spp.) are also known to lek in the fall (Sep–Nov; Hamerstrom and Hamerstrom 1951), a time when males begin to establish territories on lekking arenas (Moyles and Boag 1981). Males may use the number of females in the areas surrounding known lekking areas during the fall area as a cue for selecting which lek sites they will attend in spring. Leks might also be located in areas surrounded by late nonbreeding habitat (Dec–Mar), because males start attending leks in March (Gratson 1988) when females are still occupying nonbreeding habitat. The multiple potential reasons trying to explain why lekking arenas are located where they are indicate that this is a complex process and that evaluating all these potential reasons might lead to a better understanding of the placement of lekking arenas on the landscape.

Understanding why lek sites are located where they are is important for prairie grouse conservation, especially as current monitoring and management programs for prairie grouse focus on areas surrounding leks (Walsh et al. 2010, Hoffman et al. 2015, Hagen et al. 2016). Leks are important for monitoring populations because they are relatively fixed points that managers can visit annually and conduct surveys to count the number of individuals; in turn, managers evaluate population trends from these counts (Beck and Braun 1980, Connelly et al. 2003, Walsh et al. 2010, Fedy and Aldridge 2011, Ross et al. 2019). Generally, this monitoring strategy assumes that long-term changes in the number of birds observed on leks are due to broad changes in habitat conditions surrounding leks, either generated through anthropogenic change or abiotic factors such as drought (Hess and Beck 2012, Ross et al. 2016*a*, *b*). On a local scale, lek locations help predict female greater prairie-chicken (*T. cupido*) breeding activity with most female greater prairie-chicken activity occurring within 5 km of known leks (Winder et al. 2015). Understanding how grouse respond to habitat characteristics during different seasons and how that influences lek locations and lek size will further our understanding of lek dynamics and the establishment of new leks.

In our study, we evaluated lek-site selection and lek size (i.e., number of birds on a lek) in relation to both landscape features and seasonal habitats. for sharp-tailed grouse (*T. phasianellus*) in south-central Wyoming, USA. We evaluated the influence of landscape features on both female habitat selection and mortality risk during nesting, brood-rearing, early nonbreeding (Sep 1–Nov 30), and late nonbreeding (Dec 1–Mar 31). Our primary objective was to identify whether lek-site selection and lek size were more influenced by lek-specific habitat features or by seasonal female habitat requirements. To achieve this, we first defined two sub-objectives: 1) identify landscape features that influence female sharp-tailed grouse seasonal habitat selection and mortality risk during each season evaluated, and 2) identify landscape features influencing sharp-tailed grouse lek-site selection and lek size. Results from these two sub-objectives helped us develop models representing separate hypotheses explaining sharp-tailed grouse lek-site selection and lek size, evaluated separately: H1) lek-site selection and lek size were influenced by landscape features surrounding leks, and H2) lek-site selection and lek size were influenced by seasonal female habitat requirements. The first hypothesis suggests lek sites were selected primarily for habitat irrespective of seasonal female habitat requirements (contrary to the hotspot hypothesis) whereas the second hypothesis suggests lek sites were selected primarily for seasonal female habitat requirements (consistent with the hotspot hypothesis). Because male sharp-tailed grouse could select lek sites both because of nearby seasonal female habitat and for additional non-female-specific habitat characteristics we developed a third hypothesis: H3) lek-site selection and lek size were influenced by a combination of landscape features and seasonal female habitat requirements.

METHODS

Study Area



USGS The National Map: National Boundaries Dataset, 3DEP Elevation Program, Geographic Names Information System, National Hydrography

Esri, TomTom, Garmin, SafeGraph, FAO, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, USFWS, Esri, NASA, NGA, USGS

Our study area was located in southwestern Carbon County, Wyoming, USA (41.194°N, -107.324°E; Figure **3.1**). The study area, defined by a 95% isopleth of the fixed-kernel density polygon of known leks in Carbon County, Wyoming, encompassed 2,960 km^2 with elevation that ranged from 1900–3100 m above sea level. Ownership in our study area was composed of Bureau of Land Management (36.7%), U. S. Forest Service (23.3%), State of Wyoming (12.2%), and privately owned (27.7%) lands. During our study (2017–2020), the average annual high temperature was 13° C (30-year average = 12.4° C) and the average annual minimum temperature was -0.8° C (30-year average = -2.2° C). The average annual precipitation was 542 mm (range: 494–601; 30-year average = 618 mm; National Centers for Environmental Information, NOAA, accessed 6/10/2021, https://www.ncdc.noaa.gov/cdo-web/). Dominant vegetation communities within our study area were sagebrush steppe, mixed-shrub communities, quaking aspen (*Populus tremuloides*) forest, mixed deciduous and coniferous forests, and mixed-conifer forests. Sagebrush steppe was dominated by big sagebrush (*Artemisia tridentata*); mixed-shrub communities were primarily composed of silver sagebrush (*A. cana*), big sagebrush, serviceberry (*Amelanchier* spp.), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), antelope bitterbrush (*Purshia tridentata*), and snowberry (*Symphoricarpos* spp.); mixed deciduous and coniferous forests were primarily composed of quaking aspen, Engelmann spruce (*Picea engelmannii*) and lodgepole pine (*Pinus contorta*); and coniferous forests were primarily composed of Engelmann spruce and lodgepole pine. The primary land uses within our study area were cattle and sheep grazing, with some energy extraction, timber harvest, recreation, and irrigated hayfields.

Field Methods

We captured female sharp-tailed grouse at leks using walk-in funnel traps (Haukos et al. 1990; Schroeder and Braun 1991) continuously from ~10 Apr–11 May 2017–2019. We radio-tagged all captured females with 15-g necklace-mounted VHF transmitters (model RI-2B, Holohil, Carp, Ontario, Canada) and located individuals 2–4 times per week during the breeding season (~1 Apr–31 Aug) using triangulation at a distance of ~30–50 m. If we observed a female in the same location during two or more consecutive visits during May or June, we visually confirmed, or circled the bird within a few meters, to identify if the female was on a nest. Once we identified a nest, we monitored it 2–4 times per week from a distance of 50–100 m, until the female left the nest after it hatched or failed. We considered nests successful when ≥1 egg hatched; this was determined by examining eggshell and eggshell membranes in and near the nest after the female was no longer attending the nest. If a nest hatched, we continued to monitor each female for 7 weeks to assess brood mortality risk and habitat selection. To track brood mortality risk, we conducted night brood checks when the brood was 1-week old, and then every two weeks until broods reached 7-weeks old. Night-time checks minimized error because chicks were actively being brooded at night making it more reliable to determine chick presence (determined visually or by presence of chick droppings in the roost the following day) without causing significant disturbance to the female and chicks (Pratt and Beck 2019, Smith et al. 2019). A brood was considered to have failed if chicks were no longer observed with the female or if a female mortality was detected. We assumed failure locations to be the location where we no longer detected chicks unless the distance between the last location with known chick presence and the location where the fate was determined was >500 m away. In the case where a female moved >500 m post brood failure, we used the previous location where chicks were still present as the location where the brood likely failed, as generally broods do not move long distances in a short timespan (1–3 days). Most brood failures were the result of female mortalities (58%; brood failure locations associated with female mortality were determined to be the location of the female mortality). We considered a brood successful if there was ≥1 chick present when the brood was 7-weeks old. We located birds by airplane once per month during the fall/winter (non-breeding season; 15 Sep–31 Mar). If we were not able to locate individuals during a flight, we would continue to search for them in the next 2–3 subsequent flights; if, after subsequent flights, we were still not able to locate them, we considered them missing and right censored the individual in our survival analyses.

We obtained lek locations and counts from the Wyoming Game and Fish Department (WGFD) and the Rawlins Field Office of the Bureau of Land Management (BLM). The WGFD, BLM, and other volunteers visited leks each year (2017–2019) to count the number of sharp-tailed grouse at each lek. Each year, leks were visited once during the spring lekking season

(Mar–May). During visits, observers counted the number of birds attending leks regardless of sex because sexes can be difficult to differentiate due to poor visibility when leks are located in shrubby areas. For the few leks (<5) where all individuals could be reliably counted without flushing, leks were counted from a distance ≥50 m to minimize disturbance to lekking activities. For the majority of leks, which could not be reliably counted without flushing, leks were flushed once during each season and the number of individuals that flushed were counted. Therefore, lek counts used in analyses included both males and females and represent all birds present at the times of observations. We used all known lek locations that had ≥2 males attending the lek for at least two of the three years of our study. We evaluated lek size during each year of our study and we averaged the number of birds counted at leks each of the years of our study at each lek location and rounded to this to the nearest integer so we could use count models. We used average lek size in addition to annual lek size data to understand if there were any general trends related to lek size during our study.

Available landscape features

We used remotely sensed data to describe landscape features available in our study area. We evaluated seasonal habitats and lek locations and size in relation to vegetation cover, anthropogenic disturbances, and topographic features (TABLES
Table **3.1**). Data describing vegetation features were obtained from the Rangeland Condition Monitoring Assessment and Projection (RCMAP; Coulston et al. 2012, Xian et al. 2015, Rigge et al. 2019, 2020) and the National Land Cover Database (NLCD; Jin et al. 2019). We used the following rangeland fraction layers from 2016–2019: annual herbaceous percent cover, perennial herbaceous percent cover, herbaceous percent cover (combined annual and perennial herbaceous layers), percent bare ground, percent litter, percent cover of sagebrush (*Artemisia* sp.), percent

cover of all shrubs, percent cover of non-sagebrush shrubs, shrub height (cm), and percent canopy cover of trees (all downloaded from https://www.mrlc.gov/). We used NLCD coniferous forest and deciduous forest land cover types to derive coniferous forest and deciduous forest canopy cover from the RCMAP tree cover data. We separated out the canopy cover of different forest types (coniferous and deciduous forests) because sharp-tailed grouse are known to use some types of deciduous forests. For topographic features, we calculated heat load index (HLI; McCune and Keon 2002), terrain ruggedness index (TRI; Riley et al. 1999), and topographic position index (TPI; De Reu et al. 2014) from a digital elevation model (DEM; USGS 2011) using the *hli*, *tri*, and *tpi* functions within the *spatialEco* package in Program R 4.4.1 (Evans et al. 2021, R Core Development Team 2024). Heat load index represents an indirect measure of incident solar radiation calculated from a DEM, with zero representing the coolest areas and 1 representing the warmest areas (McCune and Keon 2002). Terrain ruggedness index represents the roughness of a surface with lower values representing smoother areas and higher values representing very rough surfaces (Riley et al. 1999). Topographic position index represents the relative position on the landscape, with positive values representing hill tops and negative values representing valleys or other positions lower on the slope (De Reu et al. 2014). For all vegetation and topographic layers, we used a moving window analysis to estimate the mean value for each layer within 6 circular distance bins (100, 200, 400, 800, 1,600, and 3,200-m) using the *focal* and *focalWeight* functions in the *terra* package in Program R (Hijmans 2023). The moving window analysis calculates the mean values for each cell within the distance of each distance bin. The combination of the moving window analysis and raw vegetation and topographic layers resulted in 7 distance bins to evaluate: 30 m (raw vegetation and topographic variables), 100 m, 200 m, 400 m, 800 m, 1,600 m, and 3,200 m. We evaluated two different anthropogenic features:

distance to oil and natural gas infrastructure and distance to all roads. We extracted oil and gas infrastructure (e.g., well pads, pipelines, settling ponds, etc.) and all road cells from the NLCD cover data and calculated the Euclidean distance to these features (Euclidean distance tool, spatial analyst toolbox, ArcGIS 10.5; ESRI Inc., 2016, Redlands, CA).

For each season that we evaluated habitat selection and mortality risk for, we used a different subset of variables mentioned above. For nest site selection and nest mortality risk, we used vegetation layers from the previous year (e.g., for a bird nest located in 2017, we used vegetation layers from 2016). We used vegetation layers from the previous year because they would better represent the residual vegetation that was present when the birds were selecting nest sites. For nest selection and mortality risk, we did not include the individual layers of annual and perennial herbaceous vegetation as we hypothesized that sharp-tailed grouse would be unable to decipher the difference between these during the dormant season; however, we did include total herbaceous vegetation (sum of annual and perennial herbaceous vegetation). We did not evaluate the 1,600 m and 3,200 m scales for nesting and brood-rearing seasons because we hypothesized that female sharp-tailed grouse were likely not selecting these habitats at those scales. For the brooding and early nonbreeding season (1 Sep–30 Nov) we used all vegetation, topographic, and anthropogenic variables from the year of the locations. During the early and late (1 Dec–31 Mar) nonbreeding seasons we did not evaluate the 30-m and 100-m scales as the accuracy of our locations during the nonbreeding season was between 50 m and 100 m and including these finer scales would not properly represent our data. Because the majority of our study area was covered in snow during the late nonbreeding season, we excluded annual and herbaceous vegetation cover, non-sagebrush shrub cover, and total shrub cover; for the final models predicting late nonbreeding season habitat selection and mortality risk we included only one of the following covariates: bare ground, herbaceous vegetation cover, and litter because any of these might represent spaces between shrubs. For bare ground, herbaceous vegetation, and litter during the late non-breeding season, we selected the variable with the lowest Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). For the late nonbreeding season, we used vegetation covariates from growth year of the vegetation. For example, if a location was from March 2018, we used vegetation data from 2017 because vegetation growth had not started yet in 2018. For a complete list of variables and scales used for modeling in each season, see TABLES

Table **3.1**.

For lek-site selection and lek size, we only included variables that we thought might influence leks. These included bare ground and herbaceous vegetation that might be selected for because they represented open ground; coniferous and deciduous forest canopy cover because we thought these might be avoided and they represented generally higher elevations in our study area; sagebrush cover because this was the dominant cover type in our study area; total shrub cover as leks might not be only in sagebrush; distance to oil and gas infrastructure and distance to roads because we wanted to know if anthropogenic features influenced leks; and all three topographic variables because topography has been found to influence prairie grouse lek locations in other studies (McKenna et al. 2012, Hovick et al. 2015, Connelly et al. 2024). Because we were not quantifying if leks moved less than 30 m (none of the leks moved more than 10 m during our study, J. D. Lautenbach, personal observation) we did not include the 30-m scale in either our lek-site selection or lek size analyses. Because leks in our study did not move, we conducted our lek-site selection analyses on the average vegetation conditions during our study. We conducted our lek size analysis for annual lek size (2017–2019) in addition to average lek size (Appendix B1: Table B1). For annual lek counts we used the prior year's vegetation conditions as these are likely what was available when male sharp-tailed grouse started attending the leks in late February/early March (e.g., for 2017 lek counts we used 2016 vegetation conditions and seasonal female habitat selection/mortality risk models predicted to 2016 vegetation data). For results on annual lek size, see Appendix C.

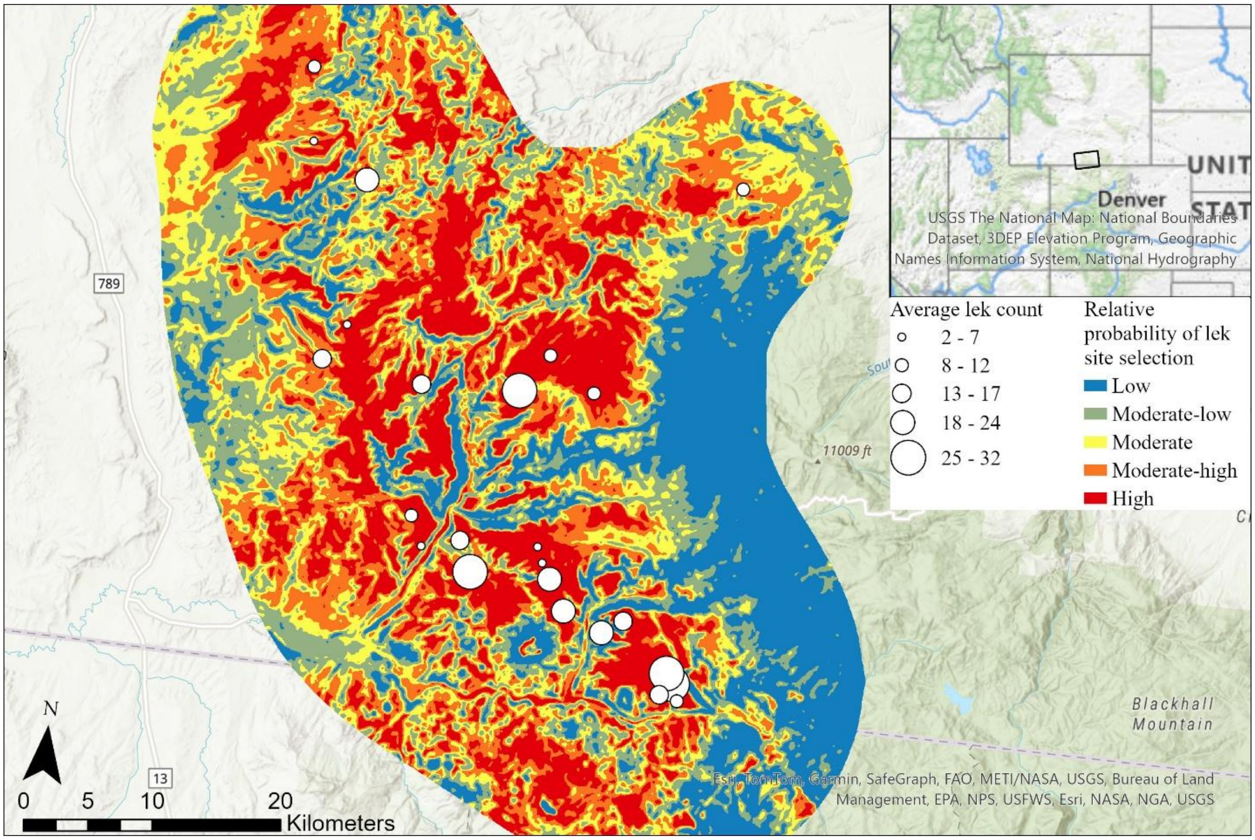
Statistical Analysis

Variable selection and model development. For all analyses, we transformed all covariates on the z-scale and back transformed them for plotting. For modeling seasonal habitat selection, seasonal mortality risk, lek-site selection, and lek size in relation to landscape features, we first screened each of the vegetation, topographic, and anthropogenic features separately (TABLES
Table **3.1**)) to identify the distance bin and relationship (linear or linear + quadratic) that most impacted the process (selection, mortality risk, or size). We tested both linear and quadratic (linear + quadratic) relationships for each scale of landscape features and a null model; we ranked these models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and selected the model with the best fit to proceed in our modeling process (Burnham and Anderson 2002). Once the scale and relationship of each covariate was identified, we prevented strong collinearity between covariates by removing covariates with the highest variance inflation factors until all covariates had variance inflation factors less than three (Zuur et al. 2010); when all covariates had a variance inflation factor less than 3, all covariates had $|r| \leq 0.65$. Pearson's correlation matrices for each season can be found in Appendix B: Tables B2–B24. Once correlated variables were removed, we developed a global model that included all non-correlated variables at their most predictive spatial scales. We used the *dredge* function from the *MuMIn*

package in Program R (Bartoń 2023) to evaluate all possible subsets of the global model and selected the model with the lowest AIC$_c$ (Burnham and Anderson 2002). To help prevent over-fitting to our data sets, we limited the number of variables in each model to one variable per every 10 events (mortality events for survival models, individuals by season for selection models, and individual leks for lek-site selection and lek size models) by limiting the number of variables allowed within the *dredge* function in the *MuMIn* package (Bartoń 2023).

Seasonal habitat selection. We evaluated seasonal habitat selection by sharp-tailed grouse using a use vs. availability study design by modeling resource selection functions (RSF; Manly et al. 2002) during four seasons: nesting (nest location), brood-rearing (from hatch to 7-weeks post hatch), female early nonbreeding (1 Sep–30 Nov), and female late nonbreeding (1 Dec–31 Mar). To evaluate availability, we generated 40 times the number of random points as used points (Northrup et al 2013) within an estimated 99.9% fixed-kernel density polygon calculated from the used locations during each season using the *kernelUD* function in the package *adehabitatHR* in Program R (Calenge 2006). We extracted vegetation, anthropogenic, and topographic features for each season (outlined in TABLES

Table **3.1**) for used and random locations. We used a binomial generalized linear model with a 'cloglog' link function to develop our seasonal RSF models; we used the 'cloglog' link within our models because of the imbalanced dataset (40 random points per used location; Fisher 1922, Alves et al. 2023). We followed the steps outlined in the 'Variable selection and model development' section to generate a top model. We generated a predictive surface from the top model from each season. For each predictive surface, we placed the predicted response values in five relative probability bins based on quantiles: 0.0–0.2 (1, low probability), 0.2–0.4 (2, moderate-low probability), 0.4–0.6 (3, moderate probability), 0.6–0.8 (4, moderate-high probability), and 0.8–1.0 (5, high probability; see Figure **3.1** for an example). We used a *k*-fold cross-validation to assess the validity of each of our RSF models using cross-validated Spearman's-rank correlations (r_s; Boyce et al. 2002); we calculated overall r_s 100 times and averaged the values to get an averaged r_s and models with higher average r_s values corresponded to better predictive performance (Boyce et al. 2002).



Seasonal mortality risk models. To quantify the mortality risk of female sharp-tailed grouse during different seasons, we evaluated the influence of landscape features on the mortality risk of nests, broods, and adult females during the early and late nonbreeding seasons using the Andersen-Gill formulation of the Cox proportional hazards model (hereafter: Andersen-Gill models; Cox 1972, Andersen and Gill 1982). For nesting and brood-rearing seasons, we calculated daily mortality risk for nests and broods; for early and late nonbreeding seasons, we calculated weekly mortality risk. To calculate hazard ratios using Andersen-Gill models, we extracted vegetation, anthropogenic, and topographic features (see TABLES

Table **3.1**) around each grouse location during each life stage (nest, brood, and non-breeding). We followed the steps outlined in the 'Variable selection and model development' section to generate a top model. We used the *coxph* function in the package *survival* in Program R (Therneau and Grambsch 2000, Therneau 2024) to develop the Andersen-Gill models. We used our final model to generate a predictive surface of daily or weekly mortality risk. We rescaled the predicted models based on 5 quantiles, with the lowest quantile (0.0–0.2) representing low mortality risk and the highest quantile (0.8–1.0) representing the highest mortality risk; intermediate quantiles (0.2–0.4, 0.4–0.6, and 0.6–0.8) represent moderate-low mortality risk, moderate mortality risk, and moderate-high mortality risk, respectively. To evaluate the fits of our models, we used the overall *C* statistic (Pencina and D'Agostino 2004); we calculated overall *C* 100 times and averaged the values to get an averaged overall *C*. We considered values of averaged overall *C* between 0.5 and 0.7 to have moderate discrimination, values between 0.7 and 0.8 to have acceptable discrimination, values ≥0.8 to have excellent discrimination, and values ≤ 0.5 indicated that the model predicted the outcome no better than random (Smith et al. 2014). We used Andersen-Gill models to estimate overall nest survival for the incubation period (25 days), overall brood survival (to 49 days), early nonbreeding season survival, late nonbreeding survival, and cumulative nonbreeding survival (1 Sep–31 Mar) using the *survfit* and *coxph* functions in the *survival* package in Program R (Therneau and Grambsch 2000, Therneau 2024).

Lek-site selection. We evaluated lek-site selection by sharp-tailed grouse using a use vs. availability study design by modeling resource selection functions (RSF; Manly et al. 2002). To evaluate availability at the second-order scale (Johnson 1980), we generated 120 times the number of random points as lek locations (Northrup et al. 2013) within an estimated 95% fixed-kernel density polygon calculated from lek locations using the *kernelUD* function in the package *adehabitatHR* in Program R (Calenge 2006). For lek-site selection, we averaged landscape features (outlined in TABLES

Table **3.1**) and seasonal female habitat covariates (female habitat selection and mortality risk) across the years of our study (2017–2019) and extracted them to our lek locations and random points; seasonal female habitat covariates were extracted at the point scale and within 100, 200, 400, 800, 1,600, and 3,200-m distance bins. We followed the steps outlined in the 'Variable selection and model development' section to generate a top model for both lek-site selection related to landscape features (Hypothesis 1) and lek-site selection related to seasonal female habitat selection and mortality risk (Hypothesis 2); for seasonal female habitat selection and mortality risk, we did not test for the relationship (linear and linear + quadratic) of the variable and only evaluated the linear term. Once we identified the top models predicting lek-site selection relative to landscape features (Hypothesis 1) and seasonal female habitat (Hypothesis 2), we developed a final set of models to identify which of our three hypotheses best predicted lek-site selection. The test of our first hypothesis, which stated that lek sites were selected primarily irrespective of female-specific habitat, was represented by the top landscape features model. The test of our second hypothesis, which stated that lek sites were selected primarily relative to seasonal female habitat selection and mortality risk, was represented by the top seasonal female habitat selection and mortality risk model. Finally, the test of our third hypothesis, which stated that lek sites were selected relative to both seasonal female habitat and landscape features, was represented by combining the seasonal female habitat selection/mortality model and the landscape features models. We compared model support for each hypothesis using AIC_c and considered the model with the lowest AIC_c to be the best predicting model (Burnham and Anderson 2002) and considered the hypothesis related to that model to be the hypothesis best explaining lek-site selection. If models had ΔAIC_c within 2, we considered them to be competitive and present results from those models (Burnham and Anderson 2002).

Lek size. We evaluated the lek size of sharp-tailed grouse using a Poisson generalized linear regression model. We evaluated lek size on two different temporal scales: annual lek size and mean lek size across the three years of our study (2017–2019) rounded to the nearest integer. We extracted annual and averaged landscape features (outlined in TABLES

Table **3.1**) and seasonal female habitat covariates (habitat selection and mortality risk) surrounding lek locations; seasonal female habitat covariates were extracted at the point scale and within 100, 200, 400, 800, 1,600, and 3,200-m scales. We followed the steps outlined in the 'Variable selection and model development' section to generate a top model for both lek size related to landscape features (Hypothesis 1) and lek size related to seasonal female habitat selection and mortality risk (Hypothesis 2); for seasonal female habitat selection and mortality risk we did not test for the relationship (linear and linear + quadratic) of the variable and only evaluated the linear term. Once we identified the top models predicting lek size relative to landscape features (Hypothesis 1) and seasonal female habitat (Hypothesis 2), we developed a final set of models to identify which of our three hypotheses best predicted lek size. The test of our first hypothesis, which stated that lek size was determined by landscape features surrounding the lek, was represented by the top landscape features model. The test of our second hypothesis, which stated that lek size was determined by seasonal female habitat selection and mortality risk, was represented by the top seasonal female habitat selection and mortality risk model. Finally, the test of our third hypothesis, which stated that lek size was determined by both seasonal female habitat and landscape features, was represented by combining the seasonal female habitat selection/mortality model and the landscape features models. We compared model support for each hypothesis using AIC_c; we considered models within ΔAIC_c of 2 to be competitive and thus we present results from those models (Burnham and Anderson 2002). We compared the models for each year and average lek counts separately and present results from each model. For results on annual lek size, see Appendix C.

RESULTS

We located 162 total nests, including 52 failed nests (*n* = 134 females), and we tracked 108 total broods, 29 of which failed (*n* = 98 females; 10 females had a successful nest during two different years of our study) for a total of 888 brood locations. During the early nonbreeding season, we radio-tracked 95 females (19 mortality events) totaling 123 bird-seasons and 350 locations. During the late nonbreeding season, we tracked 83 females (37 mortality events) totaling 104 bird-seasons and 421 locations. We estimated overall nest survival during the 25-day incubation period as 0.73 (95% CI = 0.66, 0.80). The estimated overall brood survival to 49 days was 0.64 (95% CI = 0.55, 0.74). The estimated overall early nonbreeding survival was 0.88 (95% CI = 0.82, 0.94). We estimated overall late nonbreeding survival as 0.78 (95% CI = 0.70, 0.87). We estimated cumulative nonbreeding season survival (across early and late) as 0.68 (95% CI = 0.60, 0.77). We obtained lek count information from 24 leks throughout our study area. The mean number of individual grouse attending leks during our study was 16.6 (SE: 1.90; median: 14.5; range: 3–33; Appendix B: Table B1).

Seasonal Habitat Selection

Our top model predicting nest-site selection indicated that female sharp-tailed grouse selected nest sites with less bare ground, moderate to moderate-high herbaceous vegetation cover (maximum selection probability at 54.7% canopy cover, range 0.8–83.3%), moderate to moderate-high heat loads, moderate sagebrush cover (maximum selection probability at 17% cover, range 0–33%), moderate-high shrub cover (maximum selection probability at 29.5%, cover range: 3.4–40.8%), neutral topographic positions, and less rugged terrain relative to available conditions (Table 3.2, Appendix B: Figure B1). Cross validation indicated our final nest site selection model was an acceptable fit to the data ($r_s = 0.77$, $P < 0.001$, $n = 100$). Our top model predicting brood habitat indicated that female sharp-tailed grouse areas with less bare ground, less canopy cover of coniferous forest, low canopy cover of deciduous forest (maximum selection probability at 7.3% canopy cover, range 0.0–56.5%), moderate sagebrush cover (maximum selection probability at 14.2% cover, range 0.0–31.6%), moderate-high shrub cover (maximum selection probability at 29.4%, cover range: 3.5–41.38%), higher topographic positions, and less rugged terrain relative to available conditions during the brood-rearing season (Table 3.2, Appendix B: Figure B2). Cross validation indicated our final brood site selection model was an acceptable fit to our data ($r_s = 0.90$, $P < 0.001$, $n = 100$). Our top model predicting early non-breeding season habitat selection indicated that female sharp-tailed grouse selected areas with less bare ground, increased heat loads, moderate-high cover of perennial herbaceous vegetation (maximum selection probability at 47.2%, cover range: 5.9–53.0%), higher cover of sagebrush, moderate shrub heights (maximum selection at 63.6 cm, range: 0.1–109.8 cm), less rugged terrain, and neutral to neutral-high topographic positions relative to available conditions during the early nonbreeding season (Table 3.2, Appendix B: Figure B3). Cross validation indicated our final early non-breeding site selection model was an acceptable fit to our data ($r_s =$

0.88, $P < 0.001$, $n = 100$). Our top model predicting late non-breeding season habitat indicated that female sharp-tailed grouse selected areas with less bare ground, less deciduous forest canopy cover, areas closer to oil and gas infrastructure, moderate sagebrush cover (maximum selection at 12.0% canopy cover, range: 0.0–19.0%), moderate-high shrub heights (maximum selection at 67.2 cm, range: 0.0–91.6 cm), and moderate-high topographic positions relative to available conditions during the late nonbreeding season (Table 3.2, Appendix B: Figure B4). Cross validation indicated our final model predicting female sharp-tailed grouse habitat selection during the late nonbreeding season was an acceptable fit to our data ($r_s = 0.92$, $P < 0.001$, $n = 100$).

Seasonal Mortality Risk

Our top model predicting sharp-tailed grouse nest mortality risk indicated that hazards to sharp-tailed grouse nest mortality risk were highest with intermediate herbaceous vegetation cover (mortality risk was greatest at 51.3% cover, range: 33.4–72.5%), mortality risk decreased as shrub height increased, and mortality risk was lowest at lower topographic positions (Table 3.3, Appendix B: Figure B5). Cross validation indicated our final model predicting nest mortality risk had moderate discrimination ability (Overall $C = 0.56$). Our top model predicting sharp-tailed grouse brood mortality risk indicated that hazards to sharp-tailed grouse brood mortality risk decreased as canopy cover of deciduous forest decreased and hazards were minimized at intermediate cover of perennial herbaceous vegetation (mortality risk was lowest at 48.3% cover, range: 27.7–62.0%; Table 3.3, Appendix B: Figure B6). Cross validation indicated our final model predicting brood mortality risk had moderate discrimination ability (Overall $C = 0.68$). Our top model predicting sharp-tailed grouse mortality risk during the early nonbreeding season indicated that hazards to sharp-tailed grouse mortality risk during the early nonbreeding season increased as the cover of perennial herbaceous vegetation increased and hazards decreased as topographic positions increased (Table 3.3, Appendix B: Figure B7). Cross validation indicated our final model predicting early nonbreeding mortality risk had acceptable discrimination ability (Overall *C* = 0.78). Our top model predicting mortality risk of female sharp-tailed grouse during the late nonbreeding season indicated that hazards to sharp-tailed grouse mortality risk during the late nonbreeding season decreased as bare ground cover decreased, decreased at lower heat loads, decreased as sagebrush cover decreased, and were lowest at lower topographic positions (Table 3.3, Appendix B: Figure B8). Cross validation indicated our final model predicting nonbreeding mortality risk had moderate discrimination ability (Overall *C* = 0.68).

Lek-site Selection

Our top model predicting lek-site selection based on landscape features indicated that sharp-tailed grouse lek sites were located in areas within greater herbaceous vegetation cover within 200 m, greater shrub cover within 3,200 m, and less rugged terrain relative to available (Table 3.4; Appendix B: Figure B9). Our top model predicting sharp-tailed grouse lek locations based on seasonal female habitat conditions indicated that sharp-tailed grouse leks were located in areas with lower brood mortality risk, lower nest mortality risk, and in areas with a higher proportion of selected late nonbreeding habitat relative to available (Table 3.4; Appendix B: Figure B10). Our top model evaluating lek-site selection relative to landscape features and/or seasonal female habitat was the model that included a combination of both landscape features and seasonal female habitat (H3). Nest mortality risk within 400 m and percent cover of herbaceous vegetation within 200 m were negatively correlated ($r = -0.81$) and late nonbreeding season habitat selection within 3,200 m and shrub cover within 3,200 m were positively correlated ($r = 0.87$); we did not include correlated terms in the same model and included four variations of our third hypothesis (Table 3.5, H3a–H3d). The top model predicting sharp-tailed grouse lek-site selection (H3d) indicated that sharp-tailed grouse leks were located in areas with less rugged terrain relative to available, lower brood mortality risk relative to available, lower nest mortality risk relative to available, and in areas with a higher proportion of selected late nonbreeding habitat relative to available (Table 3.4, Figure 3.2).

Lek Size

We modeled lek size as averaged lek size (2017–2019) and annual lek size (see Appendix S2 for annual lek size results). Our top model predicting average lek size based on landscape features indicated that lek sizes were larger in areas with less bare ground and lek size was larger at the highest and lowest heat load indices at lek sites (Table 3.6, Figure 3.3). Our top model predicting average lek size based on seasonal habitats indicated that lek sizes were larger in areas with higher early nonbreeding season mortality risk within 400 m, lek size was larger at leks surrounded by more early nonbreeding season habitat within 800 m, and lek size was larger at leks surrounded by lower nest mortality risk within 800 m (Table 3.6, Appendix B: Figure B11). Our top model evaluating overall sharp-tailed grouse lek size in relation to landscape features and/or seasonal female habitat was our landscape features model (H1; Table 3.7). Our top model for average lek size based on landscape features (H1) indicated that lek sizes were larger at leks surrounded by less bare ground and lek size was larger at the highest and lowest heat load indices (Table 3.6, Figure 3.3).

DISCUSSION

Identifying the mechanisms that explain lek-site selection and lek size have important conservation implications, as many management plans for prairie grouse species are focused on areas surrounding leks (Giesen and Connelly 1993, Walsh et al. 2010, Hagen et al. 2004, 2016, Hoffman et al. 2015). We found that seasonal habitat selection and mortality risk of female sharp-tailed grouse were influenced by vegetation, topographic, and anthropogenic features. Our results for sharp-tailed grouse lek-site selection supported our third hypothesis, where lek size was influenced by a combination of landscape features and seasonal female habitat selection and mortality. For sharp-tailed grouse lek size, our results indicated that features influencing lek size varied by year, with some years (average lek size and lek size in 2018) showing support for our first hypothesis (landscape features influencing lek size) and other years (lek size in 2017 and 2019) demonstrating support for our third hypothesis (combination of landscape features and seasonal female habitat selection and mortality risk). Our results suggest a complex relationship between lek dynamics (locations and size) and the habitat surrounding leks. This complex relationship with lekking sites and their environment provides some support for sharp-tailed grouse lek occurrence being related to the lek hotspot hypothesis, however it also suggests that the mechanisms that influence precise lek locations might be more nuanced.

The lek hotspot hypothesis predicts that leks will be located in areas where males are more likely to encounter females (Bradbury and Gibson 1983, Beehler and Foster 1988, Bradbury et al. 1989a). When evaluating lek site selection in relation to seasonal female habitat and mortality risk, our results indicate that lek sites were in areas with lower brood mortality risk within 3,200 m, lower nest mortality risk within 400 m, and in areas with more late nonbreeding season habitat within 3,200 m (correlated with early nonbreeding season mortality risk and brood, nest, and early nonbreeding season habitat selection). Leks are probably located in areas with more late nonbreeding habitat because females are still occupying late nonbreeding habitat during late February/early March when males start to attend leks (Gratson 1988), that might represent a transition between nonbreeding habitat and nesting habitat. This is similar to greater sage-grouse (*Centrocercus urophasianus*) lek sites, which have been found to be located in areas used by females during migration between nonbreeding and nesting habitat (Gibson 1996). We hypothesize that nest and brood mortality risk may influence lek locations because these areas are likely to produce more juveniles, and therefore, while young males are a part of a brood they might perceive the areas they are in as good habitat. More research is needed to evaluate the dispersal of juvenile sharp-tailed grouse and to identify if males and/or females remain/return to their natal areas where they were raised to evaluate this hypothesis. Within our study, female sharp-tailed grouse selected nest sites in areas with less rugged terrain, similar to how sharp-tailed grouse lek sites are selected relative to landscape features. Sharp-tailed grouse lekking sites in Saskatchewan, Canada were also located in less rugged terrain (Burda et al. 2022).

Prairie grouse leks are typically located on broad hilltops, areas with shorter vegetation, and in less rugged areas (Connelly et al. 2024, Hagen and Giesen 2020, Johnson et al. 2020). Our results indicated that at finer scales (≤400 m distance bins), sharp-tailed grouse in our study area were selecting lek sites with less rugged terrain, more herbaceous vegetation cover within 200 m, and more shrub cover within 3,200 m. Sites with less rugged terrain are less likely to impede sound waves as they propagate across the landscape (McKenna et al. 2012), however more research is needed to see if topography influences the propagation of sharp-tailed grouse calls. Sharp-tailed grouse leks in our study were located in areas with more herbaceous vegetation cover within 200 m, likely because our study area was dominated by shrub cover and areas with more herbaceous vegetation provide better opportunities for females to view and compare males on leks. Similarly, leks of prairie grouse in other areas are located in areas with sparse/shorter vegetation than the surrounding areas (Hagen and Giesen 2020, Johnson et al. 2020, Connelly et al. 2024). We hypothesize that our observed lek-site selection for increased shrub cover within

3,200 m was due to this being the primary habitat for nesting opportunities and we observed selection for increased shrub cover in all seasons. In our study, we did not observe direct selection for hilltops (higher topographic positions) typical of prairie grouse (Hagen and Giesen 2020, Johnson et al. 2020, Connelly et al. 2024); however, this was likely due to the elevational gradient at our study site with slopes generally increasing gradually until a steep valley is reached and some of the leks being located on broad hill tops while others were located on flatter locations along a hillside.

Lek size is commonly used to track trends in population changes (Ross et al. 2016b, Edmunds et al. 2018, Baines and Aebischer 2023) and differences in lek size may be a result of landscape features and female traffic patterns around leks (higher female traffic equals larger leks; Bradbury et al. 1989b). We found mixed support for lek size being related to landscape features and seasonal female habitat selection and mortality risk. Overall, we found that average lek size was most influenced by landscape features. However, when evaluating lek size on an annual basis, we found that annual lek size was influenced by a combination of landscape features and seasonal female habitat (2017 and 2019) and only landscape features (2018). There was inconsistency between the years, likely due to small sample sizes and missing data in some of the years (i.e., we were unable to visit all leks each year). We recommend continued research to evaluate the relationship between annual lek sizes and the landscape features and seasonal female habitat surrounding them. We found that sharp-tailed grouse lek size in relation to landscape features did have consistency between years and for averaged lek counts, with all analyses indicating that lek sizes were largest with the highest and lowest heat load indices at lek sites. Lek sites were generally located in areas with warmer heat load indices (HLI values ranged from 0.68–76) and the relation of lek sizes to heat load indices indicates that leks with higher and lower heat loads were larger (within the HLI range of occupied leks). Our overall findings that sharp-tailed grouse lek size was more related to landscape features then seasonal female habitat are in contrast with lesser prairie-chickens (*Tympanuchus pallidicinctus*), where larger leks are located in areas with a greater proportion of nesting habitat surrounding them (Gehrt et al. 2020). In greater sage-grouse, daily male lek attendance was correlated with female traffic patterns, with more males attending leks where more females occurred, resulting in fluctuating lek sizes within a season (Bradbury et al. 1989b). We note that the lek counts that we used might include some females because male and female sharp-tailed grouse can be difficult to distinguish from a distance and many of the leks in our study area were counted using flush counts.

Habitat selection for female sharp-tailed grouse varied by season. However, there were some similarities as they selected areas with less bare ground during all seasons. Additionally, female sharp-tailed grouse selected less rugged terrain than available during the nesting, brood-rearing, and early nonbreeding seasons, similar to lek-site selection. Selection patterns of sagebrush and shrub cover were similar during the nesting and brood-rearing seasons, where they selected areas with greater sagebrush and shrub cover, consistent with other studies on sharp-tailed grouse in mountain shrub communities (Klott and Lindzey 1990, Goddard et al. 2009). These similar uses of landscape features indicate that there is some overlap in habitat needs among seasons. The similarities between nesting and brood rearing habitats suggest that there is a close relationship between nesting and brood-rearing habitats and is likely related to brood locations being close to nesting locations (especially within 1–2 weeks of hatching). This link is further supported by a mismatch in selection for herbaceous vegetation cover at nest site that resulted in increased nest mortality risk while reducing brood mortality risk, suggesting a tradeoff in nest placement for nest survival and future brood survival. Our results also suggest that during the early nonbreeding season female sharp-tailed grouse demonstrate a potential tradeoff between foraging opportunities in areas of greater perennial herbaceous cover (which they select for) and survival, because mortality risk was higher in areas with greater herbaceous cover. Contrary to some of our findings of a mismatch between selected habitat and mortality risk, prairie-chickens select nesting and brood-rearing habitat that results in greater survival (Matthews et al. 2013, Lautenbach 2015, Lautenbach et al. 2019). Our lack of findings demonstrating that selected habitats increased survival may be because of the scale we evaluated vegetation. We recommend that future studies interested in understanding tradeoffs within seasons evaluate vegetation conditions using a combination of remotely sensed data and field surveys.

We observed minimal relationships between anthropogenic features and female habitat, lek-site selection, and lek size. We found that females selected late nonbreeding habitat closer to oil and gas infrastructure than available, potentially because oil and natural gas infrastructure were built in late nonbreeding habitat. Within our study area, oil and gas infrastructure was limited and typically occurred in lower elevations and lower elevation areas typically received less snow, so selection for areas closer to oil and natural gas might actually be selection for areas with less snow cover. Lek size in 2019 was related to oil and natural gas infrastructure, with lek size increasing as distance to oil and natural gas infrastructure increased. Throughout our study area, roads occurred at low densities and in many locations were limited to small, unimproved roads that were not identified in the NLCD data layers we used. Previous studies on lekking grouse have found relationships between anthropogenic disturbances and grouse survival and habitat selection (Hagen et al. 2011, Dinkins et al. 2014, Hovick et al. 2014, Plumb et al. 2019, Lawrence et al. 2021) and lek locations and attendance (Gregory and Beck 2014, Green et al.

2017, Burda et al. 2022). The density of anthropogenic disturbances in our study area were probably too low and too concentrated in certain areas to demonstrate any major influences on habitat selection, mortality risk, lek-site selection, and lek size.

In our study area, sharp-tailed grouse lek-site selection was influenced by a combination of landscape features and seasonal female habitat selection and mortality risk. In particular, lek-site selection was positively related to late nonbreeding habitat selection (leks were in areas with more late nonbreeding habitat) and negatively related to nest mortality risk (leks were in areas with lower nest mortality risk). Our results and results from studies of other prairie grouse species put forward that leks are generally surrounded by breeding habitat (Schroeder and White 1993, Aulicky 2020, Gehrt et al. 2020), suggesting that current management practices being focused on areas surrounding leks are appropriate. Our findings support the lek hotspot hypothesis in that sharp-tailed grouse leks were located in areas with lower brood mortality risk, lower nest mortality risk, and more late nonbreeding season habitat.

CONSERVATION IMPLICATIONS

Management decisions for prairie grouse often center on lek locations (Giesen and Connelly 1993, Hagen et al. 2004, 2016). Our results support these actions in that sharp-tailed grouse leks in south-central Wyoming occurred in areas with higher probability of late nonbreeding season habitat selection and lower nest mortality risk. Leks were located in areas important for both the nonbreeding season and nesting seasons, therefore, searching for leks in areas with no previously identified leks that fit these conditions could provide valuable insight on where sharp-tailed grouse occur. Continued monitoring and searching for sharp-tailed grouse leks may provide insight into habitat conditions surrounding them.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All capture, handling, and monitoring protocols were approved by the University of Wyoming Institutional Animal Care and Use Committee (protocol 20170324AP00266 [versions -01, -02, and -03]) and by the Wyoming Game and Fish Department (Chapter 33-1098).

DATA AVAILABILITY STATEMENT

Data and relevant code (Lautenbach et al., 2025) are available from Dryad: http://datadryad.org/stash/share/UopZzHUJC8MlMLGBIHsFQxbOHVNFTeWA7I8qbYz93ms. Lek location data are not available as these are deemed sensitive by the Wyoming Game and Fish Department; we do provide anonymized lek data with landscape feature data extracted to the lek locations. Specific lek location data may be requested from the Wyoming Game and Fish Department.

AUTHOR CONTRIBUTIONS

JDL, ACP, and JLB, formulated the questions; JDL and ACP collected data; JLB supervised research; JDL analyzed the data; JDL drafted the manuscript; JDL, ACP and JLB edited the manuscript. All authors reviewed and approved this manuscript before submission.

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TABLES

Table 3.1. List of variables, their abbreviations (abbr.), and the distance bins used in habitat models (resource selection and mortality risk models) and lek-site selection and lek size modeling for sharp-tailed grouse (*Tympanuchus phasianellus*) in south-central Wyoming, 2017–2020.

			Distance-bins included in analyses (m)					
Category	**Variable**	**Abbr.**	**Nesting**	**Brooding**	**Early non-breeding**	**Late non-breeding**	**Lek-site selection**	**Lek size**
Vegetation	Annual herbaceous vegetation cover[a]	annherb	–	30[e]–800[f]	100–3200[g]	–	–	–
	Bare ground[a]	bare	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	100–3200[g]	100–3200[g]
	Conifer canopy cover[b]	conifer	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	100–3200[g]	100–3200[g]
	Deciduous canopy cover[b]	deciduous	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	100–3200[g]	100–3200[g]
	Herbaceous vegetation cover[a]	herb	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	100–3200[g]	100–3200[g]
	Litter cover[a]	litter	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	–	–
	Non-sagebrush shrub cover[a]	nonsage	30[e]–800[f]	30[e]–800[f]	100–3200[g]	–	–	–
	Perennial herbaceous vegetation cover[a]	perherb	–	30[e]–800[f]	100–3200[g]	–	–	–
	Sagebrush (*Artemisia* sp.) cover[a]	sage	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	100–3200[g]	100–3200[g]
	Shrub height (cm)[a]	shrubht	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	–	–
	Total shrub cover[a]	totshrub	30[e]–800[f]	30[e]–800[f]	100–3200[g]	–	100–3200[g]	100–3200[g]
Anthropogenic	Distance to all roads[c]	droads	30[e]	30[e]	30[e]	30[e]	30[e]	30[e]
	Distance to oil and gas infrastructure[c]	doil	30[e]	30[e]	30[e]	30[e]	30[e]	30[e]

Topographic	Heat load index[d]	hli	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	100–3200[g]	100–3200[g]
	Terrain ruggedness index[d]	tri	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	100–3200[g]	100–3200[g]
	Topographic position index[d]	tpi	30[e]–800[f]	30[e]–800[f]	100–3200[g]	100–3200[g]	100–3200[g]	100–3200[g]

Note: En dashes (–) represent variables that were not included in a model.

[a] Derived from rangeland fractional component data set (Xian et al. 2015, Rigge et al. 2019, 2020)

[b] Derived from 30-m forest canopy cover layers (Coulston et al. 2012)

[c] Derived from National Land Cover Database layers, only calculated at the 30 m scale

[d] Derived from digital elevation model (USGS 2011)

[e] 30 represents the base spatial grain size and therefor does not contain data averaged using a moving window.

[f] Distance bins include 30 m, 100 m, 200 m, 400 m, and 800 m

[g] Distance bins include 30 m, 100 m, 200 m, 400 m, 800 m, 1,600 m, and 3,200 m.

Table 3.2. Covariates, standardized beta coefficients (β), standard errors (SE), and 95% CIs for variables from the top binomial logistic regression models for each season evaluated (nesting, brood-rearing, early nonbreeding, and late nonbreeding) for sharp-tailed grouse (*Tympanuchus phasianellus*) habitat selection in Carbon County, Wyoming, USA, 2017–2020.

Life history stage	**Covariate**	**Distance bin**	**β**	**SE**	**95% CI**
Nesting	bare	100	-6.83*	0.80	(-9.30, -5.36)
	bare^2	100	1.79*	0.27	(1.37, 2.22)
	herb	200	2.72*	0.62	(1.61, 4.03)
	herb^2	200	-1.25*	0.39	(-2.07, -0.57)
	hli	800	0.69*	0.14	(0.43, 0.97)
	hli^2	800	-0.46*	0.12	(-0.71, -0.25)
	sage	30	1.02*	0.18	(0.68, 1.38)
	sage^2	30	-0.51*	0.12	(-0.75, -0.28)
	shrub	800	0.81*	0.13	(0.30, 1.43)
	shrub^2	800	-0.35*	0.17	(-0.71, -0.28)
	tpi	800	0.40*	0.13	(0.16, 0.66)
	tpi^2	800	-0.24*	0.11	(-0.47, -0.05)
	tri	100	-1.38*	0.27	(-1.97, -0.90)
	tri^2	100	-0.50*	0.27	(-1.08, -0.01)
Brood-rearing	bare	800	-4.38*	0.24	(-4.86, -3.81)
	conif	800	-7.29*	1.06	(-9.52, -5.38)
	decid	800	0.26*	0.10	(0.06, 0.46)
	decid^2	800	-0.47*	0.10	(-0.68, -0.28)
	sage	100	0.89*	0.08	(0.73, 1.06)
	sage^2	100	-0.63*	0.06	(-0.74, -0.52)
	shrub	800	1.77*	0.16	(1.47, 2.08)
	shrub^2	800	-0.76*	0.09	(-0.94, -0.59)
	tpi	100	0.35*	0.07	(0.22, 0.47)
	tri	200	-1.66*	0.11	(-1.89, -1.46)
	tri^2	200	-0.45*	0.10	(-0.65, -0.26)
Early nonbreeding	bare	1,600	-1.02*	0.26	(-1.54, -0.51)
	bare^2	1,600	0.45*	0.06	(0.26, 0.57)
	hli	3,200	0.23*	0.06	(0.11, 0.35)
	perherb	3,200	2.12*	0.29	(1.59, 2.73)
	perherb^2	3,200	-0.75*	0.18	(-1.12, -0.42)
	sage	3,200	0.37*	0.13	(0.11, 0.63)
	shrubht	400	1.84*	0.24	(1.39, 2.34)

	shrubht^2	400	-0.49*	0.10	(-0.69, -0.30)
	tpi	200	0.64*	0.08	(0.49, 0.81)
	tpi^2	200	-0.16*	0.04	(-0.25, -0.08)
	tri	3,200	-0.15	0.08	(-0.30, 0.01)
Late nonbreeding	bare	400	-1.45*	0.23	(-1.90, -1.00)
	bare^2	400	0.32*	0.06	(0.16, 0.41)
	decid	3,200	-0.32*	0.11	(-0.54, -0.10)
	doil	30	-0.15	0.09	(-0.32, 0.01)
	sage	3,200	0.68*	0.13	(0.41, 0.94)
	sage^2	3,200	-0.64*	0.10	(-0.84, -0.46)
	shrubht	400	1.55*	0.20	(1.17, 1.96)
	shrubht^2	400	-0.36*	0.08	(-0.53, -0.21)
	tpi	400	0.47*	0.06	(0.35, 0.60)
	tpi^2	400	-0.07*	0.03	(-0.13, -0.02)

Note: An asterisk (*) denotes beta (β) coefficient whose 95% CI does not overlap zero.

Table 3.3. Covariates, standardized beta coefficients (β), standard errors (SE), and 95% CIs for variables from the top Andersen-Gill mortality risk models for each season evaluated (nesting, brood-rearing, early nonbreeding, and late nonbreeding) for sharp-tailed grouse (*Tympanuchus phasianellus*) mortality risk based on landscape features in Carbon County, Wyoming, USA, 2017–2020.

Life history stage	**Covariate**	**Distance bin**	**β**	**SE**	**95% CI**
Nesting	herb	100	4.21*	1.80	(0.68, 7.73)
	$herb^2$	100	-2.71*	1.11	(-4.88, -0.54)
	shrubht	–	-0.50	0.29	(-1.08, 0.07)
	tpi	800	1.53*	0.19	(0.06, 0.79)
Brood-rearing	decid	800	-1.08 *	0.44	(-1.95, -0.21)
	perherb	400	-3.04*	0.79	(-4.58, -1.50)
	$perherb^2$	400	1.33*	0.40	(0.54, 2.12)
Early nonbreeding	perherb	1,600	2.03*	0.56	(0.94, 3.12)
	tpi	100	-0.63	0.24	(-1.10, -0.17)
Late nonbreeding	bare	3,200	0.80	0.25	(0.30, 1.29)
	hli	3,200	0.50	0.23	(0.06, 0.95)
	sage	100	0.43	0.19	(0.05, 0.81)
	tpi	3,200	0.31	0.17	(-0.03, 0.64)

Note: An asterisk (*) denotes beta (β) coefficient whose 95% CI does not overlap zero.

Table 3.4. Covariates, standardized beta coefficients (β), standard errors (SE), and 95% CIs for the top binomial logistic regression models predicting lek-site selection based on landscape features (H1), seasonal female habitat (H2), and a combination of landscape features and seasonal female habitat (H3) in Carbon County, Wyoming, USA, 2017–2020.

Hypothesis	**Covariate**	**Distance Bin**	**β**	**SE**	**95% CI**
H1–Landscape features	herb	200	0.97*	0.27	(0.03, 0.10)
	shrub	3,200	1.63*	0.35	(0.18, 0.43)
	tri	200	-2.29*	0.57	(-3.51, -1.28)
H2–Seasonal female habitat	broodmort	3,200	-1.00*	0.32	(-1.63, -0.34)
	nestmort	400	-1.66*	0.41	(-2.50, -0.90)
	latenbRSF	3,200	0.86*	0.49	(0.02, 1.94)
H3a–Combination	tri	200	-2.71*	0.55	(-3.85, -1.73)
	broodmort	3,200	-0.94*	0.27	(-1.47, -0.39)
	nestmort	400	-1.24*	0.37	(-1.98, -0.57)
	latenbRSF	3,200	1.29*	0.52	(0.38, 2.44)

Notes: Broodmort represents mean brood mortality risk, nestmort represents mean nest mortality risk, and latenbRSF represents mean relative probability of late nonbreeding habitat selection. An asterisk (*) denotes beta (β) coefficient whose 95% CI does not overlap zero.

Table 3.5. Model selection results for binomial logistic regression models predicting sharp-tailed grouse (*Tympanuchus phasianellus*) lek-site selection as predicted by landscape features (H1), seasonal female habitat (H2), and a combination of seasonal habitat and landscape features (H3), Carbon County, Wyoming, USA, 2017–2020.

Hypothesis	**Model**	**K**[a]	**ΔAIC$_c$**[b]	***w_i***[c]
H3d	tri200 + broodmort3200 + nestmort400 + latenbRSF3200	5	0.00	0.95
H3b	shrub3200 + tri200 + broodmort3200 + nestmort400	5	5.96	0.05
H3c	herb200 + tri200 + broodmort3200 + latenbRSF3200	5	11.69	0.00
H3a	herb200 + shrub3200 + tri200 + broodmort3200	5	15.77	0.00
H1	herb200 + shrub3200 + tri200	4	17.63	0.00
H2	broodmort3200 + nestmort400 + latenbRSF3200	4	45.26	0.00
–	Null	1	92.20	0.00

Notes: There are four H3 models because shrub3200 and latenbRSF3200 were correlated (|r| = 0.87) and herb200 and nestmort400 were correlated (|r| = 0.81); therefore, we did not include any correlated terms in the same model and tested all possibilities of the models. Broodmort3200 represents mean brood mortality risk within 3,200 m of a lek, nestmort400 represents mean nest mortality risk within 400 m of a lek, and latenbRSF3200 represents mean relative probability of late nonbreeding habitat selection within 3,200 m of a lek.

[a] Number of parameters

[b] Lowest AIC$_c$ value = 187.80

[c] AIC$_c$ weight

Table 3.6. Covariates, standardized beta coefficients (β), standard errors (SE), and 95% CIs for variables included in the top Poisson regression models predicting the average lek size of sharp-tailed grouse (*Tympanuchus phasianellus*) as predicted by landscape features (H1), seasonal habitat (H2), and seasonal habitat and landscape features (H3) in Carbon County, Wyoming, USA, 2017–2020.

Hypothesis	Covariate	Distance Bin	β	SE	95% CI
H1–Landscape features	bare	400	-0.44*	0.18	(-0.81, -0.10)
	hli	200	0.52*	0.13	(0.25, 0.77)
	hli^2	200	2.33*	0.34	(1.67, 3.00)
H2–Seasonal habitat	earlynbmort	400	0.32*	0.12	(0.10, 0.55)
	earlynbRSF	800	0.45*	0.13	(0.19, 0.71)
	nestmort	800	-0.23	0.13	(-0.48, 0.02)
H3–Combination	bare	400	-0.73*	0.23	(-1.19, -0.29)
	hli	200	0.56*	0.15	(0.26, 0.86)
	hli^2	200	2.54*	0.15	(1.67, 3.41)
	earlynbmort	400	-0.18	0.14	(-0.46, 0.10)
	earlynbRSF	800	-0.24	0.18	(-0.60, 0.11)
	nestmort	800	-0.25	0.14	(-0.53, 0.03)

Notes: Earlynbmort represents early nonbreeding season mortality risk; earlynbRSF represents early nonbreeding season habitat selection; nestmort represents nest mortality risk. An asterisk (*) denotes beta (β) coefficient whose 95% CI does not overlap zero.

Table 3.7. Model selection results for Poisson regression models predicting sharp-tailed grouse (*Tympanuchus phasianellus*) lek size based on landscape features (H1), seasonal habitat (H2), and a combination of seasonal habitat and landscape features (H3) for average lek counts, Carbon County, Wyoming, USA, 2017–2020.

Model	**Hypothesis**	**K**[a]	**ΔAIC$_c$**	***w$_i$***[b]
bare400 + hli200 + hli200^2	H1	4	0.00[c]	0.95
bare400 + hli200 + hli200^2 + earlynbmort400 + earlynbRSF800 + nestmort800	H3	6	5.90	0.05
earlynbmort400 + earlynbRSF800 + nestmort800	H2	3	39.39	0.00
Null	–	1	59.37	0.00

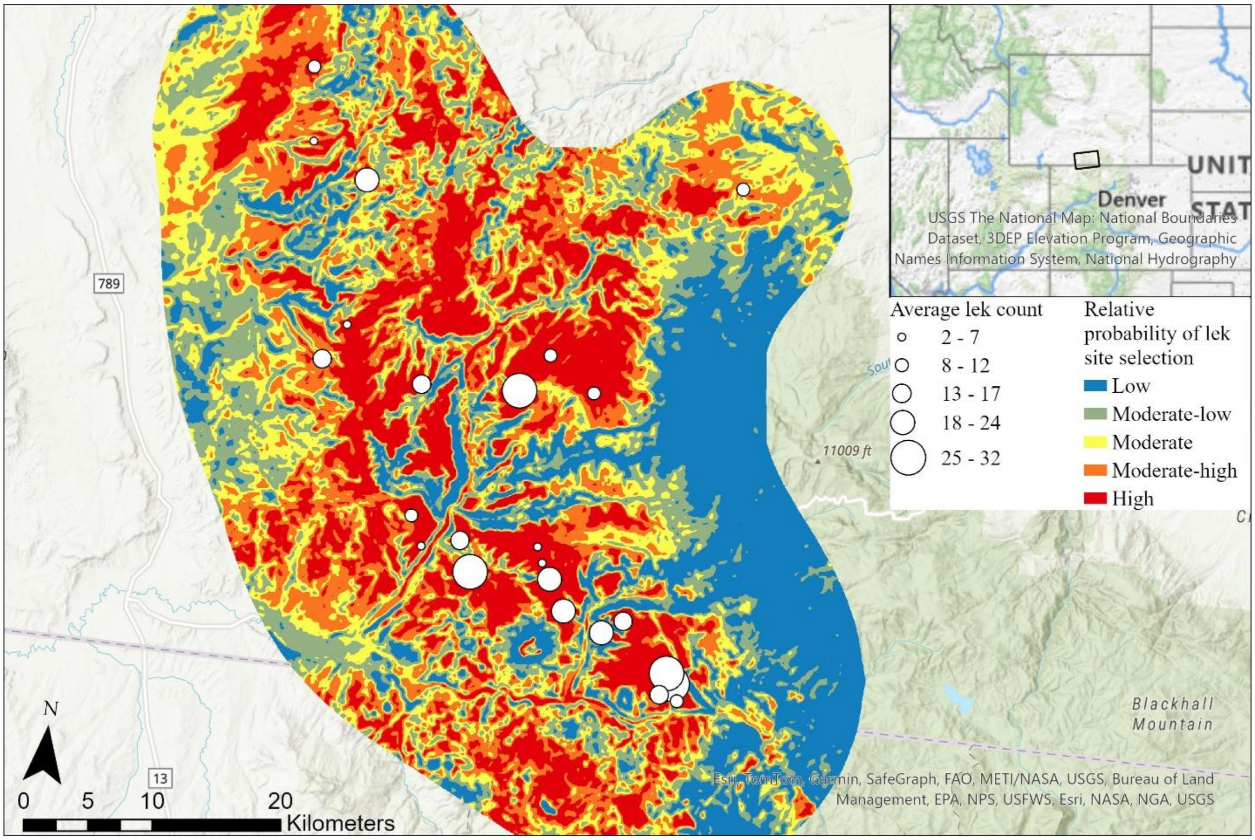
Notes: Earlynbmort represents early nonbreeding season mortality risk; earlynbRSF represents early nonbreeding season habitat selection; nestmort represents nest mortality risk.

[a] Number of parameters

[b] AIC$_c$ weight

[c] Lowest AIC$_c$ value = 164.76

FIGURES



USGS The National Map: National Boundaries Dataset, 3DEP Elevation Program, Geographic Names Information System, National Hydrography

Esri, TomTom, Garmin, SafeGraph, FAO, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, USFWS, Esri, NASA, NGA, USGS

Figure 3.1. Map of study area and known active lek locations (n = 24; white circles) for sharp-tailed grouse (*Tympanuchus phasianellus*) in Carbon County, Wyoming, USA 2017–2020. Leks are plotted on the relative probability of lek-site selection as predicted by terrain ruggedness index within 200 m, brood mortality risk within 3,200 m, nest mortality risk within 400 m, and late nonbreeding season habitat selection within 3,200 m. Cooler colors represent lower probabilities and warmer colors represent higher probabilities of selection.

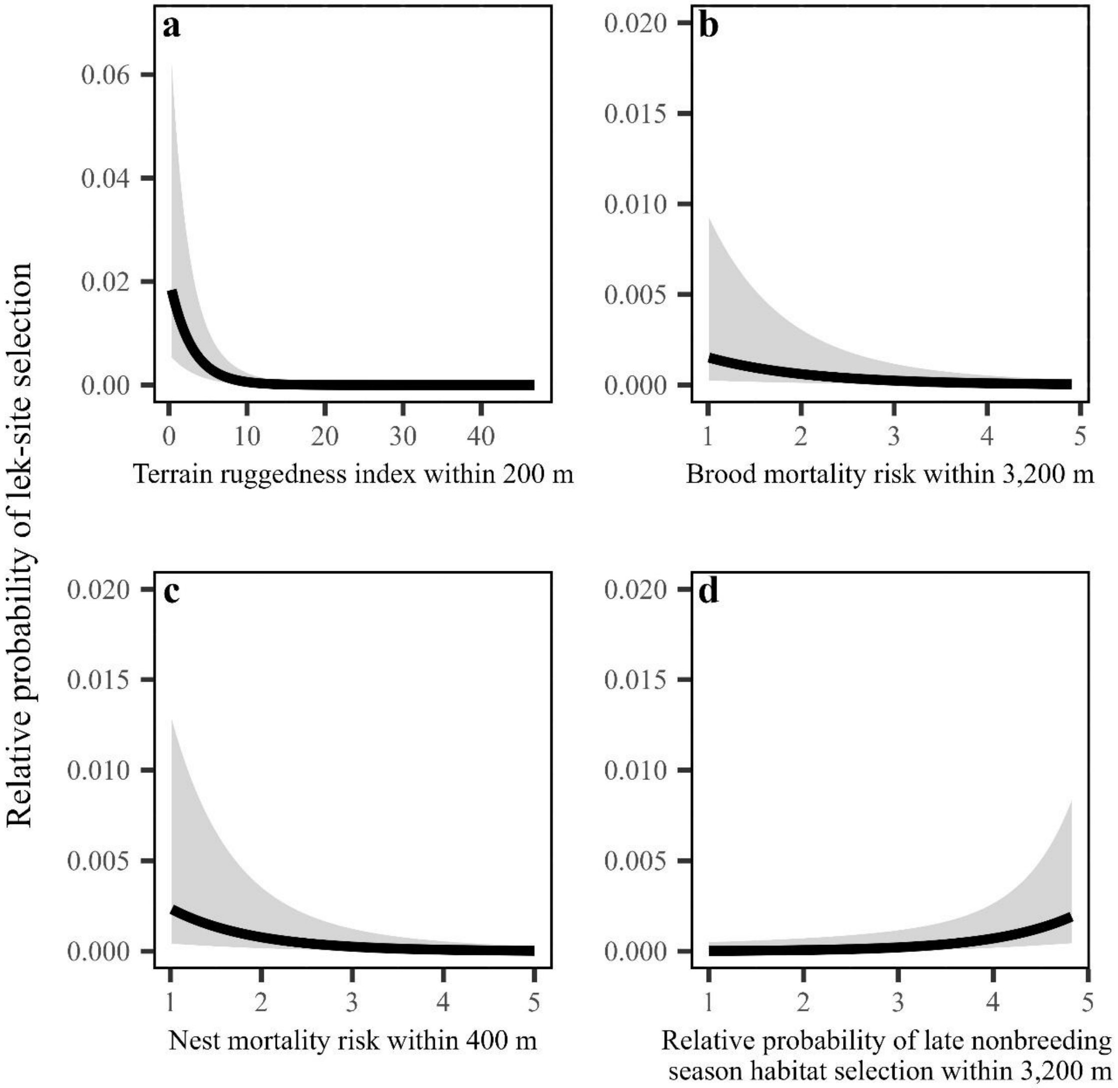


Figure 3.2. Partial effects plots (± 95% CI) for binomial logistic regression model predicting sharp-tailed grouse (*Tympanuchus phasianellus*) lek-site selection as predicted by terrain ruggedness index within 200 m (**a**), mean brood mortality risk within 3,200 m (**b**), mean nest mortality risk within 400 m (**c**), and mean relative probability of late nonbreeding habitat selection (1 Dec–31 Mar) within 3,200 m (**d**), Carbon County, Wyoming, USA, 2017–2020. For mean brood and nest mortality risk, 1 represents low nest mortality risk and 5 represents high mortality risk. For mean relative probability of late nonbreeding season selection within 3,200 m, 1 represents low probability of selection and 5 represents high probability of selection.

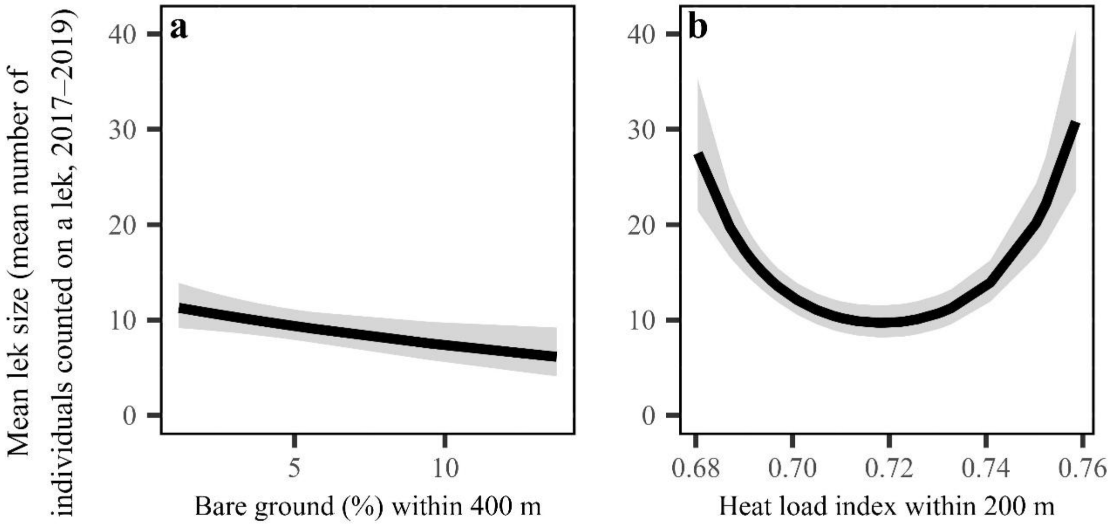


Figure 3.3. Partial effects plots (± 95% CI) for Poisson linear regression models predicting the average size of sharp-tailed grouse (*Tympanuchus phasianellus*) leks (2017–2019) as predicted by mean percent bare ground within 400 m (**a**) and mean heat load index within 200 m (**b**), Carbon County, Wyoming, USA, 2017–2020.

CHAPTER FOUR

Using an integrated population model to understand sharp-tailed grouse population growth: implications for a potential hunting season

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ABSTRACT

Understanding the demography of populations is crucial when making management decisions, including habitat management and harvest regulation. Harvest regulations typically focus on maintaining a viable population and are based on population surveys and models. It is thus imperative to understand the potential implications of existing and potential hunting seasons on population growth and size. Little is known about the population demography of sharp-tailed grouse (*Tympanuchus phasianellus*) in southcentral Wyoming, which are currently not hunted but under consideration for hunting in the future. To understand the population demographics of sharp-tailed grouse in southcentral Wyoming, we developed a stage-based, Bayesian integrated population model (IPM) and evaluated the instantaneous mortality risk for adult female and juvenile sharp-tailed grouse. We used the IPM to understand the potential impacts of reducing adult annual survival and juvenile overwinter survival (a proxy for harvest). We developed a population viability analysis using the IPM to understand extinction (no males remaining) and quasi-extinction (≤100 males remaining) probabilities under various survival reduction rates. Our IPM estimated demographic vital rates from radio-telemetry data (2017–2020), nest and brood monitoring data (2017–2019), juvenile overwinter survival data (2017–2020), and annual lek count data (2015–2022). We found that the sharp-tailed grouse population in southcentral Wyoming was declining (λ = 0.87), and most demographic rates were similar to or higher than other populations of sharp-tailed grouse. Under no survival reduction, the population had a ~70% chance the population would have <100 males after 10 years. Results from the population viability analysis demonstrated that as the survival rates decreased, the population growth rate decreased, and the extinction and quasi-extinction probabilities increased. The instantaneous risk of mortality was lowest for adults and highest for juveniles during the fall (Sep–Nov). Our results demonstrate that the population of sharp-tailed grouse in southcentral Wyoming is declining. Future research on the population of sharp-tailed grouse in southcentral Wyoming should be focused on ways to increase population growth in this area to better inform management to help increase population growth. Our results also highlight the importance of understanding population dynamics prior to implementing a hunting season and demonstrate that potential hunting seasons should consider the timing of harvest relative to biologically important seasons and try to minimize the impacts of hunting on population size and growth.

KEYWORDS harvest effects, integrated population model, population viability analysis, sharp-tailed grouse, survival, telemetry, *Tympanuchus phasianellus*, Wyoming

INTRODUCTION

Managing wildlife populations requires an understanding of population dynamics, often understood through the use of demographic models and population viability analyses (PVA; Shaffer 1981, Gilpin and Soule´ 1986, Bessinger and Westphal 1998). Population viability analyses are useful tools to help understand the potential impacts of management decisions on populations of conservation concern (e.g., Mills et al. 1996, Saunders et al. 2018, Dyck et al. 2023), including harvest management (Taylor et al. 2006, Mills 2013). Harvest regulations are often decided using adaptive harvest management plans to adjust for different environmental conditions and other uncertainties (Walters 1986, Williams and Johnson 1995, Conroy 2021). Historically, harvest for upland game birds (order Galliformes) in North America were regulated through season length, bag limits, and possession limits with limited consideration for adaptive management strategies until recently (Dahlgren et al. 2021).

Most upland game bird populations across North America have been hunted in some form since the continent was settled by Europeans, either for subsistence or sport (Leopold 1933). Hunting regulations for upland game birds have changed over the past century and adapted to better understandings of population dynamics, with regulations generally becoming more conservative (Dinkins et al. 2021) with current suggestions for harvest rates being less than 10% for some declining upland game bird species (Connelly et al. 2000, Sedinger et al. 2010, Reese and Connelly 2011, Breisjøberget et al. 2018). Population surveys provide important information about population trajectories and aid in conservation and harvest regulation decisions (Sands and Pope 2010). Upland game bird populations are monitored using a variety of methods, including territorial male counts (Blackford 1958, Gullion 1966, DeMaso et al. 1992), roadside counts (Bennett and Hendrickson 1938, Kozicky et al. 1952), aerial surveys (Shupe et al. 1987, McDonald et al. 2014), hunter surveys (Leopold 1933, Amman and Ryel 1963), wing collection (Allison 1963, Dalke et al. 1963), and lek counts (Beck and Braun 1980, Cannon and Knopf 1981). Due to declining populations detected through population monitoring and modeling, some management agencies have eliminating hunting seasons all together (Schroeder et al. 2000*a*, *b*; Haukos et al. 2016, Dinkins et al. 2021). The hunting seasons for Gunnison sage-grouse (*Centrocercus minimus*), lesser prairie-chicken (*Tympanuchus pallidicinctus*), and some populations of sharp-tailed grouse (*T. phasianellus*) and greater sage-grouse (*C. urophasianus*) have been closed over concerns that the populations were declining (Schroeder et al. 2000*a*, *b*; Reese and Connelly 2011, Haukos et al. 2016, Dinkins et al. 2021); however, the decisions to close these hunting seasons was not attributed to hunter harvest contributing to the decline of the populations (Schroeder et al. 2000*a*, *b*; Reese and Connelly 2011, USFWS 2014, Haukos et al. 2016).

Sharp-tailed grouse are found throughout much of northern North America, from as far south as Nebraska and Colorado north to Alaska and the Northwest Territories (Connelly et al. 2024). Studies on the impacts of hunting on sharp-tailed grouse populations are limited, but studies evaluating the impact of harvest on them and closely related species suggest that harvest is partially compensatory to natural mortality (Robel et al. 1972, Hamerstrom and Hamerstrom 1973, Bergerud 1988). Despite being relatively abundant with relatively stable populations across most of its range, the sharp-tailed grouse is also not hunted in different portions of their range (Miller and Graul 1980, Schroeder et al. 2000*b*, Connelly et al. 2024). Sharp-tailed grouse hunting in Washington was closed in 1998 due to low population sizes (Schroeder et al. 2000*b*), likely the results of habitat loss and degradation. In southcentral Wyoming, there has not been an established sharp-tailed grouse hunting season since at least the late 1970s (Miller and Graul 1980), with no evidence that there has ever been an established hunting season for this population. The population adjacent to the southcentral Wyoming population in northwestern Colorado has an established hunting season for “mountain” sharp-tailed grouse (https://cpw.widen.net/s/l2fgsjk9cr/colorado-small-game--waterfowl-brochure). Prior to implementing a hunting season, it is important to understand the demographic factors that influence population growth and the potential impacts that harvest might have on those factors.

Within Wyoming, there has been a growing interest in implementing a hunting season on sharp-tailed grouse in southcentral Wyoming (T. Mong, Wyoming Game and Fish Department, personal communication). The objectives of our study were to evaluate the population demography of sharp-tailed grouse in southcentral Wyoming and evaluate how population growth would change as a result of reduced adult annual survival and juvenile overwinter survival (hereafter reduced survival). We evaluated how the growth rate for this population changed in response to reduced survival. Because this population has not been hunted, we were unable to directly evaluate the impacts of hunting on population growth and because hunting directly affects adult annual survival and juvenile overwinter survival. To accomplish this goal, we developed a stage-based integrated population model (IPM) in a Bayesian framework that evaluated demographic rates, population growth, and population size under a no hunting scenario. Lastly, we used the IPM that we developed in a population viability analysis framework to evaluate the effect of reduced survival on the population growth of sharp-tailed grouse in southcentral Wyoming.

STUDY AREA

Our study area was located in western Carbon County, Wyoming, USA (41.194°N, -107.324°E) and encompassed ~2,900 km^2 with elevation that ranged from 1900–3100 m above sea level. Ownership in our study area was composed of Bureau of Land Management (36.7%), U. S. Forest Service (23.3%), State of Wyoming (12.2%), and privately owned (27.7%) lands. The primary land use within our study area was livestock grazing, with some energy extraction, timber harvest, recreation, and irrigated hayfields. During our study (2015–2022), the average annual high temperature was 12.0° C (range = 5.8–16.0° C; 30-year [1993–2022] average = 14.3° C), the average annual minimum temperature was -3.8° C (range = -8.1–-1.0° C; 30-year [1993–2022] average = -2.1° C), and the average annual precipitation was 180.1 mm (range = 65–322 mm; 30-year [1993–2022] average = 278.9 mm; National Centers for Environmental Information, NOAA, accessed 3/13/2025, https://www.ncdc.noaa.gov/cdo-web/). Common mammal species that occurred in our study area included coyote (*Canis latrans*), elk (*Cervus canadensis*), mountain lion (*Puma concolor*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), red fox (*Vulpes vulpes*), and Wyoming ground squirrel (*Urocitellus elegans*). Common avian species that occurred within our study area included American goshawk (*Astur atricapillus*), Brewer's sparrow (*Spizella breweri*), common raven (*Corvus corax*), golden eagle (*Aquila chrysaetos*), greater sage-grouse, green-tailed towhee (*Pipilo chlorurus*), sage thrasher (*Oreoscoptes montanus*), and vesper sparrow (*Pooecetes gramineus*). Dominant vegetation communities within our study area were mixed-conifer forests, mixed deciduous and coniferous forests, mixed-shrub communities, quaking aspen (*Populus tremuloides*) forest, and sagebrush (*Artemisia* spp.) steppe. Mixed deciduous and coniferous forests were primarily composed of Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and quaking aspen. Coniferous forests were primarily composed of Engelmann spruce and lodgepole pine. Mixed-shrub communities were primarily composed of antelope bitterbrush (*Purshia tridentata*), big sagebrush (*A. tridentata*), serviceberry (*Amelanchier* spp.), silver sagebrush (*A. cana*), snowberry (*Symphoricarpos* spp.), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*). Sagebrush steppe was dominated by big sagebrush, bunchgrasses, and forbs.

METHODS

Field methods

We captured female sharp-tailed grouse at leks using walk-in funnel traps (Haukos et al. 1990, Schroeder and Braun 1991) continuously from ~10 April to 11 May 2017–2019. We radio-tagged all captured females with 15-g necklace-mounted VHF transmitters (model RI-2B, Holohil, Carp, Ontario, Canada) and located individuals 2 to 4 times per week during the late spring and summer (30 Apr to 31 Aug) using triangulation at a distance of ~30 to 50 m. If we observed a female sharp-tailed grouse in the same location twice during May or June, we visually confirmed, or circled the bird within a few meters, if on a nest. Once we identified a nest, we monitored it 2 to 4 times per week from a distance of 50 to 100-m, until the female left the nest after it hatched or failed. We considered nests successful when ≥1 egg hatched; this was determined by examining eggshell and eggshell membranes in and near the nest after the female was no longer attending the nest. To obtain clutch size, we counted the number of eggs in each nest when the female was not present at the nest (i.e., on a foraging break) or after the nest had hatched. We were not able to get reliable counts from nests if they failed, given that eggs were not present or eggs shells were crushed. If a nest hatched, we continued to monitor each female for 7 weeks to assess brood mortality risk and habitat selection. To track brood mortality risk, we conducted brood checks at night when the brood was 1-week old, and then every two weeks until broods reached 7-weeks of age. During the brood-check at 7-weeks, we flushed the broods and counted the number of chicks present and attempted to capture as many of the chicks as possible. Upon capture of chicks, we fitted 10-g necklace mounted VHF transmitters (model RI-2B, Holohil, Carp, Ontario, Canada) to chicks weighing ≥250 g to ensure that the transmitter was no more than 2.5% of the chicks' mass. Night-time checks minimized error because chicks were actively being brooded at night making it more reliable to determine chick presence (determined visually or by presence of chick droppings in the roost the following day) without causing significant disturbance to the female and chicks (Pratt and Beck 2019, Smith et al. 2019). A brood was considered to have failed if chicks were no longer observed with the female or if a female mortality was detected. During the fall, winter, and early spring (1 Sep to 30 Apr) we located birds by airplane once per month. If we were unable to locate individuals during a flight, we searched for them on subsequent flights; if, after subsequent flights, we were still unable to locate them, we would consider them missing and they were right censored in survival analyses.

We obtained lek count data from the Wyoming Game and Fish Department (WGFD) and the Rawlins Field Office of the Bureau of Land Management (BLM; 2015 to 2022). The WGFD, BLM, and other volunteers visited known leks each year to count the number of sharp-tailed grouse at each lek. Each year, leks were visited once during the spring lekking season (Mar–May). For the few leks (<5) where all individuals could be reliably counted without flushing, leks were counted from a distance ≥50 m to minimize disturbance to lekking activities. For the majority of leks, which could not be reliably counted without flushing, leks were flushed once during each season and all flushed sharp-tailed grouse were counted, similar to methods described in Gillette et al. (2015). Sharp-tailed grouse are not sexually dimorphic and can be difficult to sex on leks and while in flight. Therefore, our counts of sharp-tailed grouse on leks likely included both males and females. However, we assumed that all birds counted on leks were males because we had no way of discerning how many females were included in the lek counts.

Statistical Analyses

Demographic subcomponents

We developed sub-models for each of the demographic processes that we evaluated. Demographic sub-models included: breeding season survival (1 Apr to 14 Aug; *BSS*) and annual survival (1 Apr to 31 Mar; *AnnS*); nest initiation rate of first and second nests (*Nest*1, *Nest*2); clutch size of first and second nests (*cls*1, *cls*2), daily survival of first and second nests (*N.surv*1, *N.surv*2); egg hatchability (*h*); chick survival to 49 days post hatch (*cs*); and juvenile overwinter survival (*js*, 1 Sep to 31 Mar). All sub-models except juvenile survival included a random effect of female age on demographic parameters.

We used telemetry data to estimate the monthly (months were defined as 4-week periods) survival for yearling (second year) and adult (after second year) females. Because we estimated quad-weekly survival, we defined a month as 28 days long to ensure equal length time periods across the year, and therefore a year was 13 months long. We monitored females 2-3 times per week during the breeding season (Apr–Aug) and we monitored each female once per month during the nonbreeding season (Sep–Mar; see descriptions above). Censoring occurred when the bird survived to the next breeding season, the transmitter failed, or the individual went missing and could not be relocated. We modeled survival using a random effects survival model (shared frailty model) with a constant, baseline log-hazard for every month of the study (Halstead et al. 2012), similar to Mathews et al. (2021). We included a temporal parameter (month) to allow us to calculate annual survival (*AnnS*, 1 Apr–31 Mar) and breeding season survival (*BSS*; 1 Apr–31 Aug). We fit survival models with a random effect for age (β) where we included yearlings (second year) and adults (after second year) and a random effect for year (κ). The unit (monthly) hazard (*UH*) took the form:

$$UH_{i,j} = e^{\alpha + \beta_a + \kappa_y} \tag{1}$$

where subscripts $i, j, a,$ and y reference individual, month, age, and year, respectively. The intercept (α) represents the baseline log hazard. For age, the log hazard ratio is interpreted as the change of logged magnitude in risk for each group relative to all other groups (Hernán 2010, Mathews et al. 2021). We estimated the cumulative hazard (*CH*) and survival functions as:

$$CH_i = \sum_{j=1}^{T} UH_{i,1:j} \tag{2}$$

$$S_i = e^{-CH_i} \tag{3}$$

where *T* represents the maximum number of months that an individual was monitored. We subsequently modeled survival as the probability of the Bernoulli process where the random variable *Y* indicated if an individual was dead or alive (0 and 1, respectively) between intervals.

$$Y_i \sim \text{Bernoulli}(S_i) \tag{4}$$

We derived posterior distributions for *AnnS* (*T* = 13 months) and *BSS* (*T* = 5 months) for each age class included in the study.

For first nest initiation (*Nest*1), we used informative priors from the Beta distribution for each age class:

$$Nest1_{asy} \sim \text{Beta}(97, 5) \tag{5}$$

$$Nest1_{sy} \sim \text{Beta}(90, 12) \tag{6}$$

where *asy* and *sy* represent adults and yearling age classes, respectively. These informative priors indicate that the probability of initiating a first nest is higher for adult females than yearling females, but the probability of initiating first nests is still relatively high for both age classes. We used informative priors for first nest initiation because we could not be certain that we detected all first nest attempts on the landscape, as some nests likely failed during the egg laying period. Second nests attempts are typically easier to detect because second nests typically have fewer eggs leading to a shorter laying period and they typically are initiated shortly after a failed nest making them easier to predict when they will be initiated. Therefore, we estimated the probability of initiating a second nest following a Binomial distribution for all age classes combined. The probability of initiating a second nest took on the form:

$$RN \sim \text{Binomial}(fn1, ni2) \tag{7}$$

$$\text{Logit}(Nest2) = \alpha \tag{8}$$

where *fn*1 represents the number of failed first nests, *RN* represents the number of individuals that attempted to renest, and *Nest*2 is the apparent probability of second nest initiation. The logit-transformed probability was described by the intercept (α). Because we used informative priors for first nest initiation and did not have enough renests each year, we did not include annual variation as a component of nest initiation.

We modeled the expected clutch size of first (*cls*1) and second nests (*cls*2) using a Poisson distribution and it took the form:

$$clutch1_i \sim \text{Poisson}(cls1_i) \tag{9}$$

$$Log(cls1_i) = \alpha + \theta_y \tag{10}$$

where *i* and *y* represent nest and year, respectively, and $clutch1_i$ represents observed clutch sizes. We described expected clutch size (*cls*1) by a linear combination of the intercept (α) and the random effect of year (θ). We calculated clutch size for second nests (*cls*2) using the same equations that were used for first nest clutch size.

We modeled first (*N.surv*1) and second (*N.surv*2) nest survival using a shared frailty model, similar to how we modeled adult survival (eqs. 1–4), over a 24-day incubation period (Johnsgard 1973, Hoffman 2001, Barker et al. 2023). We did not include the egg laying period in our analysis because we could not be certain that we detected all nests that our marked female grouse in our study initiated prior to incubation starting. We used a random effect for female ID and female age to account for females that had nests during multiple years and different nest survival probabilities for adult and yearling females. We modeled second nest survival similar to first nest survival, except we did not include random effects for age because we had a small sample size.

We modeled egg hatchability (h) using eggshell remains from successful nests with no signs of scavenging. We modeled hatchability using a Binomial distribution where the number of eggs laid represented the number of trials and the number of hatched eggs represented the number of successes. We modeled hatchability with a random effect for year (θ) and the model took the form:

$$he \sim Binomial(cls, h) \tag{11}$$

$$\text{Logit}(h) = \alpha + \theta_y \tag{12}$$

where y represents the year of the nest and he represents the number of eggs hatched, and cls represents the initial clutch size of the nest. The logit-transformed probability of egg hatchability was described by the linear combination of the intercept (α) and the random effect of year (θ). We assumed that egg hatchability was the same for first and second nesting attempts.

We modeled chick survival (cs) from brood count data when broods were 7-weeks of age using a Binomial distribution. The initial number of chicks (number of trials) was considered to be the number of eggs that hatched, whereas the number of chicks that survived were the number of chicks at 49-days (number of successes). We modeled chick survival similar to equations 11 and 12. The logit-transformed probability of chick survival included the intercept and a random effect for year. We assumed that chick survival was similar between age classes because we had a relatively small sample size for each age class.

We modeled juvenile overwinter survival (*js*) from monthly telemetry data using a shared frailty model, similar to how we modeled adult survival (Eqs. 1–4). For this model we included a random effect for year. We modeled monthly juvenile overwinter survival from 1 September to 31 March. We assumed that juvenile overwinter survival was similar between male and female juveniles.

Integrated population model framework

To understand the population dynamics and the potential influence of hunting on sharp-tailed grouse in southcentral Wyoming, we developed a Bayesian integrated population model (IPM). We used this model to estimate the demographic subcomponents outlined above, productivity, population growth rates, and abundance of sharp-tailed grouse in southcentral Wyoming (Schaub and Abadi 2011, Kéry and Schaub 2012). We developed a lek-based IPM, similar to Mathews et al. (2021). Within our population model, we assumed that there was a 1:1 sex ratio on the landscape and every grouse counted on a lek was a male (i.e., every grouse counted on a lek was a male and there was a corresponding female not occurring at the lek), there was a 1:1 sex ratio at fledging, breeding began at age one, and there was no immigration into the population. Previous research on sharp-tailed grouse and other *Tympanuchus* species indicates an approximate 1:1 sex ratio on the landscape (Robel et al. 1972, Giesen 1999) and this ratio is used in population models for *Tympanuchus* grouse (Cummings et al. 2017, Ross et al. 2018, Mathews et al. 2021). There is potentially immigration into the focal population of sharp-tailed grouse in southcentral Wyoming from an adjacent population in Colorado, however, we also observed emigration from our focal population to the adjacent population in Colorado, potentially negating any immigration from the population in Colorado. Because we did not have a way to identify the rates of immigration and emigration, we assumed that they were equal and used a closed population model.

We used a stage-based pre-breeding season model, which decomposed population dynamics into a state process based on breeding season survival, annual survival (see above), and annual recruitment. Annual recruitment (R) took the form:

$$R_{\mathrm{a,y}} = \{(Nest1_a \times cls1 \times N.surv1_{a,y} \times h_y \times cs_y \times js_y) + \\ ([1 - Nest1_a] \times Nest2 \times cls2 \times N.surv2 \times h_y \times cs_y \times js_y)\}/2 \tag{13}$$

where the subscripts a and y represent age class and year of study, respectively. We assumed an even sex ratio of chicks, as this has been found to be true at hatch in another population of sharp-tailed grouse (Mathews et al. 2018).

We used a time-series analysis via Markovian processes to model annual sharp-tailed grouse lek counts (Baumgart 2011, Mathews et al. 2021). We used a Normal distribution to model the observation process allowing demographic estimates to inform apparent abundance (Mathews et al. 2021). We linked lek counts (see above) in year y to male abundance ($N_{\mathrm{male,y}}$):

$$C_y \sim Normal(N_{male,y},\ \sigma_C^2) \tag{14}$$

where σ_C^2 represented the observation error, which we assigned a Uniform prior distribution between 0 and 100. We calculated the finite rate of population change on an annual basis by dividing the total population size in year y + 1 by the total population size in year y:

$$\hat{\lambda}_y = \frac{N_{male,y+1}}{N_{male,y}} \tag{15}$$

Lek counts in year y represent the survival and recruitment of year y – 1, therefore lek counts and corresponding $\hat{\lambda}$ were staggered and we averaged all population change metrics from 2016 to 2022 (Mathews et al. 2021). Additionally, we calculated the geometric mean of the log-transformed annual $\hat{\lambda}_y$ estimates to understand historical population changes. To understand the contributions of demographic processes to annual variation in population growth ($\hat{\lambda}_y$), we correlated population growth with yearling and adult breeding season survival probability, yearling and adult annual survival probability, yearling and adult nest survival probability, chick survival probability, and juvenile overwinter survival probability (Schaub et al. 2013, Tempel et al. 2014, Saunders et al. 2018, Schaub and Kéry 2021).

Population viability analysis

We used a population viability analysis (PVA) based on the integrated population model described above to understand the effects of reduced adult annual survival and juvenile over winter survival on sharp-tailed grouse. We simulated the population 10 years into the future for the PVA. We used a PVA to estimate the probability of absolute extinction (no males remain in the population) and quasi-extinction (≤100 males) after 10 years. We choose the quasi-extinction rate of ≤100 males because, assuming a 1:1 sex ratio on the landscape, this results in 200 individuals in the population, which is considered a minimum viable population size for the persistence of sharp-tailed grouse populations (Toepfer et al. 1990, Milligan et al. 2018).

To reduce adult annual survival and juvenile overwinter survival, we derived survival reduction rates based on published results from Sandercock et al. (2011). Sandercock et al. (2011) found that willow ptarmigan (*Lagopus lagopus*) had annual survival rates of 0.54, similar to annual survival rates for sharp-tailed grouse (Gillette 2014, Milligan et al. 2020*b*, Mathews et al. 2021), and that survival rates of willow ptarmigan populations were reduced by hunter harvest at 15% and 30% harvest compared to the population without harvest. To understand how lower and intermediate harvest rates, and therefore intermediate reductions in survival (e.g., 5%, 10%, 20%, and 25% harvest), might influence survival, we used a linear model in Program R 4.4.1 (R Core Team 2024) to fit a quadratic equation to the published survival rates for no harvest, 15%

harvest, and 30% harvest and used this equation to estimate survival rates at 5%, 10%, 20%, and 25% harvest. Once we had estimated the survival rates at intermediate harvest, we divided the predicted survival rates by the survival rates when there was no harvest on willow ptarmigan from Sandercock et al. (2011) to get the reduction in survival (*Reduction*). The *Reduction* rates that we used were 0% (no survival reduction), 2.3%, 6.6%, 13.0%, 21.4%, 31.9%, and 44.4% reduction in survival. Because we did not know exactly how hunting would impact survival, we allowed the influence of hunting (*SurvReduction*) on survival to vary for both adult annual and juvenile overwinter survival. We used a Normal distribution with a mean of *Reduction* and a standard deviation of 0.005 and truncated at 0 and 1:

$$SurvReduction \sim Normal(Reduction, 1/(0.005 * 0.005)\ )T(0,1) \qquad (16)$$

We only decreased adult annual and juvenile overwinter survival during the prospective analyses and not during the retrospective analysis by multiplying the respective survival rate by *SurvReduction*.

Model fitting

We conducted modeling using Bayesian Markov Chain Monte Carlo (MCMC) sampling in the program JAGS V4.3.2 (Plummer 2003), implemented using Program R and the R package *jagsUI* (Kellner 2024). We report all results as the median posterior estimate and 95% credible intervals (CI) unless otherwise noted. We ran three independent chains for 800,000 iterations following a 200,000 iteration burn-in and thinned chains by five. Model convergence was assessed using the Rhat ($\hat{R}$) statistic (Gelman and Hill 2006) and we visually inspected the chains. We observed convergence ($\hat{R} \leq 1.1$) for all parameter estimates.

Timing of mortality

To evaluate seasonal timing of mortality, we calculated hazards functions using smoothing spline functions (DelGiudice et al. 2006, Winder et al. 2018). To calculate hazard functions, we used the *sshzd* function from the *gss* package in Program R (Gu 2014). This allowed us to evaluate when adult females (yearlings and adults) and juveniles encounter natural hazard risks during the year (1 Apr–31 Mar; adult females) and over winter (1 Sep–31 Mar; juveniles) for potentially harvested populations.

RESULTS

Our IPM estimated that the population of sharp-tailed grouse in Carbon County, Wyoming declined from 824 males (95% credible interval [CI] = 744–919) in 2015 to a low of 174 (CI = 133–215) in 2020 and then increased to 308 (CI = 243–384) in 2022 (

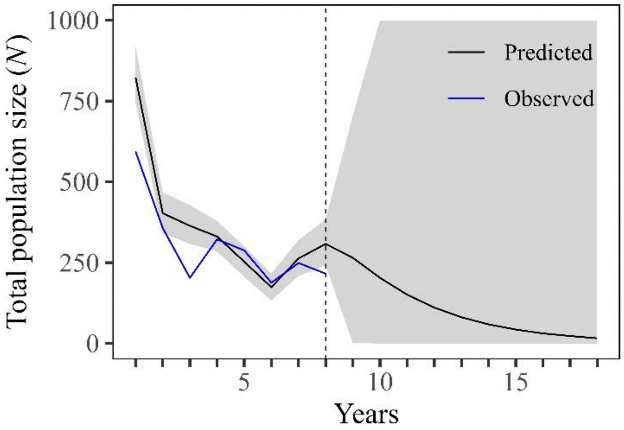

Figure **4.1**). Our population estimates from the IPM roughly tracked the observed lek counts, though the modeled population was generally higher than the observed counts (

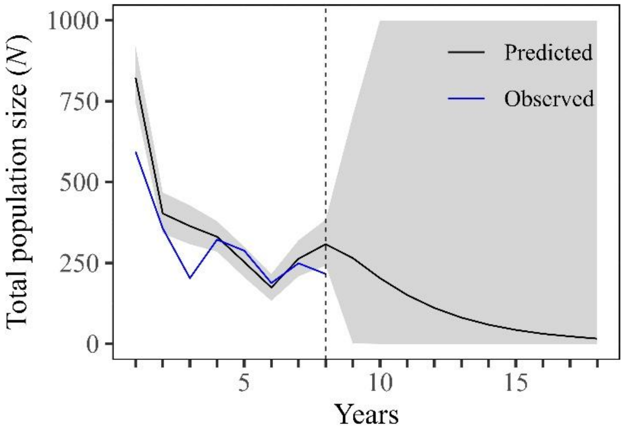

Figure **4.1**). Annual population growth ($\hat{\lambda}_y$) varied from 0.49–1.51 with a geometric mean of 0.87 (CI = 0.84–0.90) from 2016 to 2022. In the prospective analysis without hunting, the estimated population 10 years into the future was 16 males (TABLES

Table **4.1**); the geometric mean of population growth in the prospective model was 0.65 (TABLES

Table **4.1**). Mean annual estimates of annual survival and breeding season survival of yearling females were slightly higher than annual survival and breeding season survival of adult females from 2017 to 2020 (Table 4.2). Estimated annual nest survival of yearling females was higher than nest survival of adult females from 2017 to 2019 (Table 4.2). Mean annual estimates of chick survival varied from 0.19 to 0.40, with a geometric median of 0.28 from 2017 to 2019 (Table 4.2). The mean annual estimates of juvenile over-winter survival during our study varied from 0.53 to 0.64 with a geometric median of 0.59 (Table 4.2) from 2017 to 2020. We found that population growth ($\hat{\lambda}_y$) was positively correlated with yearling and adult female breeding season and annual survival (*r* = 0.77; CI = -0.48–1.00); the correlation coefficient and credible intervals were similar for all adult and yearling survival parameters. Chick survival was also positively correlated with population growth (*r* = 0.64; CI = -0.38–1.00). Population growth was negatively correlated with nest survival (yearling and adult; *r* = -0.23; CI = -1.00–0.99) and juvenile over-winter survival (*r* = -0.45; CI = -1.00–0.94), though the credible intervals overlapped zero and ranged from nearly -1.00–1.00.

Population viability analysis

When adult annual survival and juvenile overwinter survival were reduced, the predicted population growth rates (λ) during 2023–2033 decreased as the rate at which survival was reduced increased (TABLES

Table **4.1**, Figure 4.2), and suggested that the population was declining under all scenarios, though the credible intervals for population growth under no survival reduction to 12.96% survival reduction overlapped 1.0 due to model uncertainty (TABLES

Table **4.1**). The projected populations under each survival reduction rate approached zero after 10 years (TABLES

Table **4.1**, Figure 4.2). After 10 years, there was an estimated 33.9% chance that the population will go extinct without a reduction in survival (TABLES

Table **4.1**, Figure 4.3A) and the probability of extinction increased as the reduction in survival increased, with a maximum of 81.5% probability of extinction under the 44.44% reduction in survival scenario (TABLES

Table **4.1**, Figure 4.3A). The quasi-extinction rate (≤100 males) was 72.7% under reduction in survival and increased as the reduction in survival increased (TABLES

Table **4.1**, Figure 4.3B), with a maximum of 99.6% probability of quasi-extinction after 10 years with a 44.44% reduction in survival (TABLES

Table **4.1**, Figure 4.3B).

Timing of mortality

To evaluate the patterns of mortality to adult female and juvenile sharp-tailed grouse, we calculated hazard functions across the year, with the year starting on 1 April. We found that the instantaneous risk of mortality was highest for adult females during the early breeding season (weeks 6–14, 29 Apr–7 Jul) with other peaks in instantaneous risk to mortality occurring during the late breeding season (weeks 18–25, 29 Jul–22 Sep) and the late nonbreeding season (weeks 43–50, 20 Jan–17 Mar; Figure 4.4). The lowest instantaneous risk of mortality for adults occurred during the early nonbreeding season (weeks 27–42, 30 Sep–19 Jan). For juveniles, instantaneous risk of mortality was greatest during the early nonbreeding season (weeks 27–42, 30 Sep–19 Jan).

DISCUSSION

There is limited research on the population demography of sharp-tailed grouse in southcentral Wyoming, and to our knowledge, there has not been an official, regulated hunting season for sharp-tailed grouse in southcentral Wyoming since at least the late 1970s (Miller and Graul 1980). We sought to evaluate the population demography of sharp-tailed grouse in southcentral Wyoming and to understand the potential influence of reduced adult annual survival and juvenile overwinter survival on population growth. We found that the population of sharp-tailed grouse in southcentral Wyoming declined from 2015–2022, with a mean population growth of 0.87 over the duration of our study. Population growth during this period was most correlated with the annual survival of yearling and adult females. Projected population growth rates indicated a declining population, with projected future populations predicted to have an approximate 30% chance of extinction and an approximate 72% chance of quasi-extinction (≤100 males remaining in the population) after 10 years. Under predicted scenarios where adult annual survival and juvenile overwinter survival were reduced, we found that extinction and quasi-extinction probabilities increased as the rate at which survival was reduced increased. The predicted population growth rate, extinction probability, and quasi-extinction for survival reduction rates less than 6.7% were similar, but all analyses still resulted in declining populations.

We found that the population of sharp-tailed grouse in southcentral Wyoming was declining during our study. We only evaluated sharp-tailed grouse population growth in southcentral Wyoming for a relatively short period (2015 to 2022) and grouse populations are historically cyclical over time, experiencing growth pulses and declines (Moss and Watson 2001, Williams et al. 2004*b*, Fedy and Doherty 2011). Because of the cyclical nature of grouse populations, we may have only evaluated the southcentral Wyoming population during a downturn in population growth and this may need to be evaluated over a longer period. We observed a slight population increase in the final year of our study (2022), suggesting that the population may have reached the low of a cycle and was starting to recover. Because of the nature of the simulated models that we used, there is significant uncertainty in them with credible intervals of most projected population growth rates overlapping 1 and we do not know the exact causes for the decline. However, population growth in our retrospective analysis was correlated with adult, yearling survival, and chick survival. To help better manage this population, it is important that future research helps to identify management actions that could improve adult, yearling, and chick survival.

During our study, trends in the estimated population size and lek counts generally were similar, with the estimated population size being higher than the cumulative lek counts (

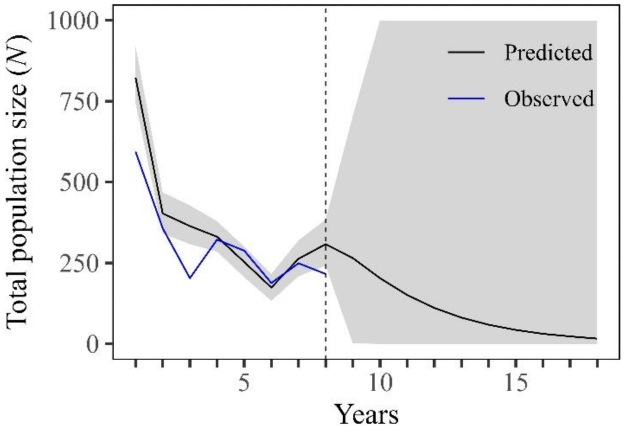

Figure **4.1**). We hypothesize that this is because there was missing lek count data because within our study area, some leks were inaccessible during years with deep snow. Additionally, lek counts in our study area were only conducted once per year per lek, this might result in inaccurate lek sizes as male attendance on leks varies during the lekking season (Emmons and Braun 1984, Drummer et al. 2011, Wann et al. 2019). Finally, we likely do not know the locations of all the leks within our study area because much of the area is inaccessible by established roads and the area is characterized by high shrub cover, making it difficult to identify new leks (Smith et al. 2016). Because of this, it would be beneficial for agencies using lek counts to guide management and harvest recommendations to conduct multiple lek counts during the spring lekking season and to establish a consistent lek count protocol and to search for additional leks every 2 to 4 years to ensure a complete survey of the population of interest.

Factors that are most influential on population growth in grouse populations vary depending on the species and population, yet has frequently been attributed to breeding success and adult female survival (Johnson and Braun 1999, Hagen et al. 2009, Taylor et al. 2012, Gillette 2014, Sullins 2017). We found that population growth was positively correlated with adult and yearling survival and chick survival, though the credible intervals overlapped zero, which is congruent with other populations of grouse (Johnson and Braun 1999, Hagen et al. 2009, Taylor et al. 2012, Gillette 2014). Population growth was negatively correlated with nest survival and juvenile overwinter survival with the credible intervals for both ranging from -1 to 1. The consistent overlap of zero with correlation suggests that we do not have enough data to understand which factors were most correlated with population growth, likely related to only having three years of demographic data. However, our estimated demographic rates were similar to other studies evaluating sharp-tailed grouse populations in the adjacent population of Colorado (Barker et al, 2022, 2023). Our observed nest survival of 0.85 and 0.76 for yearlings and adults, respectively, which was higher than observed apparent nest success or modeled nest survival rates from other portions of the sharp-tailed grouse range (range: 0.29–0.62; Gillette 2014, Burr et al. 2017, Proett et al. 2019, Milligan et al. 2020*a*). Additionally, we observed similar or lower adult annual survival rates (yearlings = 0.45, adults = 0.33) compared with other studies on sharp-tailed grouse (range 0.28–0.86; Gillette 2014, Milligan et al. 2018, 2020*b*, Mathews et al. 2021; for additional sources see Table 2 in Milligan et al. 2018).

Identifying factors that might be influenced by harvest regulations is important to understand prior to implementing a hunting season. Hunting seasons for grouse typically occur during the fall and early winter (September through December), with hunters harvesting both adults and juveniles. We observed opposite trends for risks of mortality for adults and juvenile sharp-tailed grouse during the nonbreeding season (1 Sep–31 Mar) in our study area. We found that juveniles had the highest risk of mortality during fall and early winter, while adults had their lowest risk of mortality for annual survival during this same period, suggesting that hunter harvest during the fall might be more compensatory for juveniles and more additive for adults.

Juvenile grouse likely have a higher risk of mortality during the early nonbreeding season because they are naïve as they are just starting to become independent from the brood female that raised them (Hannon and Marting 2006). In areas where sharp-tailed grouse have been hunted, juvenile-to-adult harvest ratios varied, but were close to 1:1 in some populations (Robel et al. 1972, Giesen 1999, Stevens et al. 2023). Adult risk of mortality was greatest during the first half of the breeding season (29 Apr–7 Jul), similar to greater prairie-chickens in Kansas (Winder et al. 2014). During the first part of the breeding season, females are visiting leks, laying eggs and incubating nests, and attending broods, therefore, decreased survival during these periods is common in similar species (Hagen et al. 2007, Augustine and Sandercock 2011, Winder et al. 2014, Milligan et al. 2020*b*).

Because sharp-tailed grouse are located in spatially and temporally predictable patterns (Smith et al. 2016, Lautenbach et al. 2022) and are known to lek in the fall (Hamerstron and Hamerstrom 1951), this may make males attending leks more susceptible to harvest (Chen et al. 2023). Within sharp-tailed grouse, fall lekking is when many juvenile and adult males begin establishing territories on leks (Myles and Boag 1981). The timing and duration of fall lekking is a little less known, but it typically occurs from September through October with males visiting leks throughout the winter (Myles and Boag 1981). Sharp-tailed grouse hunting seasons across much of North America overlap with fall lekking, potentially facilitating hunters to target known leks. Many of the known leks within the population of sharp-tailed grouse in southcentral Wyoming were located along or near roads (improved and unimproved; J. Lautenbach, personal observation) and might be easy for hunters to locate and target their hunting efforts, potentially reducing the size of leks and potentially greatly reducing numbers of sharp-tailed grouse during some years. Therefore, identifying the timing of peak fall lekking and implementing hunting outside of this period might reduce the potential influence of hunting on leks in populations where leks are easy for hunters to access.

The sharp-tailed grouse population in southcentral Wyoming is declining and our population viability analyses demonstrate that the population has a 72% chance of having fewer than 100 males after 10 years, suggesting that the population will likely fall below the minimum population size for population persistence (Toepfer et al. 1990, Hoffman et al. 2015, Milligan et al. 2018). Population growth was most correlated with adult, yearling, and chick survival and the instantaneous risk of mortality to adult females suggests that hunting would be additive to adult female mortality. Prior to implementing a hunting season, it is important to understand all potential impacts of harvest on populations, including seasonal mortality risk, important biological events (e.g., fall lekking), and factors limiting population growth. If a hunting season is implemented on a previously non-hunted population, this would provide a great opportunity to better understand the influence of hunting on population dynamics and could be studied through banding, telemetry, and/or wing collection (Hagen et al. 2018).

MANAGEMENT IMPLICATIONS

The population of sharp-tailed grouse was declining during our study. We found that population growth in our population was most correlated with adult annual survival and chick survival. Identifying management objectives that improve habitat conditions that benefit adult annual survival and chick survival will help grow the population. We found that the instantaneous risk of mortality. Harvest during the fall would likely be additive for adults, however this is when mortality risk for juveniles is highest, suggesting that a fall harvest could be partially compensatory for juveniles. If a hunting season is implemented on a previously non-harvested population, managers should consider the timing of the hunting season relevant to important life-history stages (e.g., annual survival, fall lekking, etc.) and try to minimize the impacts of hunting on population size and growth.

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ETHICS STATEMENT

All capture, handling, and monitoring protocols were approved by the University of Wyoming Institutional Animal Care and Use Committee (protocol 20170324AP00266 [versions -01, -02, and -03]) and by the Wyoming Game and Fish Department (Chapter 33-1098 permit).

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TABLES

Table 4.1. Estimates of posterior median (50th percentile) population growth (λ) and 95% credible intervals (CI), posterior median (50th percentile) population size (*N*) and 95% credible intervals (CI), absolute extinction probability, and quasi-extinction probability (≤100 males) for sharp-tailed grouse in southcentral Wyoming after the population was projected 10 years into the future when adult annual survival and juvenile overwinter survival were reduced (survival reduction rate) based on estimates from Sandercock et al (2011).

Survival reduction rate	λ	*N*	Absolute extinction probability	Quasi-extinction probability
0%	0.65 (0.47–1.21)	16 (0–4612)	0.28	0.71
2.26%	0.63 (0.47–1.18)	13 (0–3747)	0.30	0.74
6.58%	0.60 (0.47–1.12)	8 (0–2368)	0.33	0.79
12.96%	0.56 (0.47–1.04)	3 (0–1182)	0.38	0.86
21.40%	0.51 (0.47–0.93)	1 (0–414)	0.47	0.92
31.90%	0.48 (0.47–0.79)	0 (0–98)	0.62	0.98
44.44%	0.48 (0.47–0.64)	0 (0–13)	0.81	1.00

Table 4.2. Posterior median estimates (50% quantile) of various demographic parameters and 95% credible intervals (CI) for sharp-tailed grouse in southcentral Wyoming using an integrated population model; estimates are based on data telemetry data collected from female sharp-tailed grouse fitted with radio-transmitters from 2017–2020.

			95% CI	
Parameter	Age[a]	50%	2.5%	97.5%
Annual Survival (*AnnS)*	Yearling female	0.45	0.35	0.55
	Adult female	0.33	0.27	0.41
Breeding season survival (*BSS*)	Yearling female	0.73	0.66	0.79
	Adult female	0.65	0.60	0.70
Nest initiation; first nest (*Nest*1)[b]	Yearling female	0.90	0.83	0.94
	Adult female	0.96	0.91	0.99
Nest initiation; second nest (*Nest*2)	Combined	0.17	0.08	0.30
Clutch size; first nest (*cls*1)	Combined	9.93	9.40	10.48
Clutch size; first nest (*cls*2)	Combined	8.77	6.59	11.38
Nest survival; first nest (*N.surv*1)	Yearling female	0.85	0.74	0.92
	Adult female	0.76	0.68	0.83
Nest survival; first nest (*N.surv*2)	Combined	0.97	0.56	1.00
Egg hatchability (*h*)	Combined	0.88	0.86	0.90
Chick survival (*cs*)	Combined	0.28	0.25	0.31
Juvenile survival (*js*)	Combined	0.59	0.51	0.67

[a] Age designations represent that vital rates were estimated for “Yearling female” and “Adult female” age classes; a “Combined” designation represents vital rates that were pooled across age classes.

[b] First nest initiation was derived from an informative prior with a Beta distribution with a mean of 90 and a standard deviation of 12 for yearlings and a mean of 97 and a standard deviation of 5 for adults.

FIGURES

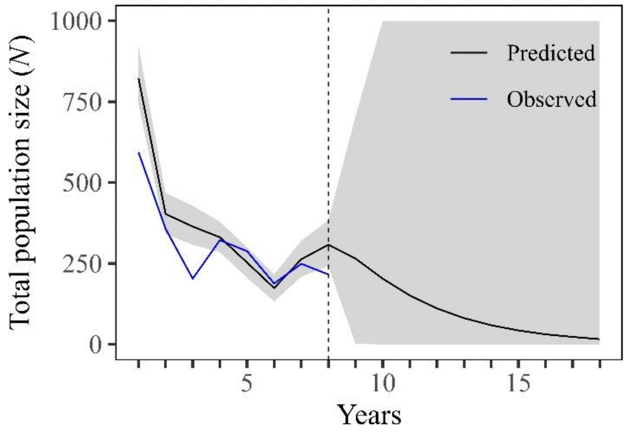

Figure 4.1. Estimated retrospective (years 1–8, 2015–2022; before vertical dashed line) and prospective (years 9–18; after vertical dashed line) population size (blue line) and raw total number of males counted on leks (black) for sharp-tailed grouse in southcentral Wyoming. Gray shaded area represents 95% credible intervals.

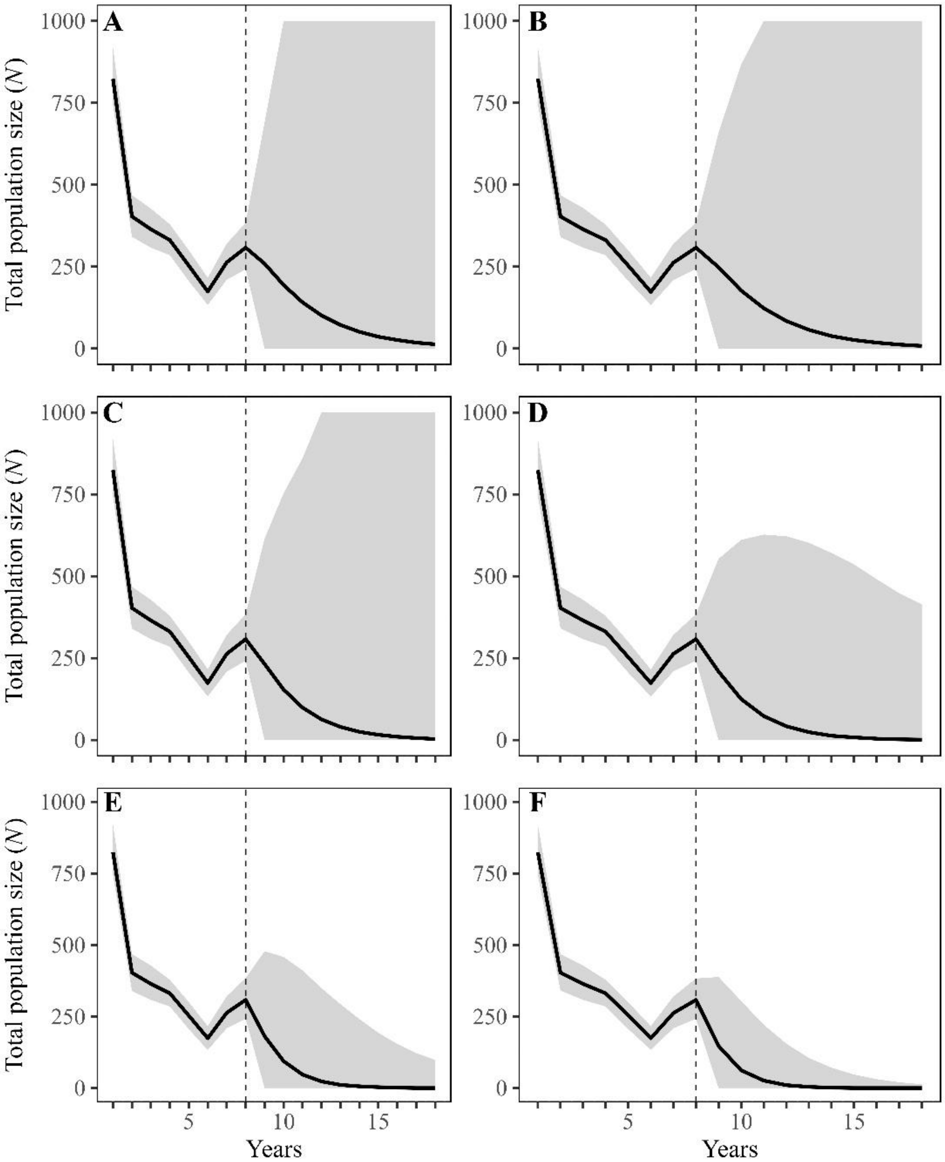

Figure 4.2. Estimated retrospective (years 1–8, 2015–2022; before vertical dashed line) and prospective (years 9–18; after vertical dashed line) population size for sharp-tailed grouse in southcentral Wyoming under different survival reduction rates simulated by reducing adult annual survival and juvenile over-winter survival when predicted 10 years into the future (survival reduction approach). Simulated survival reduction rates were 2.3% (**A**), 6.6% (**B**), 13.0% (**C**), 21.4% (**D**), 31.9% (**E**), and 44.4% (**F**) reductions in survival. Gray shaded areas represent 95% credible intervals.

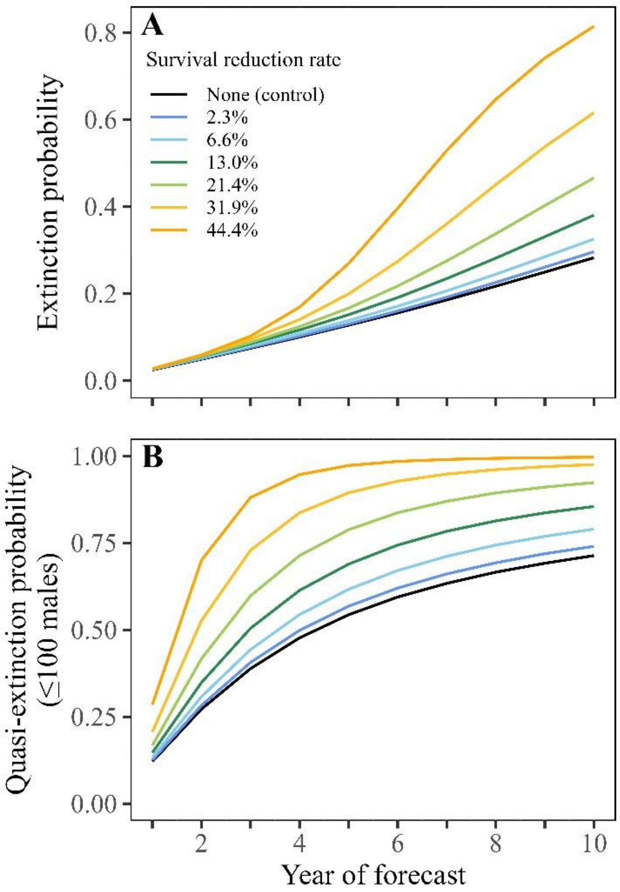

Figure 4.3. Cumulative absolute extinction (**A**) and quasi-extinction (≤100 males; **B**) probabilities from a Bayesian population viability analysis for sharp-tailed grouse in southcentral Wyoming predicted 10 years into the future under different survival reduction rates simulated by reducing adult annual survival and juvenile over-winter survival when predicted 10 years into the future. Simulated survival reduction rates were no reduction in survival (control), 2.3%, 6.6%, 13.0%, 21.4%, 31.9%, and 44.4% reductions in survival.

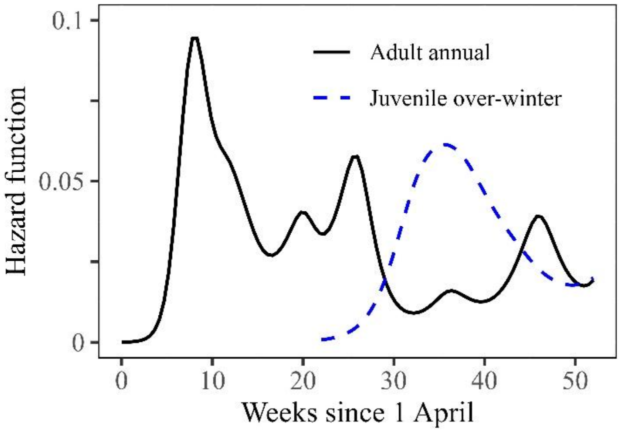

Figure 4.4. Bi-weekly hazard functions for adult female (solid black) and juvenile (blue dashed) sharp-tailed grouse in southcentral Wyoming, USA, 2017–2020. The horizontal axis was scaled to weekly hazards to minimize confusion. Juvenile overwinter survival starts at week 22 because that is when our juvenile overwinter season started and is approximately when juvenile sharp-tailed grouse become independent from females. Confidence intervals were omitted for clarity.

APPENDIX A

Results from Chapter 2 including Lesser Prairie-Chicken as an out group

INTRODUCTION

Appendix A reports results for the discriminatory analysis including Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) as an outgroup when evaluating the relationship of three populations of Sharp-tailed Grouse: Columbian Sharp-tailed Grouse (*T. phasianellus columbianus*), plains Sharp-tailed Grouse (*T. phasianellus jamesi*), and a population of unknown subspecific status in south-central Wyoming (hereafter unknown Sharp-tailed Grouse). Please see the Methods section in the main manuscript for a description of the methods used. Note, we do not include results for microsatellite analyses in this Appendix because we did not collect data on microsatellite loci for Lesser Prairie-Chickens.

RESULTS

Habitat— A discriminant analysis of principal components (DAPC) on habitat conditions surrounding observed locations correctly predicted 100.0% of Lesser Prairie-Chicken observations, 66.0% of Columbian Sharp-tailed Grouse observations, 97.8% of plains Sharp-tailed Grouse observations, and 83.7% of unknown Sharp-tailed Grouse observations (Table 1, Figure A1C). Average membership probabilities for Lesser Prairie-Chicken, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse observations were relatively high (1.00, 0.98, and 0.85, respectively) while Columbian Sharp-tailed Grouse were intermediate (0.66; Table A2). Average membership probabilities for Columbian Sharp-tailed Grouse were 0.25 plains Sharp-tailed Grouse and 0.09 unknown Sharp-tailed Grouse (Table A2). In general, Lesser Prairie-Chickens occupied their own principal components space while the principal components space of Columbian Sharp-tailed Grouse overlapped both plains and unknown Sharp-tailed Grouse;

unknown and plains Sharp-tailed Grouse did not overlap in principal components space (Figure A4D). Our Random Forests model evaluating habitat conditions for Lesser Prairie-Chickens and three Sharp-tailed Grouse populations correctly classified 100% of Lesser Prairie-Chickens, 93.3% of Columbian Sharp-tailed Grouse, 100% of plains Sharp-tailed Grouse, and 98.4% of unknown Sharp-tailed Grouse (Table A5). The three habitat characteristics with the highest importance in the Random Forests model were mean annual maximum temperature (1.00), shrub cover (0.55), and precipitation (0.21; Table A4).

When evaluating the species distribution models for the populations, we observed a similar relationship to the DAPC analysis, with Columbian Sharp-tailed Grouse habitat occurring in portions of unknown and plains Sharp-tailed Grouse with no overlap of habitat between plains Sharp-tailed Grouse, unknown Sharp-tailed Grouse, and Lesser Prairie-Chickens (Figure 1).

Morphology—Using morphological measurements from the four populations, we found that there was a difference in average tail length between populations (χ^2_3 = 372.26, $P \leq 0.001$), with Lesser Prairie-Chickens having the shortest tail (mean = 89.28 mm, SD = 9.90 mm), Columbian (mean = 109.59, SD = 4.55 mm) and unknown Sharp-tailed Grouse (mean = 110.58 mm, SD = 5.92 mm) had intermediate tail lengths that did not differ from each other (P = 0.09), and plains Sharp-tailed Grouse had the longest tails (mean = 112.87 mm, SD = 7.05 mm; Figure 2.2A). Wing cord length differed between populations (χ^2_3 = 88.85, $P \leq 0.001$) with unknown Sharp-tailed Grouse having the shortest wing cord (mean = 209.58 mm, SD = 4.02 mm), Lesser Prairie-Chicken (mean = 211.89 mm, SD = 6.52) and Columbian Sharp-tailed Grouse (mean = 211.53 mm, SD = 3.82 mm) having intermediate wing cord lengths that did not differ from each other (P = 0.32), and plains Sharp-tailed Grouse had the longest wing cord lengths (mean = 216.59 mm, SD = 5.11 mm; Figure 2.2B). We found that tarsus + longest toe length differed between the populations (χ_3^2 = 88.85, $P \leq 0.001$) with Columbian Sharp-tailed Grouse having the shortest tarsus + longest toe length (mean = 90.95 mm, SD = 2.41 mm) followed by Lesser Prairie-Chickens (mean = 92.30 mm, SD = 5.95), unknown Sharp-tailed Grouse (mean = 96.74, SD = 2.91 mm), and plains Sharp-tailed Grouse had the longest tarsus + longest toe length (mean = 98.00 mm, SD = 2.74 mm; Figure 2.2C). We found that mass differed between the four populations (χ_3^2 = 194.57, $P \leq 0.001$) with Columbian Sharp-tailed Grouse having the lowest mass (mean = 741.80 g, SD = 35.03 g), Lesser Prairie-Chicken (mean = 760.02 g, 46.55 g) and unknown Sharp-tailed Grouse (mean = 758.92 g, SD = 34.91 g) having intermediate mass that did not differ from each other (*P* = 0.98), and plains Sharp-tailed Grouse had the greatest mass (mean = 930.05 g, SD = 40.77 g; Figure 2.2D).

Using a discriminant analysis of principal components (DAPC) on morphological characteristics including mass on all populations, we found that this model correctly predicted the population 84.2% of the time for Lesser Prairie-Chickens, 93.2% of the time for Columbian Sharp-tailed Grouse, 96.8% of the time for plains Sharp-tailed Grouse, and 81.8% of the time for unknown Sharp-tailed Grouse (Table A1, Figure A1A). Average membership probabilities for Lesser Prairie-Chicken and plains Sharp-tailed Grouse individuals were relatively high (0.81 and 0.96, respectively), while average membership probabilities for Columbian Sharp-tailed Grouse and unknown Sharp-tailed Grouse individuals were intermediate (0.75 and 0.65; Table A2). Average membership probabilities for Columbian Sharp-tailed Grouse were 0.04 Lesser Prairie-Chicken and 0.21 unknown Sharp-tailed Grouse (Table A2). Average membership probabilities for unknown Sharp-tailed Grouse were 0.04 Lesser Prairie-Chicken and 0.30 Columbian Sharp-tailed Grouse (Table A2). In general, the morphological spaces of Columbian Sharp-tailed Grouse and unknown Sharp-tailed Grouse occupied similar spaces while Lesser Prairie-Chickens and plains Sharp-tailed Grouse occupied their own spaces (Figure A2A). Our Random Forests model evaluating four populations including mass correctly classified 87.4% of Lesser Prairie-Chickens, 88.1% of Columbian Sharp-tailed Grouse, 95.2% of plains Sharp-tailed Grouse, and 84.9% unknown Sharp-tailed Grouse (Table A3). The three morphological factors with the highest importance in the Random Forests model when including mass were the wing cord length to tail length ratio (1.00), tarsus + longest toe length (0.91), and wing cord length to tarsus + longest toe length ratio (0.76; Table A5).

When excluding mass from the DAPC analysis on all populations, we found that this model correctly predicted the population 83.9% of the time for Lesser Prairie-Chickens, 94.5% of the time for Columbian Sharp-tailed Grouse, 41.3% of the time for plains Sharp-tailed Grouse, and 77.0 % of the time for unknown Sharp-tailed Grouse (Table A1, Figure A3A). Average membership probabilities for Lesser Prairie-Chicken individuals were relatively high (0.80), while average membership probabilities for Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse individuals were intermediate to low (0.74, 0.40, and 0.59, respectively; Table A2). Average membership probabilities for Columbian Sharp-tailed Grouse were 0.03 Lesser Prairie-Chicken, 0.05 plains Sharp-tailed Grouse, and 0.18 unknown Sharp-tailed Grouse (Table A2). Average membership probabilities for plains Sharp-tailed Grouse were 0.05 Lesser Prairie-Chicken, 0.19 Columbian Sharp-tailed Grouse, and 0.36 unknown Sharp-tailed Grouse (Table A2). Average membership probabilities for unknown Sharp-tailed Grouse were 0.04 Lesser Prairie-Chicken, 0.25 Columbian Sharp-tailed Grouse, and 0.12 plains Sharp-tailed Grouse (Table A2). In general, in this model excluding mass, plains Sharp-tailed Grouse and unknown Sharp-tailed Grouse occupied similar morphological spaces (Figure A3B), while Columbian Sharp-tailed Grouse occupied a mostly unique morphological spaces, and Lesser Prairie-Chickens occupied their own space (Figure A3A). Our Random Forests model evaluating four populations while excluding mass correctly classified 87.4% of Lesser Prairie-Chickens, 88.1% of Columbian Sharp-tailed Grouse, 52.4% of plains Sharp-tailed Grouse, and 76.4% of unknown Sharp-tailed Grouse (Table A3). The three morphological factors with the highest importance in the wing cord length to tail length ratio (1.00), tarsus + longest toe length (0.93), and tail length (0.74; Table A6).

When evaluating morphological differences between Lesser Prairie-Chicken, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse using 15 covariates, we found that the model correctly predicted the population 92.8% of the time for Lesser Prairie-Chickens, 71.4% of the time for plains Sharp-tailed Grouse, and 74.3% of the time for unknown Sharp-tailed Grouse (Table A1, Supplemental Figure A4A). Average membership probabilities for Lesser Prairie-Chicken individuals were relatively high (0.91), while average membership probabilities for plains Sharp-tailed Grouse and unknown Sharp-tailed Grouse individuals were intermediate to low (0.68, and 0.67, respectively; Table A2). Average membership probabilities for plains Sharp-tailed Grouse were 0.10 Lesser Prairie-Chicken, 0.68 plains Sharp-tailed Grouse, and 0.22 unknown Sharp-tailed Grouse (Table A2). Average membership probabilities for unknown Sharp-tailed Grouse were 0.14 Lesser Prairie-Chicken, 0.19 plains Sharp-tailed Grouse, and 0.67 unknown Sharp-tailed Grouse (Table A2). In general, from this model on 3 populations using 15 covariates, Lesser Prairie-Chickens occupied their own morphological spaces while plains Sharp-tailed Grouse and unknown Sharp-tailed Grouse mostly occupied their own space, however there was some overlap (Figure A4B). Our Random Forests model evaluating 15 covariates on three populations correctly classified 92.8% of Lesser Prairie-Chickens, 79.4% of plains Sharp-tailed Grouse, and 83.4% of unknown Sharp-tailed Grouse (Table A3). The three morphological factors with the highest importance in the expanded morphological covariates Random Forests model were the wing cord length to tail length ratio (1.00), tail length (0.81), and the tail length to total head length ratio (0.80; Table A7).

Microsatellite Genotyping—We did not collect microsatellite loci from Lesser Prairie-Chicken samples; therefore, we do not have any microsatellite loci results including Lesser Prairie-Chickens.

Whole Genome Resequencing—Using a DAPC analysis on low-resolution whole genome resequencing single nucleotide variants (SNVs) data, the model correctly predicted 100.0% of Lesser Prairie-Chicken, 66.7% of Columbian Sharp-tailed Grouse, 33.3% of plains Sharp-tailed Grouse, and 76.9% of unknown Sharp-tailed Grouse (Table 1, Figure A1B). The average membership probabilities for Lesser Prairie-Chicken individuals was high (1.00), while average membership probabilities for Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, and unknown Sharp-tailed Grouse individuals were low (0.56, 0.39, and 0.49, respectively; Table A2). In general, Lesser Prairie-Chicken occupied a unique principal components space while Columbian, plains, and unknown Sharp-tailed Grouse generally shared a principal components space (Figure A2B). Our Random Forests model evaluating 453 single nucleotide variants across all sequenced individuals correctly classified 0.0% of Lesser Prairie-Chickens, 50.0% of Columbian Sharp-tailed Grouse, 33.3% of plains Sharp-tailed Grouse, and 53.9% of unknown Sharp-tailed Grouse (Table A3). Population genetic statistics for single nucleotide variants are reported in Table 4.

Table A1. Number of variables, sample sizes, and assignment probabilities of discriminant analysis of principal components on habitat characteristics, morphological characteristic, and single nucleotide variants (SNVs) for populations of Lesser Prairie-Chicken (LEPC), Columbian Sharp-tailed Grouse (STGRc), plains Sharp-tailed Grouse (STGRp), and a population with unknown subspecific status of Sharp-tailed Grouse in south-central Wyoming (STGRu). Habitat data (eBird observation locations) from Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, Washington, and Wyoming, 2010–2023. Morphological data were collected in Kansas and Colorado (LEPC; 2013–2017), Idaho and Washington (STGRc; 2005–2013), and Wyoming (STGRp, 2019; STGRu, 2017–2019). Single nucleotide variant data were collected on individuals sampled from Kansas (LEPC, 2013), Idaho (STGRc, 2018), and Wyoming (STGRp 2019; STGRu, 2017–2018). Empty cells (—) represent populations that were not included in that particular analysis.

		Sample size				Assignment probability			
Analyses	Number of variables	LEPC	cSTGR	pSTGR	uSTGR	LEPC	cSTGR	pSTGR	uSTGR
Habitat	22	1,576	812	7,951	509	1.00	0.66	0.98	0.84
Morphology	6[a]	222	219	63	165	0.84	0.95	0.41	0.77
	10[b]	222	219	63	165	0.84	0.93	0.97	0.82
	15[c]	210	—	63	74	0.93	—	0.71	0.74
SNVs	453	2	12	12	13	1.00	0.67	0.33	0.77

[a] Morphological analysis using tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons.

[b] Morphological analysis using mass (g), tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons

[c] Morphological analysis using tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), culmen length, total head length, and all pairwise combinations

Table A2. Mean and median average membership probability of each individual assigned to each population of prairie-grouse evaluated using a discriminant analysis of principal components based on habitat characteristics, morphological characteristics, and single nucleotide variants (SNVs) for 4 populations of prairie-grouse: Lesser Prairie-Chicken (LEPC), Columbian Sharp-tailed Grouse (STGRc), plains Sharp-tailed Grouse (STGRp), and a population of Sharp-tailed Grouse with unknown subspecific status (STGRu) in south-central Wyoming. Habitat data (eBird observation locations) from Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, Washington, and Wyoming, 2010–2023. Morphological data were collected in Kansas and Colorado (LEPC; 2013–2017), Idaho and Washington (STGRc; 2005–2013), and Wyoming (STGRp, 2019; STGRu, 2017–2019). Single nucleotide variant data were collected on individuals sampled from Kansas (LEPC, 2013), Idaho (STGRc, 2018), and Wyoming (STGRp 2019; STGRu, 2017–2018).

		Mean (median) average membership probability of individs.			
Analyses	**Population**	**LEPC**	**STGRc**	**STGRp**	**STGRu**
Habitat	LEPC	1.00 (1.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
	STGRc	<0.01 (0.00)	0.66 (0.96)	0.25 (0.01)	0.09 (0.00)
	STGRp	0.01 (0.00)	0.02 (0.00)	0.98 (1.00)	<0.01 (0.00)
	STGRu	<0.01 (0.00)	0.15 (0.00)	<0.01 (0.00)	0.85 (1.00)
Morphological[a]	LEPC	0.80 (0.99)	0.11 (0.01)	0.02 (0.00)	0.07 (0.01)
	STGRc	0.03 (0.01)	0.74 (0.78)	0.05 (0.03)	0.18 (0.16)
	STGRp	0.05 (0.01)	0.19 (0.14)	0.40 (0.38)	0.36 (0.35)
	STGRu	0.04 (0.01)	0.25 (0.21)	0.12 (0.08)	0.59 (0.64)
Morphological[b]	LEPC	0.81 (0.99)	0.10 (0.01)	0.01 (0.00)	0.08 (0.00)
	STGRc	0.04 (0.01)	0.75 (0.80)	0.00 (0.00)	0.21 (0.18)
	STGRp	0.01 (0.00)	0.01 (0.00)	0.96 (1.00)	0.02 (0.00)
	STGRu	0.04 (0.01)	0.30 (0.27)	0.00 (0.00)	0.65 (0.70)
Morphological[c]	LEPC	0.91 (1.00)	—	0.02 (0.00)	0.06 (0.00)
	STGRp	0.10 (0.01)	—	0.68 (0.91)	0.22 (0.07)
	STGRc	0.14 (0.04)	—	0.19 (0.07)	0.67 (0.76)
SNVs	LEPC	1.00 (1.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
	STGRc	0.00 (0.00)	0.56 (0.54)	0.24 (0.24)	0.20 (0.14)
	STGRp	0.00 (0.00)	0.23 (0.12)	0.39 (0.36)	0.38 (0.34)
	STGRu	0.00 (0.00)	0.16 (0.09)	0.35 (0.33)	0.49 (0.52)

[a] Morphological analysis using tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons.

[b] Morphological analysis using mass (g), tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons

[c] Morphological analysis using tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), culmen length, total head length, and all pairwise combinations

Table A3. Pairwise comparisons and classification error (%) of Random Forests classification for four populations of prairie-grouse based on habitat characteristics, morphological characteristics, and single nucleotide variants. Populations evaluated were Lesser Prairie-Chicken (LEPC), Columbian Sharp-tailed Grouse (STGRc), plains Sharp-tailed Grouse (STGRp), and unknown Sharp-tailed Grouse (STGRu). Habitat data (eBird observation locations) from Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, Washington, and Wyoming, 2010–2023. Morphological data were collected in Kansas and Colorado (LEPC; 2013–2017), Idaho and Washington (STGRc; 2005–2013), and Wyoming (STGRp, 2019; STGRu, 2017–2019). Single nucleotide variant data were collected on individuals sampled from Kansas (LEPC, 2013), Idaho (STGRc, 2018), and Wyoming (STGRp 2019; STGRu, 2017–2018).

Analysis		LEPC	STGRc	STGRp	STGRu	Classification error (%)
Habitat	LEPC	1,576	0	0	0	0.0
	STGRc	0	757	54	1	6.8
	STGRp	1	7	7943	0	0.1
	STGRu	0	8	1	500	1.8
Morphological[a]	LEPC	194	15	0	13	12.6
	STGRc	14	193	0	12	11.9
	STGRp	2	0	60	1	4.8
	STGRu	11	13	1	140	15.2
Morphological[b]	LEPC	194	14	0	14	12.6
	STGRc	11	193	3	12	11.9
	STGRp	4	5	33	21	47.6
	STGRu	10	14	15	126	23.6

Morphological[c]	LEPC	194	–	3	12	7.2
	STGRp	9	–	50	4	20.6
	STGRu	5	–	7	62	16.2
Single nucleotide variants	LEPC	0	1	0	1	100.0
	STGRc	0	6	3	3	50.0
	STGRp	0	3	5	4	58.3
	STGRu	0	4	3	6	53.8

[a] Morphological analysis using tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons.

[b] Morphological analysis using mass (g), tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), and all pairwise comparisons

[c] Morphological analysis using tail length (mm), wing cord length (mm), tarsus + longest toe length (mm), culmen length, total head length, and all pairwise combinations

Table A4. Standardized variable importance for Random Forests model predicting prairie-grouse populations based on habitat characteristics at observed locations (eBird), 2010–2023. Prairie-grouse populations evaluated were Lesser Prairie-Chicken, Columbian Sharp-tailed Grouse, plains Sharp-tailed Grouse, and a population of Sharp-tailed Grouse with unknown subspecific status. Variable importance values were standardized so the top variable equals 1 and the remaining variables are proportions derived by dividing by the top variable (Doherty et al. 2018). PRISM represents 30-year average annual climate data (PRISM Climate Group 2014); RAP represents rangeland analysis platform data (Robinson et al. 2019, Alred et al. 2021, Jones et al. 2021); and NLCD represents the National Land Cover Database from 2011, 2013, 2016, 2019, and 2021 (Jin et al. 2019).

Variable	Importance Value
Mean maximum annual temperature (PRISM)	1.00
Percent cover of shrubs (RAP)	0.55
Mean annual precipitation (PRISM)	0.21
Terrain ruggedness index	0.16
Emergent wetland (NLCD)	0.14
Perennial herbaceous vegetation biomass (RAP)	0.11
Heat load index	0.11
Percent cover of litter (RAP)	0.10
Annual herbaceous vegetation biomass (RAP)	0.09
Percent cover of perennial herbaceous vegetation (RAP)	0.08
Water (NLCD)	0.07
Percent cover of annual herbaceous vegetation (RAP)	0.07
Canopy cover of coniferous forests (RAP)	0.07
Topographic position index	0.07
Canopy cover of deciduous forests (RAP)	0.07
Croplands (NLCD)	0.06
Unclassified forests canopy cover (RAP)	0.05
Canopy cover of all forest types (RAP)	0.05
Percent bare ground (RAP)	0.05
Pasture lands (NLCD)	0.05
Anthropogenic development (NLCD)	0.04
Canopy cover of mixed forests (RAP)	0.02

Table A5. Standardized variable importance for Random Forests model predicting prairie-grouse populations based on morphological characteristics (mass (g), tail length (mm), wing cord length (mm), tarsus + longest toe length (mm) [tarsus + toe length], and all pairwise comparisons). Prairie-grouse populations evaluated were Lesser Prairie-Chicken (2013–2017; Kansas and Colorado), Columbian Sharp-tailed Grouse (2005–2013; Idaho and Washington), plains Sharp-tailed Grouse (2019; Wyoming), and a population of Sharp-tailed Grouse with unknown subspecific status (2017–2019; Wyoming). Variable importance values were standardized so the top variable equals 1 and the remaining variables are proportions derived by dividing by the top variable (Doherty et al. 2018).

Variable	Importance value
Wing cord length to tail length ratio	1.00
Tarsus + toe length	0.91
Wing cord length to tarsus + toe length ratio	0.76
Tail length	0.71
Tail length to mass ratio	0.66
Tail length to tarsus + toe length ratio	0.53
Mass	0.52
Tarsus + toe length to mass ratio	0.40
Wing cord length:mass	0.40
Wing cord length	0.16

Table A6**.** Standardized variable importance for Random Forests model predicting prairie-grouse populations based on morphological characteristics (tail length (mm), wing cord length (mm), tarsus + longest toe length (mm) [tarsus + toe length], and all pairwise comparisons). Prairie-grouse populations evaluated were Lesser Prairie-Chicken (2013–2017; Kansas and Colorado), Columbian Sharp-tailed Grouse (2005–2013; Idaho and Washington), plains Sharp-tailed Grouse (2019; Wyoming), and a population of Sharp-tailed Grouse with unknown subspecific status (2017–2019; Wyoming). Variable importance values were standardized so the top variable equals 1 and the remaining variables are proportions derived by dividing by the top variable (Doherty et al. 2018).

Variable	Importance value
Wing cord length to tail length ratio	1.00
Tarsus + toe length	0.93
Tail length	0.74
Wing cord length to tarsus + toe length ratio	0.72
Tail length to tarsus +toe length ratio	0.71
Wing cord length	0.41

Table A7. Standardized variable importance for Random Forests model predicting prairie-grouse populations based on morphological characteristics (tail length (mm), wing cord length (mm), tarsus + longest toe length (mm; tarsus + toe), culmen length, total head length, and all pairwise combinations). Prairie-grouse populations evaluated were Lesser Prairie-Chicken (2013–2017; Kansas and Colorado), plains Sharp-tailed Grouse (2019; Wyoming), and a population of Sharp-tailed Grouse with unknown subspecific status (2017–2019; Wyoming). Variable importance values were standardized so the top variable equals 1 and the remaining variables are proportions derived by dividing by the top variable (Doherty et al. 2018).

Variable	**Importance value**
Wing cord length to tail length ratio	1.00
Tail length	0.81
Tail length to total head length ratio	0.80
Tail length to culmen length ratio	0.63
Tail length to tarsus +toe length ratio	0.46
Total head length	0.45
Total head length to tarsus +toe length ratio	0.43
Wing cord length	0.34
Wing cord length to total head length ratio	0.32
Tarsus +toe length	0.32
Total head length to culmen length ratio	0.30
Wing cord length to tarsus +toe length ratio	0.26
Culmen length	0.20
Culmen length to tarsus +toe length ratio	0.19
Wing cord length to culmen length ratio	0.17

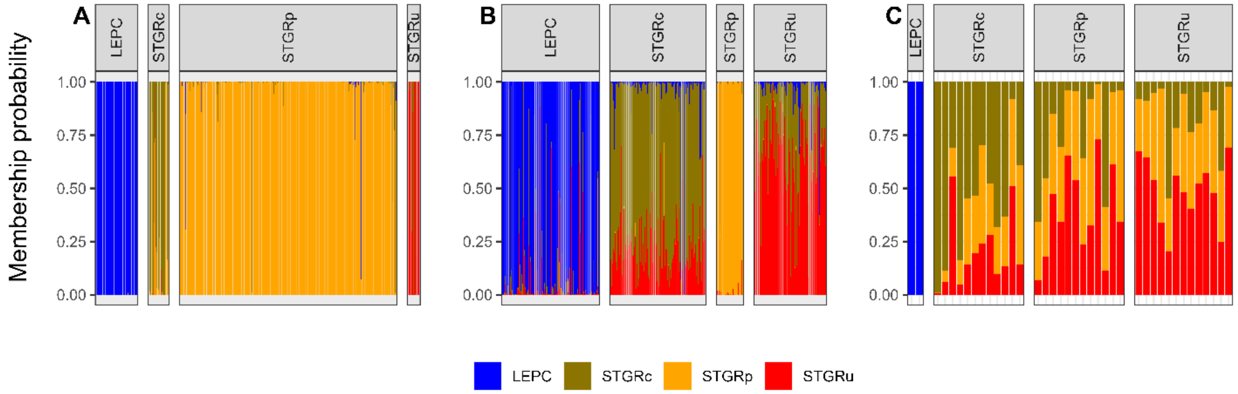

Figure A1. Membership probability (admixture) plots for discriminant analysis of principal components for habitat characteristics (**A**), morphological characteristics (mass, wing cord length, tarsus + longest toe length, tail length, and all pairwise combinations; **B**), single nucleotide variants (SNVs; **C**), and for Lesser Prairie-Chicken (LEPC), Columbian Sharp-tailed Grouse (STGRc), plains Sharp-tailed Grouse (STGRp), and unknown Sharp-tailed Grouse subspecies (STGRu). Membership probability plot depicts the proportion of assignment to each population, with different colors representing the proportion of each population in each individual. Facets represent the original population of each individual (morphology and SNVs) or observations (habitat). Habitat data (eBird observation locations) from Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, Washington, and Wyoming, 2010–2023. Morphological data were collected in Kansas and Colorado (LEPC; 2013–2017), Idaho and Washington (STGRc; 2005–2013), and Wyoming (STGRp, 2019; STGRu, 2017–2019). Single nucleotide variant data were collected on individuals sampled from Kansas (LEPC, 2013), Idaho (STGRc, 2018), and Wyoming (STGRp 2019; STGRu, 2017–2018).

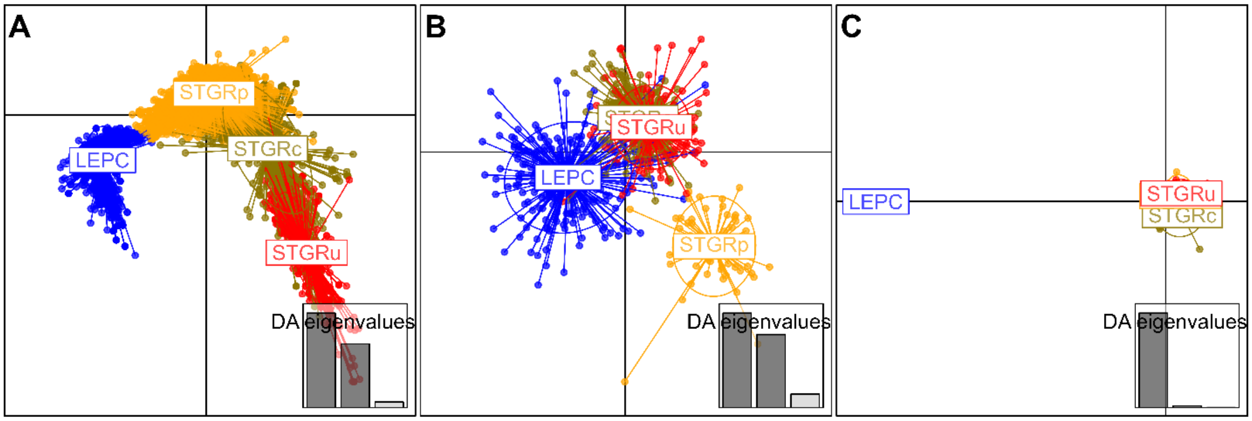

Figure A2. Principal components plots from discriminant analysis of principal components for habitat characteristics (**A**), morphological characteristics (mass, wing cord length, tarsus + longest toe length, tail length, and all pairwise combinations; **B**), and 453 single nucleotide variants (SNVs; **C**) for Lesser Prairie-Chicken (LEPC; blue), Columbian Sharp-tailed Grouse (STGRc; greenish-gold), plains Sharp-tailed Grouse (STGRp; yellow-orange), and unknown Sharp-tailed Grouse subspecies (STGRu; red). Habitat data (eBird observation locations) from Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, Washington, and Wyoming, 2010–2023. Morphological data were collected in Kansas and Colorado (LEPC; 2013–2017), Idaho and Washington (STGRc; 2005–2013), and Wyoming (STGRp, 2019; STGRu, 2017–2019). Single nucleotide variant data were collected on individuals sampled from Kansas (LEPC, 2013), Idaho (STGRc, 2018), and Wyoming (STGRp 2019; STGRu, 2017–2018). Points represent individuals (morphology and SNVs) or individual observations (habitat).

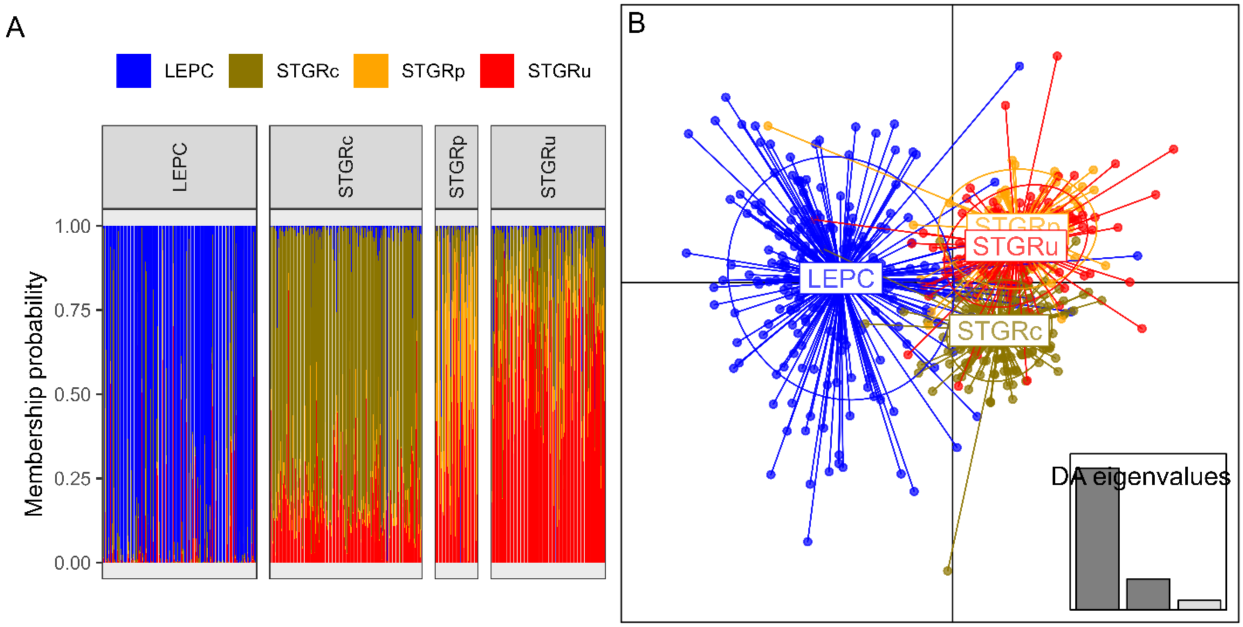

Figure A3. Membership probability (admixture) plot (**A**) and principal components plot (**B**) from discriminant analysis of principal components (DAPC) for morphological characteristics excluding mass (wing cord length, tarsus + longest toe length, tail length, and all pairwise combinations) for Lesser Prairie-Chicken (LEPC), Columbian Sharp-tailed Grouse (STGRc), plains Sharp-tailed Grouse (STGRp), and unknown Sharp-tailed Grouse (STGRu). Morphological data were collected in Kansas and Colorado (LEPC; 2013–2017), Idaho and Washington (STGRc; 2005–2013), and Wyoming (STGRp, 2019; STGRu, 2017–2019).

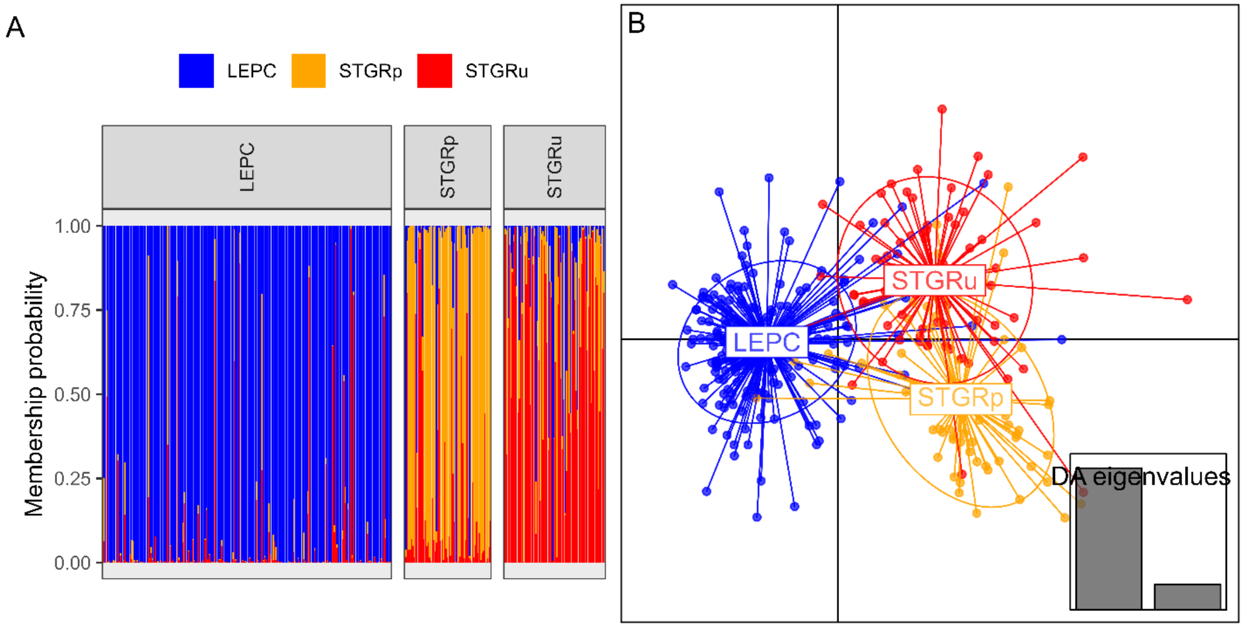

Figure A4. Membership probability (admixture) plot (**A**) and principal components plot (**B**) from discriminant analysis of principal components (DAPC) for expanded morphological characteristics (total head length, culmen length, wing cord length, tarsus + longest toe length, tail length, and all pairwise combinations) for Lesser Prairie-Chicken (LEPC), plains Sharp-tailed Grouse (STGRp), and unknown Sharp-tailed Grouse (STGRu). Morphological data were collected in Kansas and Colorado (LEPC; 2013–2017) and Wyoming (STGRp, 2019; STGRu, 2017–2019).

APPENDIX B

Supplemental tables and figures for the Chapter 3.

Table B1. 2017–2019 annual lek counts and averaged lek count over the three years of the study, Carbon County, Wyoming, USA, 2017–2019. Numbers in parentheses are the rank of the lek size; leks with an en dash (–) represent leks that were not counted/visited during that year; zero's represent leks that were visited but no birds were observed on the lek.

Lek ID	2017 lek count	2018 lek count	2019 lek count	Average lek count
10	2 (1)	4 (1)	0 (1)	2 (1)
22	3 (2)	4 (1)	3 (3)	3 (2)
7	6 (3)	5 (4)	4 (5)	5 (3)
1	9 (5)	7 (5)	4 (5)	7 (4)
23	– (–)	8 (6)	6 (9.5)	7 (4)
14	21 (16)	4 (1)	1 (2)	9 (6)
3	6 (3)	10 (8)	15 (14)	10 (7)
6	12 (6)	16 (14)	5 (7.5)	11 (8)
15	17 (10)	12 (9)	4 (5)	11 (8)
24	17 (10)	12 (9)	5 (7.5)	11 (8)
9	17 (10)	13 (12)	7 (11)	12 (11)
12	13 (8)	– (–)	– (–)	13 (12)
16	26 (21)	8 (6)	6 (9.5)	13 (12)
21	15 (9)	16 (14)	9 (12)	13 (12)
8	12 (6)	12 (9)	22 (15)	15 (15)
17	20 (14)	14 (13)	– (–)	17 (16)
4	23 (17)	18 (18)	12 (13)	18 (17)
11	20 (14)	17 (17)	26 (17)	21 (18)
20	17 (10)	16 (14)	30 (18.5)	21 (18)
2	25 (18)	23 (19)	24 (16)	24 (20)
13	25 (18)	26 (21)	– (–)	26 (21)
5	25 (18)	28 (22)	36 (20)	30 (22)
18	26 (21)	24 (20)	42 (21)	31 (23)
19	35 (23)	30 (23)	30 (18.5)	32 (24)

Table B2. Pearson's correlation matrix for variables used to identify sharp-tailed grouse nest mortality risk based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 30	**shrubht 30**	**sage 100**	**litter 400**	**herb 100**	**nonsageshr 30**	**bare 100**	**tpi 800**
shrub 30	–	–	–	–	–	–	–	–
shrubht 30	0.82	–	–	–	–	–	–	–
sage 100	0.17	-0.13	–	–	–	–	–	–
litter 400	-0.3	-0.45	0.69	–	–	–	–	–
herb 100	-0.76	-0.55	-0.36	0.08	–	–	–	–
nonsageshr 30	0.65	0.77	-0.54	-0.71	-0.4	–	–	–
bare 100	-0.44	-0.58	0.08	0.42	0.16	-0.42	–	–
tpi 800	-0.1	-0.09	-0.05	0.08	0	-0.03	0.05	–
tri 100	0.21	0.16	0.04	0.11	-0.3	0.1	0.06	0.09

Table B3. Pearson's correlation matrix for variables used to identify sharp-tailed grouse brood mortality risk based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	sage 30	**perherb 400**	**litter 30**	**herb 200**	**bare 30**	**decid 800**	**hli 400**	**tpi 100**
perherb 400	-0.06	–	–	–	–	–	–	–
litter 30	0.78	0.08	–	–	–	–	–	–
herb 200	-0.12	0.86	0.08	–	–	–	–	–
bare 30	0.09	-0.05	0.19	0.01	–	–	–	–
decid 800	-0.08	-0.5	-0.2	-0.39	-0.12	–	–	–
hli 400	0.09	0.41	0.13	0.25	0.05	-0.36	–	–
tpi 100	0.06	-0.32	0.04	-0.29	0	0.21	-0.23	–
tri 30	0.05	-0.22	0.02	-0.33	0.06	-0.04	0.01	-0.02

Table B4. Pearson’s correlation matrix for variables used to identify sharp-tailed grouse early nonbreeding season mortality risk based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	sage 100	**perherb 1600**	**litter 100**	**herb 1600**	**nonsageshr 100**	**bare 100**	**decid 200**	**hli 3200**	**tpi 100**
perherb 1600	0.26	–	–	–	–	–	–	–	–
litter 100	0.85	0.29	–	–	–	–	–	–	–
herb 1600	0.35	0.89	0.47	–	–	–	–	–	–
nonsageshr 100	-0.62	-0.16	-0.69	-0.34	–	–	–	–	–
bare 100	0.15	-0.25	0.34	0.07	-0.47	–	–	–	–
decid 200	-0.5	-0.36	-0.67	-0.49	0.32	-0.26	–	–	–
hli 3200	0.17	0.25	0.18	0.24	-0.16	0.01	-0.19	–	–
tpi 100	-0.03	-0.05	-0.02	-0.05	-0.06	0.13	0.19	0.05	–
tri 800	-0.25	-0.23	-0.32	-0.31	0.3	-0.09	0.31	-0.06	0.21

Table B5. Pearson's correlation matrix for variables used to identify sharp-tailed grouse late nonbreeding season mortality risk based on environmental variables, Carbon County, Wyoming, USA, 2017–2020. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 3200	**shrubht 3200**	**sage 100**	**litter 100**	**herb 3200**	**bare 3200**	**decid 3200**	**doil**	**droads**	**hli 3200**	**tpi 3200**
shrubht 3200	0.73	–	–	–	–	–	–	–	–	–	–
sage 100	-0.04	-0.22	–	–	–	–	–	–	–	–	–
litter 100	-0.20	-0.03	0.86	–	–	–	–	–	–	–	–
herb 3200	-0.06	-0.07	0.40	0.51	–	–	–	–	–	–	–
bare 3200	-0.50	-0.82	0.29	0.38	0.17	–	–	–	–	–	–
decid 3200	0.13	0.49	-0.49	-0.55	-0.66	-0.60	–	–	–	–	–
doil	-0.10	0.15	-0.31	-0.38	-0.47	-0.28	0.68	–	–	–	–
droads	0.03	0.14	-0.14	-0.06	-0.01	-0.04	0.06	-0.02	–	–	–
hli 3200	0.02	0.04	0.07	0.07	0.04	-0.15	0.03	0.09	-0.30	–	–
tpi 3200	0.10	0.02	-0.17	-0.20	0.01	0.02	-0.03	-0.11	-0.01	-0.17	–
tri 100	0.08	0.12	-0.41	-0.36	-0.06	-0.17	0.15	0.06	0.10	-0.02	0.13

Table B6. Pearson's correlation matrix for variables used to identify sharp-tailed grouse nest-site selection based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 800	**shrubht 800**	**sage 30**	**litter 30**	**herb 200**	**bare 100**	**nonsageshr 200**	**decid 800**	**conif 800**	**doil**	**hli 800**	**tpi 800**
shrubht 800	0.87	–	–	–	–	–	–	–	–	–	–	–
sage 30	0.33	0.11	–	–	–	–	–	–	–	–	–	–
litter 30	0.18	0.07	0.74	–	–	–	–	–	–	–	–	–
herb 200	0.16	0.18	0.41	0.69	–	–	–	–	–	–	–	–
bare 100	-0.20	-0.38	0.16	0.17	0.08	–	–	–	–	–	–	–
nonsageshr 200	0.58	0.67	-0.30	-0.31	-0.22	-0.44	–	–	–	–	–	–
decid 800	0.13	0.32	-0.46	-0.53	-0.50	-0.40	0.55	–	–	–	–	–
conif 800	-0.46	-0.44	-0.45	-0.53	-0.67	-0.27	0.04	0.20	–	–	–	–
doil	-0.18	-0.03	-0.48	-0.52	-0.51	-0.45	0.33	0.56	0.63	–	–	–
hli 800	-0.04	-0.06	-0.04	-0.02	-0.02	0.05	0.02	-0.11	0.09	0.15	–	–
tpi 800	0.06	0.01	-0.04	-0.03	-0.05	0.02	0.12	0.03	0.01	0.00	0.00	–
tri 100	0.01	0.06	-0.26	-0.27	-0.28	-0.09	0.25	0.27	0.21	0.27	0.17	0.07

Table B7. Pearson's correlation matrix for variables used to identify sharp-tailed grouse brood habitat selection based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 800	**shrub-ht 800**	**sage 100**	**per-herb 200**	**litter 800**	**herb 100**	**nonsage-shr 800**	**bare 800**	**ann-herb 200**	**decid 800**	**conif 800**	**doil**	**droads**	**hli 30**	**tpi 100**
shrubht 800	0.81	–	–	–	–	–	–	–	–	–	–	–	–	–	–
sage 100	0.31	0.00	–	–	–	–	–	–	–	–	–	–	–	–	–
perherb 200	0.16	0.25	0.34	–	–	–	–	–	–	–	–	–	–	–	–
litter 800	0.14	-0.07	0.76	0.57	–	–	–	–	–	–	–	–	–	–	–
herb 100	0.04	0.08	0.37	0.92	0.65	–	–	–	–	–	–	–	–	–	–
nonsage-shr 800	0.55	0.72	-0.51	-0.19	-0.66	-0.34	–	–	–	–	–	–	–	–	–
bare 800	-0.28	-0.58	0.33	-0.08	0.44	0.13	-0.60	–	–	–	–	–	–	–	–
annherb 200	-0.33	-0.48	0.31	0.12	0.59	0.39	-0.64	0.70	–	–	–	–	–	–	–
decid 800	0.02	0.26	-0.57	-0.45	-0.77	-0.53	0.61	-0.49	-0.52	–	–	–	–	–	–
conif 800	-0.3	-0.28	-0.46	-0.57	-0.68	-0.59	0.23	-0.31	-0.36	0.29	–	–	–	–	–
doil	-0.07	0.16	-0.52	-0.29	-0.70	-0.42	0.49	-0.56	-0.61	0.66	0.51	–	–	–	–
droads	-0.05	-0.09	-0.13	-0.13	-0.17	-0.14	0.09	-0.07	-0.11	0.05	0.27	0.13	–	–	–
hli 30	0.03	0.02	0.00	0.04	-0.01	0.04	0.05	0.02	0.00	-0.05	0.01	0.05	0.02	–	–

tpi 100	0.00	0.00	0.03	-0.02	-0.01	-0.03	0.01	0.00	0.00	0.00	0.01	0.00	0.01	-0.02	–
tri 200	0.02	0.11	-0.31	-0.14	-0.28	-0.24	0.27	-0.14	-0.37	0.26	0.13	0.23	0.20	0.13	-0.02

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Table B8. Pearson's correlation matrix for variables used to identify sharp-tailed grouse early nonbreeding season habitat selection based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 400	**shrubht 400**	**sage 3200**	**perherb 3200**	**herb 1600**	**nonsage-shr 400**	**bare 1600**	**annherb 800**	**decid 3200**	**conif 1600**	**hli 3200**	**tpi 200**
shrubht 400	0.91	–	–	–	–	–	–	–	–	–	–	–
sage 3200	0.31	0.13	–	–	–	–	–	–	–	–	–	–
perherb 3200	0.39	0.41	0.65	–	–	–	–	–	–	–	–	–
herb 1600	0.22	0.26	0.67	0.89	–	–	–	–	–	–	–	–
nonsageshr 400	0.71	0.77	-0.37	-0.05	-0.25	–	–	–	–	–	–	–
bare 1600	-0.26	-0.38	0.40	-0.03	0.21	-0.52	–	–	–	–	–	–
annherb 800	-0.29	-0.27	0.37	0.15	0.51	-0.55	0.61	–	–	–	–	–
decid 3200	0.20	0.35	-0.65	-0.38	-0.54	0.65	-0.57	-0.58	–	–	–	–
conif 1600	-0.43	-0.45	-0.63	-0.73	-0.80	-0.01	-0.34	-0.43	0.23	–	–	–
hli 3200	-0.03	-0.07	0.01	0.03	0.01	-0.04	-0.08	-0.06	-0.12	0.13	–	–
tpi 200	0.02	-0.01	0.00	0.00	-0.01	0.02	0.00	-0.02	0.00	0.01	0.00	–
tri 3200	0.13	0.17	-0.37	-0.17	-0.41	0.38	-0.58	-0.64	0.52	0.42	0.28	0.02

Table B9. Pearson's correlation matrix for variables used to identify sharp-tailed grouse late nonbreeding season habitat selection based on environmental variables, Carbon County, Wyoming, USA, 2017–2020. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 400	**shrubht 400**	**sage 3200**	**herb 3200**	**bare 400**	**decid 3200**	**conif 1600**	**doil**	**tpi 400**
shrubht 400	0.91	–	–	–	–	–	–	–	–
sage 3200	0.37	0.19	–	–	–	–	–	–	–
herb 3200	0.28	0.31	0.70	–	–	–	–	–	–
bare 400	-0.32	-0.42	0.26	0.08	–	–	–	–	–
decid 3200	0.24	0.38	-0.59	-0.49	-0.48	–	–	–	–
conif 1600	-0.44	-0.45	-0.64	-0.78	-0.32	0.19	–	–	–
doil	-0.20	-0.18	-0.62	-0.66	-0.24	0.45	0.60	–	–
tpi 400	0.02	-0.02	0.00	0.01	0.04	0.00	0.01	0.00	–
tri 3200	0.14	0.20	-0.36	-0.37	-0.58	0.52	0.45	0.39	0.02

Table B10. Pearson's correlation matrix for variables used to identify sharp-tailed grouse lek-site selection based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 3200	**sage 400**	**herb 200**	**conif 800**	**tpi 100**
sage 400	0.46	–	–	–	–
herb 200	0.36	0.92	–	–	–
conif 800	-0.63	-0.71	-0.72	–	–
tpi 100	0.00	0.00	-0.01	0.00	–
tri 200	-0.02	-0.16	-0.27	0.18	-0.04

Table B11. Pearson's correlation matrix for variables used to identify sharp-tailed grouse lek-site selection based on seasonal habitat selection and mortality risk, Carbon County, Wyoming, USA, 2017–2019. MR stands for mortality risk; NB stands for nonbreeding season; and RSF represents resource selection function or habitat selection. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	Brood MR 3200	**Nest MR 400**	**Early NB MR 800**	**Brood RSF 400**	**Nest RSF 800**	**Early NB RSF 1600**
Nest MR 400	-0.29	–	–	–	–	–
Early NB MR 800	-0.01	-0.69	–	–	–	–
Brood RSF 400	-0.23	-0.58	0.74	–	–	–
Nest RSF 800	-0.28	-0.59	0.77	0.94	–	–
Early NB RSF 1600	-0.25	-0.56	0.84	0.85	0.84	–
Late NB RSF 3200	-0.35	-0.51	0.73	0.82	0.81	0.93

Table B12. Pearson's correlation matrix for variables used to identify sharp-tailed grouse lek size (average lek count from 2017–2019) based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 1600	**sage 3200**	**herb 1600**	**bare 400**	**decid 1600**	**conif 400**	**doil**	**hli 200**
sage 3200	-0.65	–	–	–	–	–	–	–
herb 1600	-0.72	0.45	–	–	–	–	–	–
bare 400	-0.44	0.56	-0.05	–	–	–	–	–
decid 1600	0.73	-0.80	-0.69	-0.49	–	–	–	–
conif 400	0.64	-0.65	-0.44	-0.27	0.60	–	–	–
doil	0.17	-0.42	-0.18	-0.10	0.33	0.06	–	–
hli 200	0.11	-0.13	-0.20	-0.15	0.42	-0.03	0.11	–
tri 200	0.01	0.02	-0.04	0.16	0.07	-0.13	0.29	0.37

Table B13. Pearson's correlation matrix for variables used to identify sharp-tailed grouse lek size in 2017 based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 1600	**herb 1600**	**bare 800**	**decid 1600**	**conif 1600**	**doil**	**hli 200**	**tpi 400**
herb 1600	-0.73	–	–	–	–	–	–	–
bare 800	-0.52	0.08	–	–	–	–	–	–
decid 1600	0.73	-0.69	-0.56	–	–	–	–	–
conif 1600	0.25	-0.33	-0.20	0.13	–	–	–	–
doil	0.17	-0.19	-0.21	0.33	0.29	–	–	–
hli 200	0.11	-0.20	-0.19	0.42	-0.18	0.11	–	–
tpi 400	-0.10	-0.14	-0.14	-0.03	0.10	-0.07	-0.16	–
tri 200	0.02	-0.06	0.14	0.07	-0.17	0.29	0.37	-0.36

Table B14. Pearson's correlation matrix for variables used to identify sharp-tailed grouse lek size in 2018 based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 1600	**sage 3200**	**herb 800**	**bare 400**	**decid 1600**	**conif 1600**	**hli 200**
sage 3200	-0.65	–	–	–	–	–	–
herb 800	-0.58	0.15	–	–	–	–	–
bare 400	-0.44	0.57	-0.24	–	–	–	–
decid 1600	0.73	-0.79	-0.46	-0.48	–	–	–
conif 1600	0.25	-0.41	-0.03	-0.18	0.14	–	–
hli 200	0.11	-0.12	-0.15	-0.14	0.42	-0.18	–
tri 200	0.01	0.03	-0.19	0.17	0.07	-0.19	0.37

Table B15. Pearson's correlation matrix for variables used to identify sharp-tailed grouse lek size in 2019 based on environmental variables, Carbon County, Wyoming, USA, 2017–2019. For description of variables, see Table 1. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	shrub 200	**sage 3200**	**herb 100**	**bare 400**	**decid 1600**	**conif 800**	**doil**	**droads**	**hli 200**	**tpi 100**
sage 3200	-0.39	–	–	–	–	–	–	–	–	–
herb 100	-0.51	-0.13	–	–	–	–	–	–	–	–
bare 400	-0.25	0.57	-0.50	–	–	–	–	–	–	–
decid 1600	0.60	-0.80	-0.07	-0.50	–	–	–	–	–	–
conif 800	0.07	0.23	0.03	-0.02	-0.12	–	–	–	–	–
doil	0.11	-0.42	-0.01	-0.11	0.34	-0.17	–	–	–	–
droads	0.39	0.16	-0.44	0.08	0.19	-0.06	-0.28	–	–	–
hli 200	0.11	-0.14	0.00	-0.16	0.42	-0.20	0.11	0.27	–	–
tpi 100	0.29	0.03	-0.53	0.36	-0.05	-0.06	0.32	0.01	-0.43	–
tri 3200	0.15	0.14	-0.03	-0.17	0.07	-0.02	-0.29	0.60	0.21	-0.33

Table B16. Pearson's correlation matrix for variables used to identify sharp-tailed grouse lek size (average lek count from 2017–2019) based on seasonal habitat selection and mortality risk, Carbon County, Wyoming, USA, 2017–2019. MR stands for mortality risk; NB stands for nonbreeding season; and RSF represents resource selection function or habitat selection. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	Brood MR 800	**Nest MR 800**	**Early NB MR 400**	**Late NB MR 3200**	**Brood RSF 800**	**Nest RSF 800**	**Early NB RSF 800**
Nest MR 800	0.01	–	–	–	–	–	–
Early NB MR 400	0.39	-0.09	–	–	–	–	–
Late NB MR 3200	0.44	-0.27	-0.24	–	–	–	–
Brood RSF 800	-0.65	0.00	0.13	-0.52	–	–	–
Nest RSF 800	-0.55	0.07	0.20	-0.57	0.96	–	–
Early NB RSF 800	-0.55	-0.06	0.06	-0.17	0.84	0.75	–
Late NB RSF 800	-0.59	-0.21	0.02	-0.21	0.88	0.77	0.90

Table B17. Pearson’s correlation matrix for variables used to identify sharp-tailed grouse lek size in 2017 based on seasonal habitat selection and mortality risk, Carbon County, Wyoming, USA, 2017–2019. MR stands for mortality risk; NB stands for nonbreeding season; and RSF represents resource selection function or habitat selection. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	Brood MR 1600	**Nest MR 30**	**Early NB MR 400**	**Brood RSF 400**	**Nest RSF 800**	**Early NB RSF 800**
Nest MR 30	0.02	–	–	–	–	–
Early NB MR 400	-0.59	0.17	–	–	–	–
Brood RSF 400	-0.46	0.05	0.00	–	–	–
Nest RSF 800	-0.59	-0.05	0.16	0.87	–	–
Early NB RSF 800	-0.50	-0.15	0.05	0.85	0.74	–
Late NB RSF 400	-0.48	0.26	0.22	0.79	0.70	0.77

Table B18. Pearson's correlation matrix for variables used to identify sharp-tailed grouse lek size in 2018 based on seasonal habitat selection and mortality risk, Carbon County, Wyoming, USA, 2017–2019. MR stands for mortality risk; NB stands for nonbreeding season; and RSF represents resource selection function or habitat selection. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	Brood MR 800	**Nest MR 800**	**Early NB MR 400**	**Late NB MR 3200**	**Brood RSF 800**	**Nest RSF 800**	**Early NB RSF 30**
Nest MR 800	0.24	–	–	–	–	–	–
Early NB MR 400	-0.25	-0.08	–	–	–	–	–
Late NB MR 3200	0.71	-0.30	-0.21	–	–	–	–
Brood RSF 800	-0.62	0.00	0.10	-0.52	–	–	–
Nest RSF 800	-0.63	0.07	0.18	-0.57	0.95	–	–
Early NB RSF 30	-0.35	-0.29	-0.09	0.12	0.59	0.49	–
Late NB RSF 1600	-0.59	0.24	0.44	-0.63	0.78	0.83	0.38

Table B19. Pearson's correlation matrix for variables used to identify sharp-tailed grouse lek size in 2019 based on seasonal habitat selection and mortality risk, Carbon County, Wyoming, USA, 2017–2019. MR stands for mortality risk; NB stands for nonbreeding season; and RSF represents resource selection function or habitat selection. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	Brood MR 1600	**Nest MR 30**	**Early NB MR 400**	**Late NB MR 3200**	**Brood RSF 800**	**Nest RSF 400**	**Early NB RSF 1600**
Nest MR 30	0.12	–	–	–	–	–	–
Early NB MR 400	-0.63	0.13	–	–	–	–	–
Late NB MR 3200	0.69	-0.14	-0.30	–	–	–	–
Brood RSF 800	-0.59	-0.09	0.19	-0.53	–	–	–
Nest RSF 400	0.65	0.14	-0.28	0.57	-0.92	–	–
Early NB RSF 1600	-0.66	-0.21	0.30	-0.43	0.84	-0.83	–
Late NB RSF 1600	-0.75	0.03	0.48	-0.64	0.79	-0.88	0.85

Table B20. Pearson's correlation matrix for variables in final hypothesis testing used to identify sharp-tailed grouse lek-site selection based on environmental variables (H1), seasonal habitat selection and mortality risk (H2), or a combination of the environmental variables and seasonal habitat selection and mortality risk (H3), Carbon County, Wyoming, USA, 2017–2019. For description of environmental variables, see Table 1. MR stands for mortality risk; NB stands for nonbreeding season; and RSF represents resource selection function or habitat selection. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	herb 200	**shrub 3200**	**tri 200**	**Brood MR 3200**	**Nest MR 400**
shrub 3200	0.37	–	–	–	–
tri 200	-0.27	-0.03	–	–	–
Brood MR 3200	0.17	-0.57	-0.29	–	–
Nest MR 400	-0.81	-0.31	0.20	-0.29	–
Late NB RSF 3200	0.56	0.87	-0.04	-0.35	-0.51

Table B21. Pearson's correlation matrix for variables in final hypothesis testing used to identify sharp-tailed grouse lek size (average lek count from 2017–2019) based on environmental variables (H1), seasonal habitat selection and mortality risk (H2), or a combination of the environmental variables and seasonal habitat selection and mortality risk (H3), Carbon County, Wyoming, USA, 2017–2019. For description of environmental variables, see Table 1. MR stands for mortality risk; NB stands for nonbreeding season. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	bare 400	**hli 200**	**Early NB MR 400**	**Early NB RSF 800**
hli 200	-0.15	–	–	–
Early NB MR 400	-0.33	-0.09	–	–
Early NB RSF 800	-0.58	0.27	0.06	–
Nest MR 800	-0.26	-0.02	-0.09	-0.06

Table B22. Pearson's correlation matrix for variables in final hypothesis testing used to identify sharp-tailed grouse 2017 lek size based on environmental variables (H1), seasonal habitat selection and mortality risk (H2), or a combination of the environmental variables and seasonal habitat selection and mortality risk (H3), Carbon County, Wyoming, USA, 2017–2019. For description of environmental variables, see Table 1. MR stands for mortality risk; NB stands for nonbreeding season. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	conif 1600	**hli 200**	**Brood RSF 400**
hli 200	-0.18	–	–
Brood RSF 400	0.22	0.22	–
Nest MR 30	0.01	0.22	0.05

Table B23. Pearson's correlation matrix for variables in final hypothesis testing used to identify sharp-tailed grouse 2018 lek size based on environmental variables (H1), seasonal habitat selection and mortality risk (H2), or a combination of the environmental variables and seasonal habitat selection and mortality risk (H3), Carbon County, Wyoming, USA, 2017–2019. For description of environmental variables, see Table 1. MR stands for mortality risk; NB stands for nonbreeding season. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	conif 1600	**hli 200**	**Nest RSF 800**
hli 200	-0.18	–	–
Nest RSF 800	0.25	0.26	–
Nest MR 800	-0.26	-0.03	0.07

Table B24. Pearson's correlation matrix for variables in final hypothesis testing used to identify sharp-tailed grouse 2019 lek size based on environmental variables (H1), seasonal habitat selection and mortality risk (H2), or a combination of the environmental variables and seasonal habitat selection and mortality risk (H3), Carbon County, Wyoming, USA, 2017–2019. For description of environmental variables, see Table 1. MR stands for mortality risk; NB stands for nonbreeding season. The number following each variable is the distance that the variable is averaged over (i.e., the distance bin).

	bare 400	**hli 200**	**Brood RSF 800**	**Early NB MR 400**
hli 200	-0.16	–	–	–
Brood RSF 800	-0.83	0.20	–	–
Early NB MR 400	-0.36	-0.10	0.19	–
Nest MR 30	0.05	0.18	-0.09	0.13

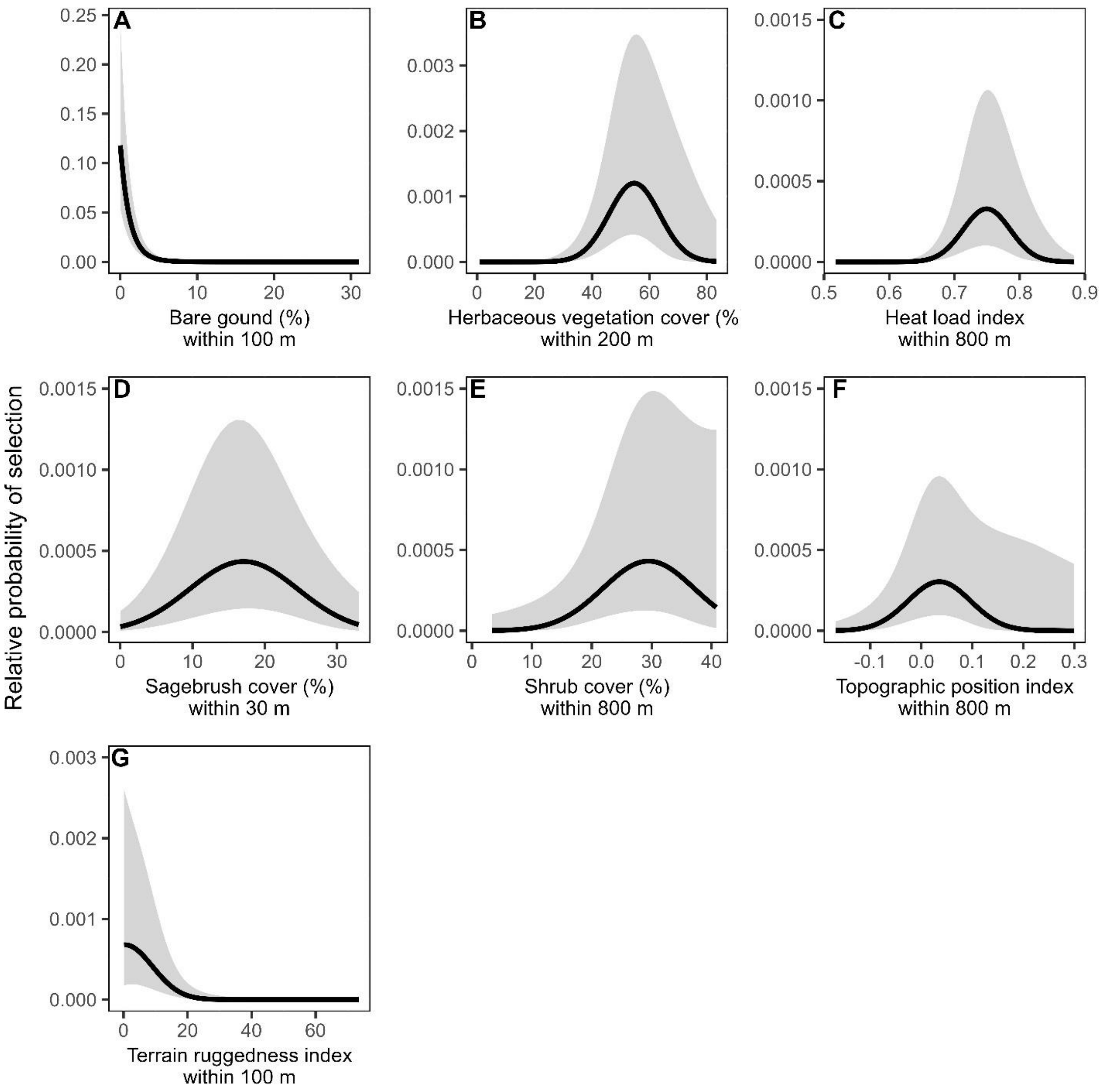

Figure B1. Partial effects plots from the top model predicting the relative probability of sharp-tailed grouse nest-site selection (± 95% CI) as predicted by mean bare ground cover (%) within 100 m (**a**), mean herbaceous vegetation cover (%) within 200 m (**b**), mean heat load index within 800 m (**c**), mean sagebrush (*Artemisia* sp.) cover (%) within 15 m (**d**), mean shrub cover (%) within 800 m (**e**), mean topographic position index within 800 m (**f**), and mean terrain ruggedness index within 100 m (**g**), Carbon County, Wyoming, USA, 2017–2019.

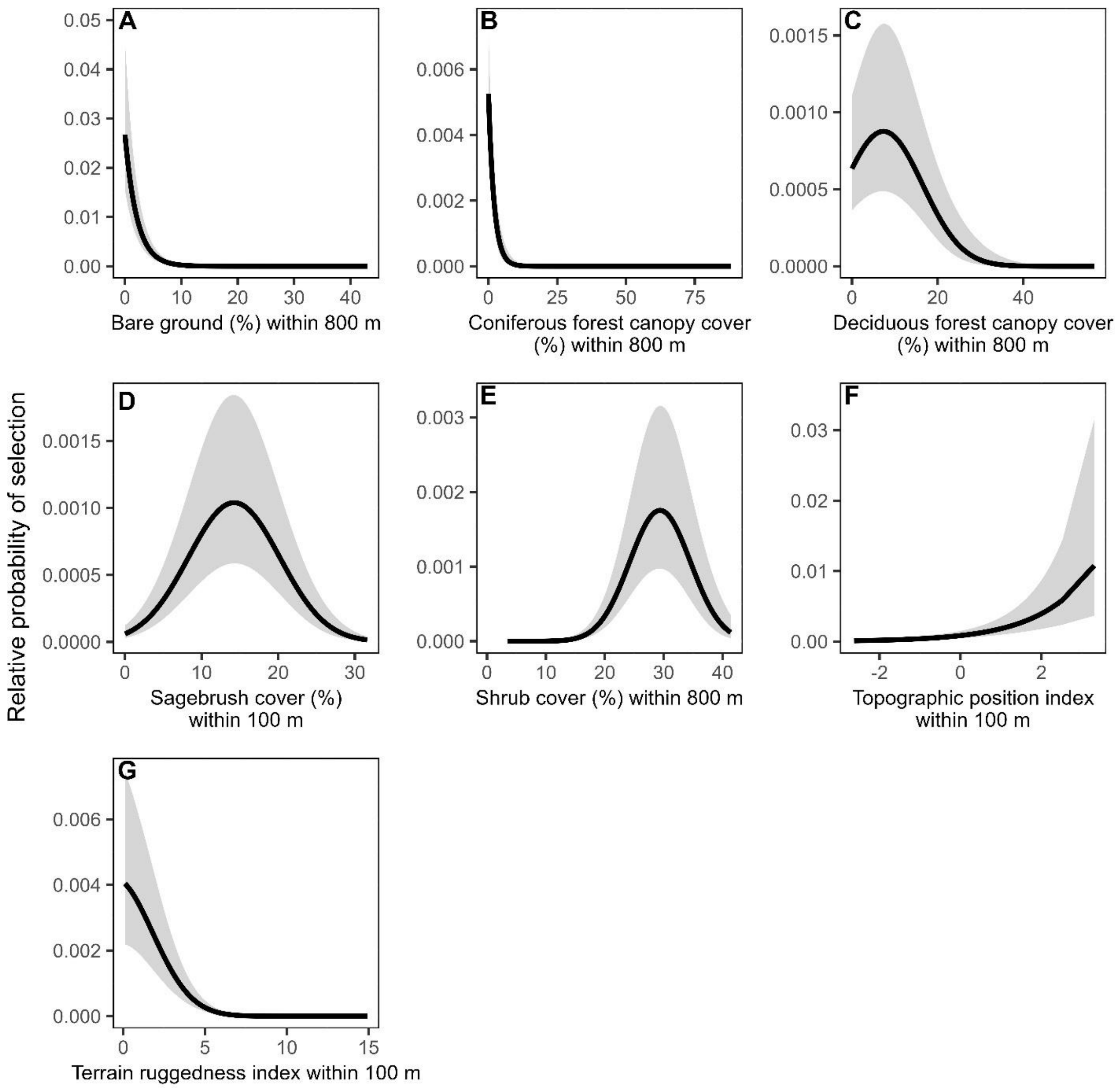

Figure B2. Partial effects plots from the top model predicting the relative probability of sharp-tailed grouse brood-site selection (± 95% CI) as predicted by mean bare ground (%) within 800 m (**a**), mean coniferous forest canopy cover (%) within 800 m (**b**), mean deciduous forest canopy cover (%) within 800 m (**c**), mean sagebrush shrub cover (%) within 100 m (**d**), mean shrub cover (%) within 800 m (**e**), mean topographic position index within 100 m (**f**), and mean terrain ruggedness index within 100 m (**g**), Carbon County, Wyoming, USA, 2017–2019.

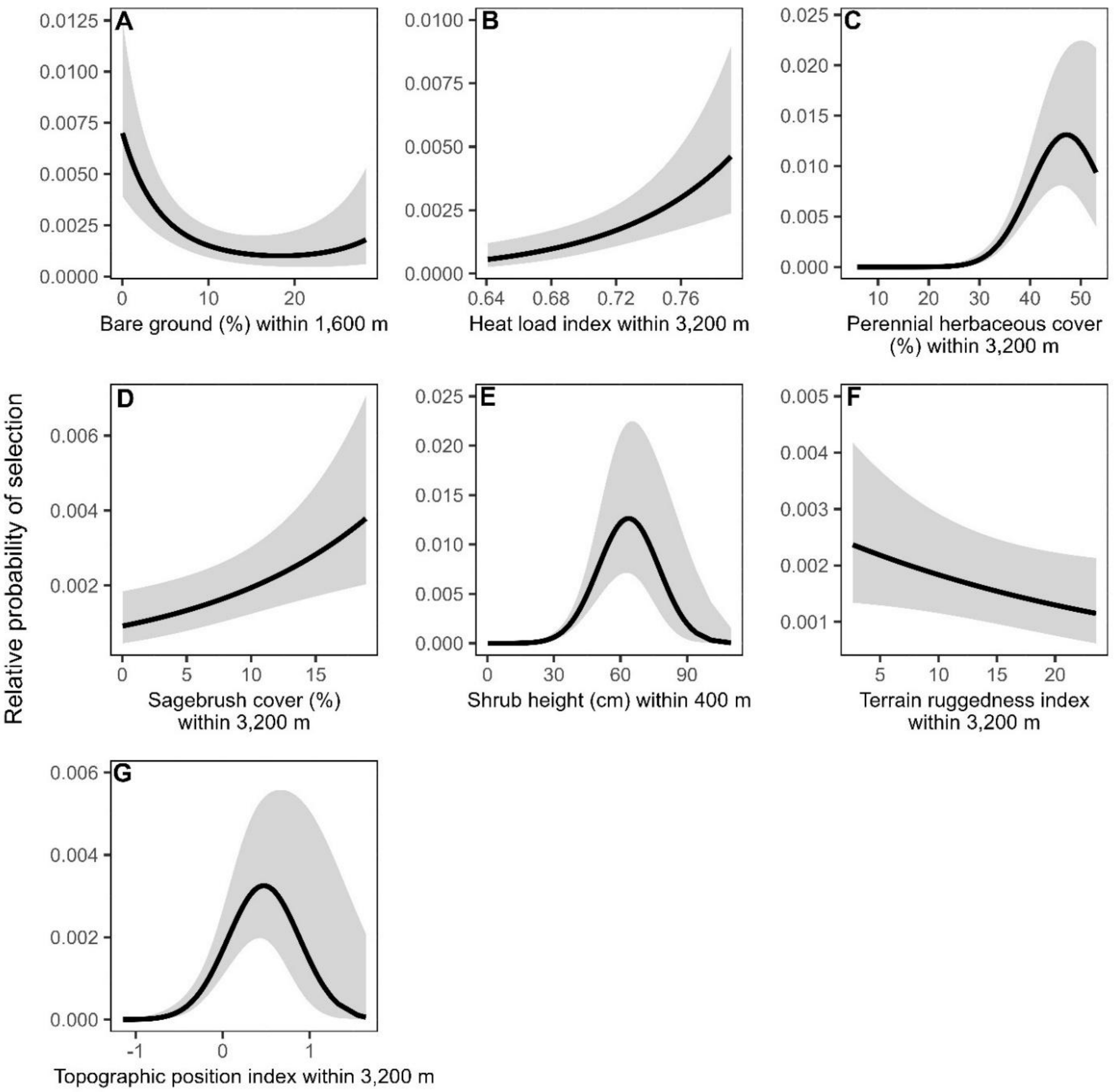

Figure B3. Partial effects plots from the top model predicting the relative probability of female sharp-tailed grouse early non-breeding season habitat selection (Sept 1–Nov 30; ± 95% CI) as predicted by mean bare ground (%) within 1,600 m (**a**), mean heat load index within 3,200 m (**b**), mean perennial herbaceous vegetation cover (%) within 3,200 m (**c**), mean sagebrush cover (%) within 3,200 m (**d**), mean shrub height (cm) within 400 m (**e**), mean terrain ruggedness index within 3,200 m (**f**), and mean topographic position index within 3,200-m (**g**), Carbon County, Wyoming, USA, 2017–2020.

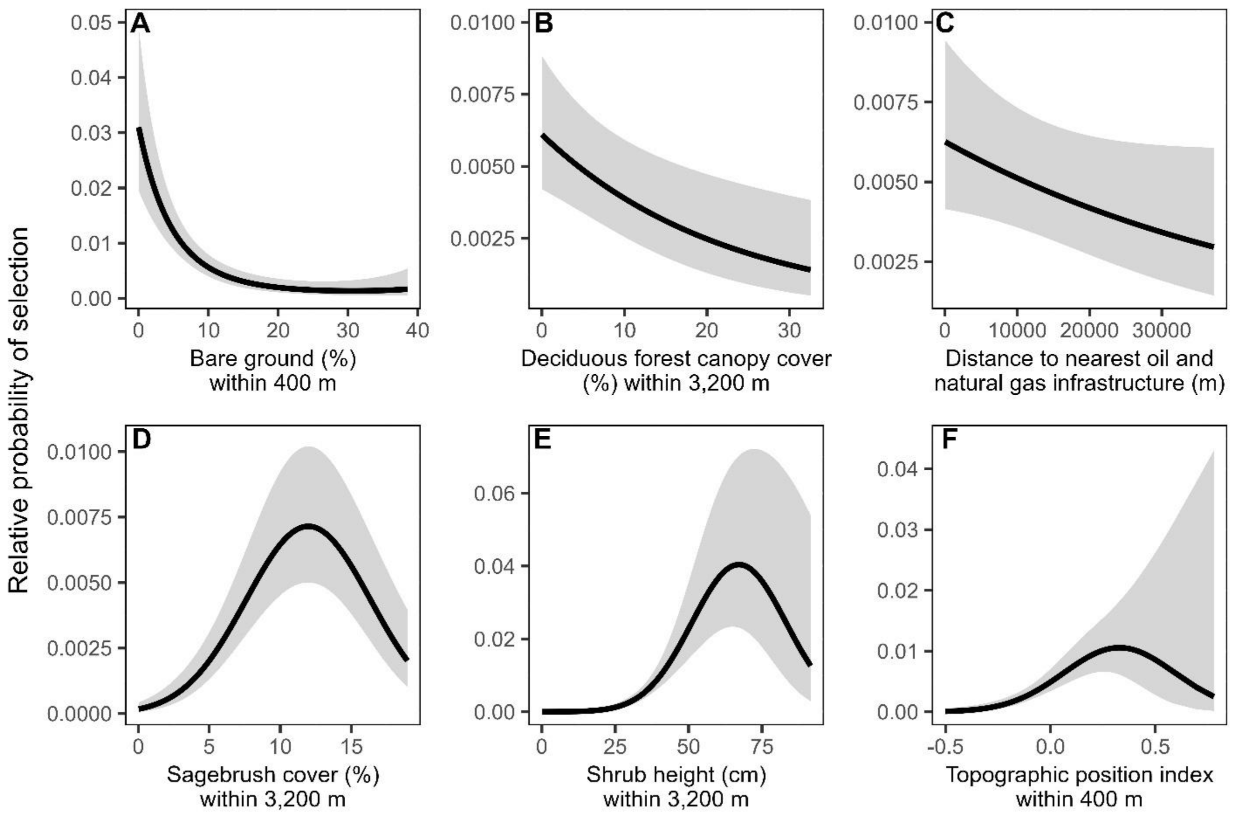

Figure B4. Partial effects plots from the top model predicting the relative probability of female sharp-tailed grouse late non-breeding season habitat selection (Dec 1–Mar 31; ± 95% CI) as predicted by mean bare ground (%) within 400 m (**a**), mean deciduous forest canopy cover (%) within 3,200 m (**b**), distance to oil and natural gas infrastructure (m; **c**), mean sagebrush cover (%) within 3,200 m (**d**), mean shrub height (cm) within 3,200 m (**e**), and mean topographic position index within 400-m (**f**), Carbon County, Wyoming, USA, 2017–2020.

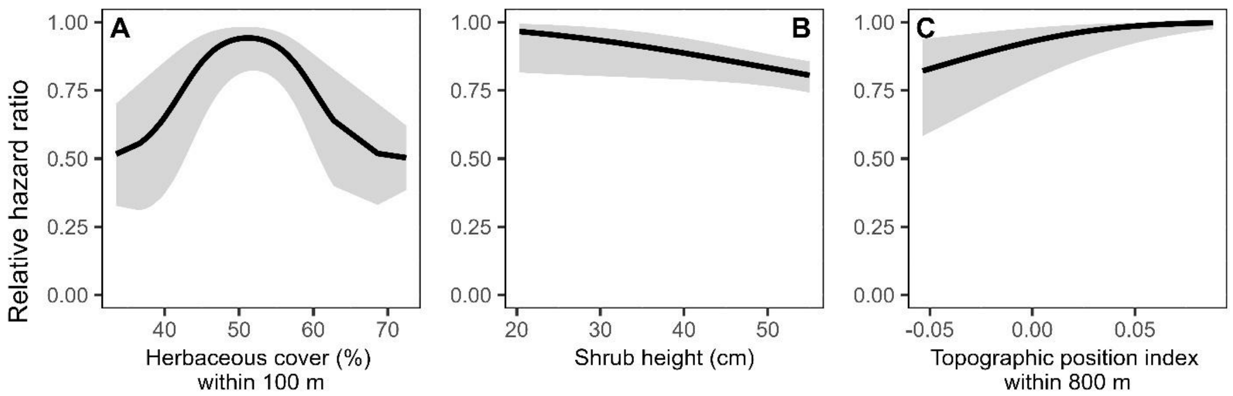

Figure B5. Partial effects plots from the top model predicting hazards to sharp-tailed grouse nest mortality risk (± 95% CI) as predicted by mean herbaceous vegetation cover within 100 m (**a**), shrub height (cm) within 15 m (**b**), and mean topographic position index within 800 m (**c**), Carbon County, Wyoming, USA, 2017–2019.

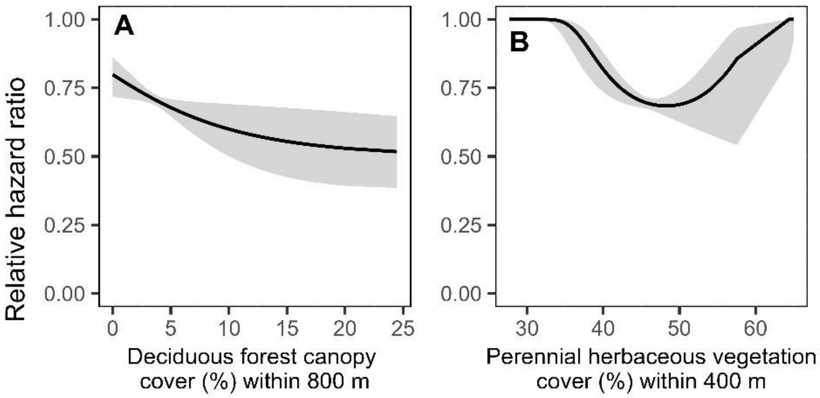

Figure B6. Partial effects plots from the top model predicting hazards to sharp-tailed grouse brood mortality risk (± 95% CI) as predicted by mean deciduous forest canopy cover (%) within 800 m (**a**) and mean perennial herbaceous vegetation cover (%) within 400 m (**b**), Carbon County, Wyoming, USA, 2017–2019.

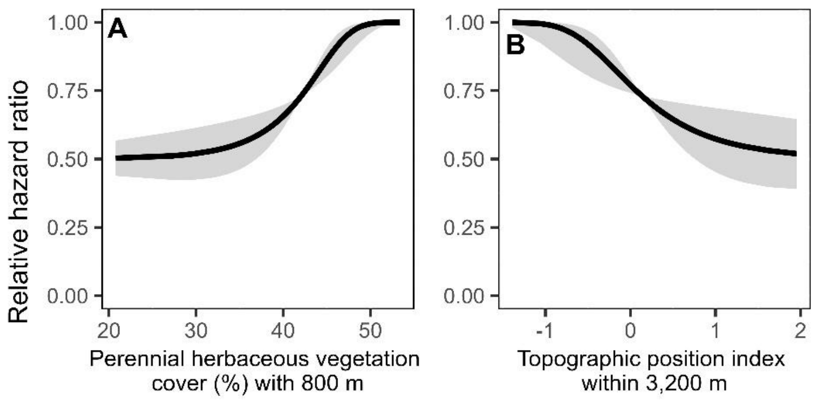

Figure B7. Partial effects plots from the top model predicting hazards to sharp-tailed grouse early non-breeding season mortality risk (Sept 1–Nov 30; ± 95% CI) as predicted by perennial herbaceous vegetation cover (%) within 800 m (**a**) and mean topographic position index within 3,200-m (**b**), Carbon County, Wyoming, USA, 2017–2020.

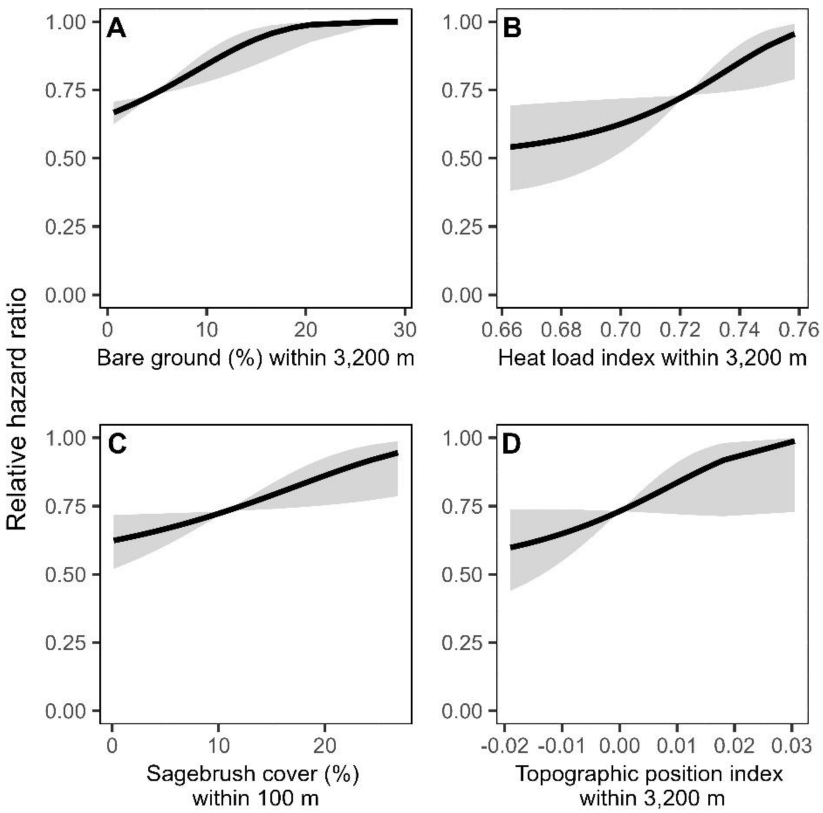

Figure B8. Partial effects plots from the top model predicting hazards to sharp-tailed grouse late non-breeding season mortality risk (Dec 1–Mar 31; ± 95% CI) as predicted by bare ground (%) within 3,200 m (**a**), mean heat load index within 3,200 m (**b**), mean sagebrush (*Artemisia* sp.) cover within 100 m (**c**), and mean topographic position index within 3,200-m (**d**), Carbon County, Wyoming, USA, 2017–2020.

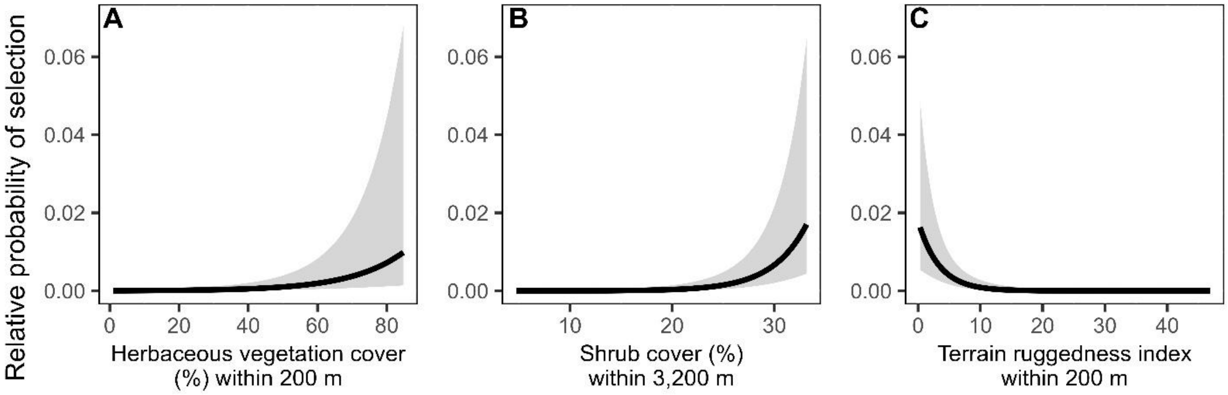

Figure B9. Partial effects plots for the top binomial logistic regression model predicting sharp-tailed grouse lek-site selection based on three landscape features: mean herbaceous vegetation cover (%) within 200 m (**a**), mean shrub cover (%) within 3,200 m (**b**), and mean terrain ruggedness index within 200 m (**c**), Carbon County Wyoming, USA, 2017–2019.

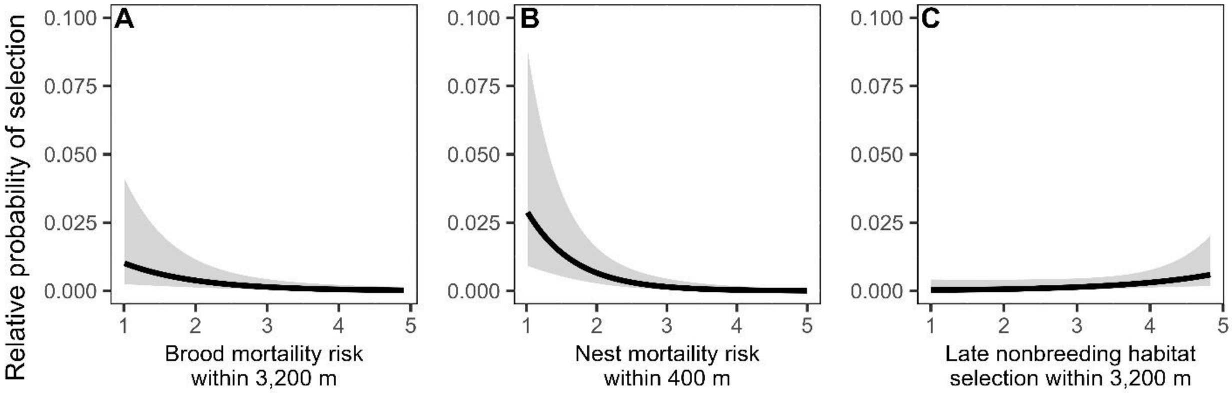

Figure B10. Partial effects plots for the top binomial logistic regression model predicting sharp-tailed grouse lek locations based on seasonal habitat selection and mortality risk models: mean brood mortality risk within 3,200 m (**a**), mean nest mortality risk within 400 m (**b**), and mean relative probability of late nonbreeding habitat selection within 3,200 m (**c**), Carbon County Wyoming, USA, 2017–2020. For brood and nest mortality risk, 1 represents low nest mortality risk and 5 represents high mortality risk. For mean relative probability of late nonbreeding season selection within 3,200 m, 1 represents low probability of selection and 5 represents high probability of selection.

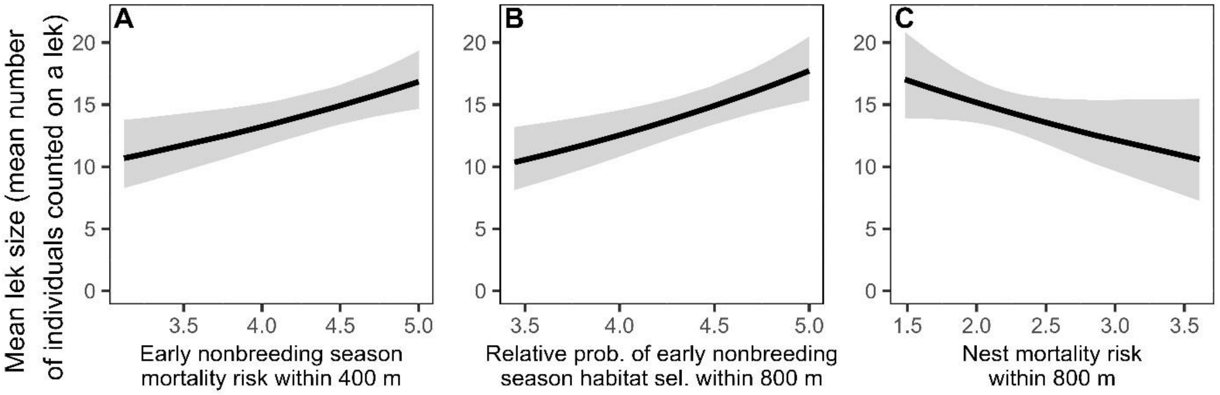

Figure B11. Partial effects plots for the top Poisson regression model predicting average (2017–2019) sharp-tailed grouse lek size (number of individuals counted on leks) based on seasonal habitat and mortality risk predictors: mean early nonbreeding season mortality risk within 400 m (**a**), mean relative probability of early nonbreeding season habitat selection within 800 m (**b**), and mean nest mortality risk within 800 m of leks (**c**), Carbon County, Wyoming, USA, 2017–2019. For early nonbreeding season mortality risk and nest mortality risk, 1 represents low mortality risk and 5 represents high mortality risk. For mean relative probability of early nonbreeding season habitat selection within 400 m, 1 represents low probability of selection and 5 represents high probability of selection.

APPENDIX C

Results for annual lek size analysis as described in Chapter 3

We modeled lek size as averaged lek size across the years of our study (2017–2019). Our top models predicting lek size in 2017 and 2018 included percent canopy cover of coniferous forest within 1,600 m and the quadratic of heat load index within 200 m and our top model predicting lek size in 2019 included percent bare ground cover within 400 m and the quadratic of heat load index within 200 m (Appendix S2: Table S1, Figure S1–S3). In 2017 and 2018, our top model indicated that lek size increased with greater cover of coniferous forest canopy cover (max within 1,600 m was 5.3% canopy cover) and lek size was larger at the highest and lowest heat load indices (Appendix S2: Table S1, Figures S1 and S2). Our top model predicting lek size in 2019 indicated that lek sizes were larger in areas with less bare ground and lek size was larger at the highest and lowest heat load indices at lek sites (Appendix S2: Table S1, Figure S3).

Our top model predicting lek size in 2017 based on seasonal female habitat indicated that lek size was smaller at leks surrounded by more brood rearing habitat within 1,600 m and lek size was larger at leks surrounded by areas with higher nest mortality risk within 30 m (Appendix S2: Table S1, Figure S4). Our top model predicting lek size in 2018 indicated lek size was larger at leks surrounded by more nesting habitat within 800 m and lek size was larger at leks surrounded by areas with lower nest mortality risk within 800 m (Appendix S2: Table S1, Figure S5). Our top model predicting lek size in 2019 indicated that lek size was larger at leks surrounded by more brood rearing habitat within 800 m, lek size was larger at leks surrounded by areas with higher early nonbreeding season mortality risk, and lek was larger at leks surrounded by areas with lower nest mortality risk within 30 m (Appendix S2: Table S1, Figure S6).

Our top model with the lowest AIC_c predicting sharp-tailed grouse lek size was the combination of landscape features and seasonal female habitat model (H3) in 2017, the landscape features model (H1) in 2018, and the combination of landscape features and seasonal female habitat (H3; Appendix S2: Table S2). The top model predicting sharp-tailed grouse lek size in 2017 (H3) indicated that lek size increased as percent canopy cover of coniferous forest increased within 3,200 m, lek size was larger at the highest and lowest heat load indices, and lek size increased as nest mortality within 30 m increased (Table 6, Figure S18); confidence intervals for both brood mortality risk within 1,600 m overlapped zero, indicating these variables were uninformative in predicting lek size in this model (Appendix S2: Table S1). Our top models for average lek size and lek size in 2018 based on landscape features (H1) indicated that lek sizes were larger at leks in areas with greater canopy cover of coniferous forest (max within 1,600 m was 5.3% canopy cover) and lek size was larger at the highest and lowest heat load indices (Appendix S2: Table S1 and Figure S2). For our model predicting sharp-tailed grouse lek size in 2019 based on a combination of landscape features and seasonal female habitat, bare ground within 400 m and brood habitat selection within 800 m were correlated, therefor we developed two models for our third hypothesis to avoid including correlated features in the same model (Appendix S2: Table S2). The top model predicting sharp-tailed grouse lek size in 2019 (H3a) indicated that lek sizes were larger in areas within less bare ground within 400 m, lek size was larger at the highest and lowest heat load indices, and lek size was larger at leks with surrounded by lower nest mortality risk (Appendix S2: Table S1 and Figure S2); confidence intervals for early nonbreeding season mortality risk within 200 overlapped zero, indicating it was uninformative in predicting lek size in this model (Appendix S2: Table S1).

Table C1. Covariates, standardized beta coefficients (β), standard errors (SE), and 95% CIs for variables included in Poisson regression models predicting the annual lek size of sharp-tailed grouse (*Tympanuchus phasianellus*) as predicted by landscape features (H1), seasonal female habitat (H2), and seasonal female habitat and landscape features (H3) in Carbon County, Wyoming, USA, 2017–2020. Earlynbmort represents early nonbreeding season mortality risk; earlynbRSF represents early nonbreeding season habitat selection; nestmort represents nest mortality risk; broodmort represents mean brood mortality risk; broodRSF represents brood habitat selection. An asterisk (*) denotes beta (β) coefficient whose 95% CI does not overlap zero.

Hypothesis	**Year**	**Covariate**	**Distance Bin**	**β**	**SE**	**95% CI**
H1–Landscape features	2017	conif	1600	1.64*	0.57	(0.48, 2.73)
		hli	200	0.49*	0.13	(0.23, 0.74)
		hli^2	200	2.07*	0.33	(1.42, 2.72)
	2018	conif	1600	2.65*	0.64	(1.35, 3.87)
		hli	200	0.62*	0.14	(0.35, 0.89)
		hli^2	200	2.57*	0.36	(1.87, 3.27)
	2019	bare	400	-1.08*	0.24	(-1.58, -0.62)
		hli	200	0.57*	0.13	(0.31, 0.83)
		hli^2	200	3.34*	0.44	(2.49, 4.20)
H2–Seasonal habitat	2017	broodmort	1600	-0.35*	0.13	(-0.62, -0.10)
		nestmort	–	0.25*	0.07	(0.10, 0.39)
	2018	nestmort	800	-0.44*	0.14	(-0.71, -0.17)
		nestRSF	800	0.63*	0.16	(0.33, 0.94)
	2019	broodRSF	800	1.04*	0.23	(0.61, 1.50)
		earlynbmort	400	0.71*	0.15	(0.42, 1.01)
		nestmort	–	-0.40*	0.10	(-0.61, -0.21)
H3–Combination	2017	conif	1600	1.65*	0.58	(0.47, 2.77)

	hli	200	0.39*	0.15	(0.08, 0.69)
	hli^2	200	2.09*	0.40	(1.31, 2.88)
	broodmort	1600	-0.03	0.16	(-0.37, 0.28)
	nestmort	30	0.25*	0.08	(0.09, 0.41)
2018	conif	1600	2.70*	0.92	(0.86, 4.49)
	hli	200	0.55*	0.17	(0.22, 0.88)
	hli^2	200	2.43*	0.42	(1.62, 3.25)
	nestRSF	800	0.11	0.18	(-0.23, 0.47)
	nestmort	800	-0.06	0.16	(-0.37, 0.24)
2019	bare	400	-1.02*	0.25	(-1.53, -0.54)
	hli	200	0.63*	0.14	(0.35, 0.90)
	hli^2	200	2.89*	0.50	(1.92, 3.88)
	earlynbmort	400	0.01	0.18	(-0.35, 0.37)
	nestmort	30	-0.35*	0.11	(-0.57, -0.14)

Table C2. Model selection results for Poisson regression models predicting sharp-tailed grouse (*Tympanuchus phasianellus*) lek size environmental covariates (H1), seasonal habitat (H2), and environmental and seasonal (H3) for average, 2017, 2018, and 2019 lek counts, Carbon County, Wyoming, USA, 2017–2020. There are two H3 models in 2019 (H3a and H3b) because bare400 and broodRSF800 were correlated ($|r| = 0.83$); because these were correlated we did not include these terms in the same model and tested all possibilities of the model. Earlynbmort represents early nonbreeding season mortality risk; earlynbRSF represents early nonbreeding season habitat selection; nestmort represents nest mortality risk; broodmort represents mean brood mortality risk; broodRSF represents brood habitat selection.

Year	**Model**	**Hypothesis**	**K**[a]	**ΔAIC$_c$**	***w_i***[b]
2017	conif1600 + hli200 + hli200^2 + broodmort1600 + nestmort	H3	6	0.00[c]	0.78
	conif1600 + hli200 + hli200^2	H1	4	2.49	0.22
	broodmort1600 + nestmort	H2	3	25.14	0.00
	Null	–	1	37.54	0.00
2018	conif1600 + hli200 + hli200^2	H1	4	0.00[c]	0.96
	conif1600 + hli200 + hli200^2 + broodmort800 + nestmort800	H3	6	6.60	0.04
	broodmort800 + nestmort800	H2	3	32.82	0.00
	Null	–	1	55.38	0.00
2019	bare400 + hli200 + hli200^2 + earlynbmort200 + nestmort	H3a	7	0.00[c]	0.88
	bare400 + hli200 + hli200^2	H1	4	3.94	0.12
	hli200 + hli200^2 + broodRSF800 + earlynbmort200 + nestmort	H3b	7	15.89	0.00
	broodRSF800 + earlynbmort200 + nestmort	H2	4	49.96	0.00
	Null	–	1	115.84	0.00

[a] Number of parameters

[b] AIC$_c$ weight

[c] 2017 lowest AIC_c value = 171.85; 2018 lowest AIC_c value = 142.90; 2019 lowest AIC_c value = 167.11

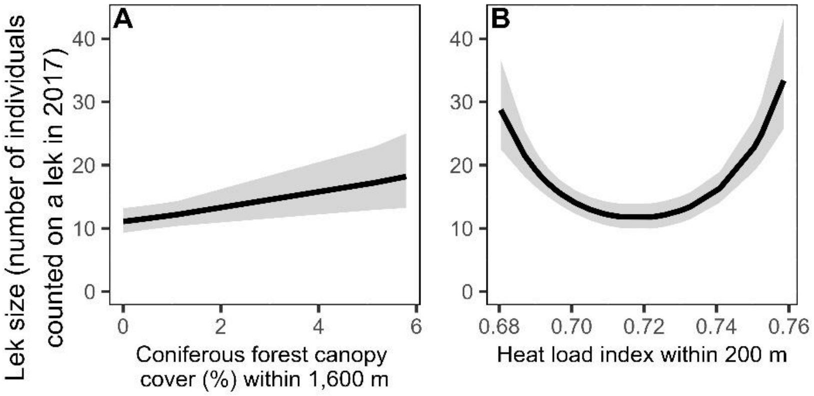

Figure C1. Partial effects plots for the top linear Poisson regression model predicting 2017 sharp-tailed grouse lek size (number of individuals counted on leks) based on landscape features: mean coniferous forest canopy cover (%) within 1,600 m (**a**) and mean heat load index within 200 m (**b**), Carbon County, Wyoming, USA, 2017.

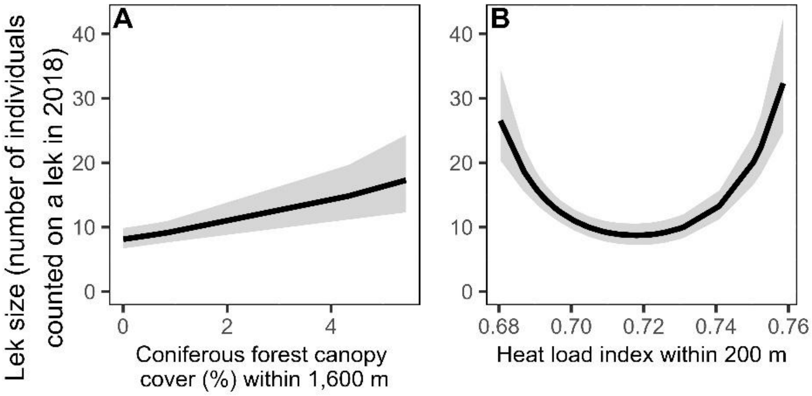

Figure C2. Partial effects plots for the top linear Poisson regression model predicting 2018 sharp-tailed grouse lek size (number of individuals counted on leks) based on landscape features: mean coniferous forest canopy cover (%) within 1,600 m (**a**) and mean heat load index within 200 m (**b**), Carbon County, Wyoming, USA, 2018.

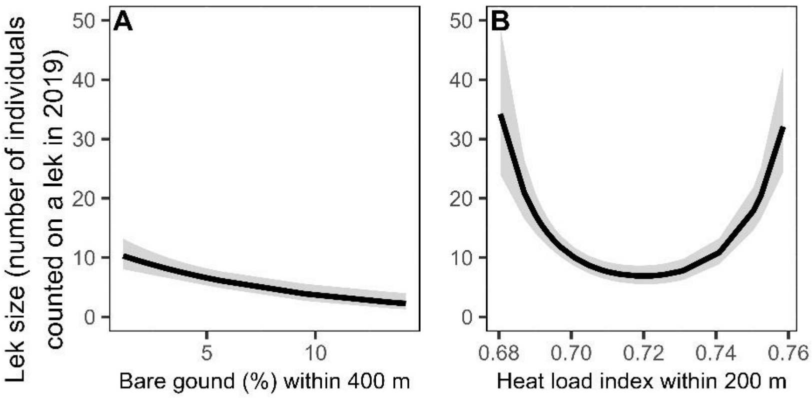

Figure C3. Partial effects plots for the top linear Poisson regression model predicting 2019 sharp-tailed grouse lek size (number of individuals counted on leks) based on landscape features: percent bare ground within 400 m (**a**) and mean heat load index within 200 m (**b**), Carbon County, Wyoming, USA, 2019.

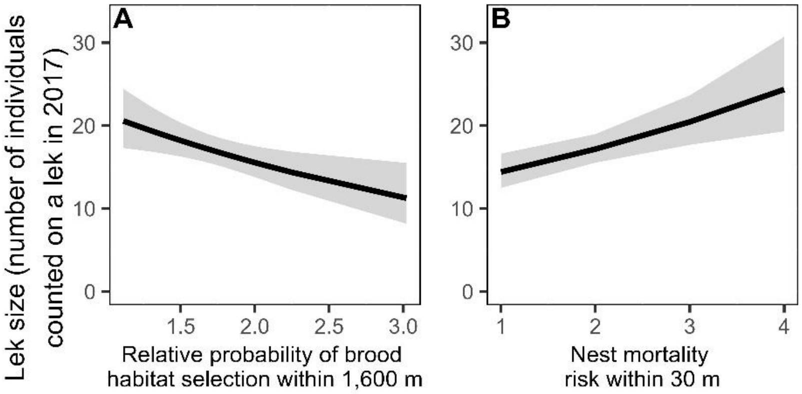

Figure C4. Partial effects plots for the top Poisson regression model predicting 2017 sharp-tailed grouse lek size (number of individuals counted on leks) based on seasonal female habitat and mortality risk predictors: mean relative probability of brood habitat selection within 1,600 m of leks (**a**) and nest mortality risk within 30 m (**b**), Carbon County, Wyoming, USA, 2017. For probability of brood habitat selection within 1,600 m, 1 represents low probability of brood habitat selection and 5 represents high probability of brood habitat selection. For nest mortality risk, 1 represents low mortality risk and 5 represents high mortality risk.

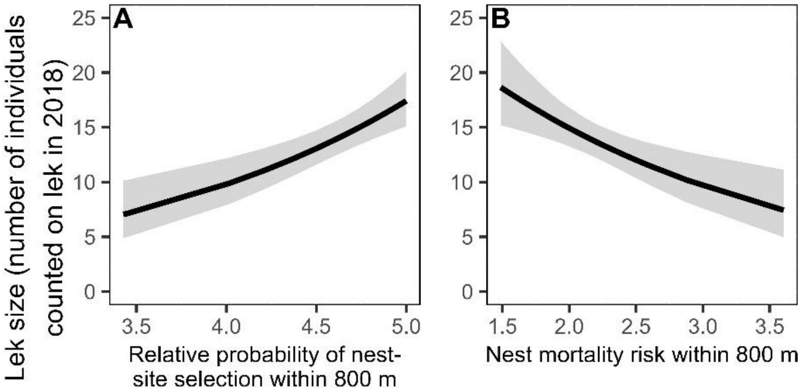

Figure C5. Partial effects plots for the top linear Poisson regression model predicting 2018 sharp-tailed grouse lek size (number of individuals counted on leks) based on seasonal female habitat and mortality risk predictors: mean relative probability of nest site selection within 800 m of leks (**a**) and mean nest mortality risk within 800 m of leks (**b**), Carbon County, Wyoming, USA, 2018. For nest site selection, 1 represents low probability of selection and 5 represents high probability of selection; for nest mortality risk within 800 m, 1 represents low nest mortality risk and 5 represents high mortality risk.

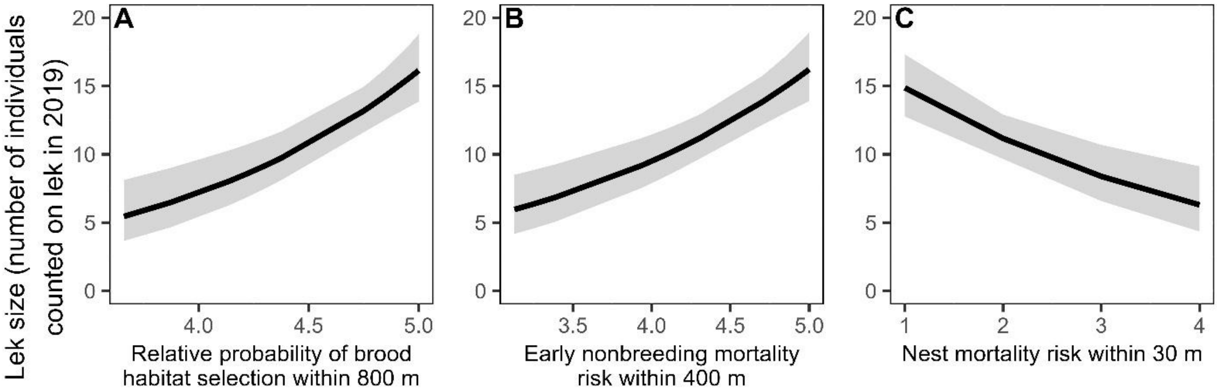

Figure C6. Partial effects plots for the top linear Poisson regression model predicting 2019 sharp-tailed grouse lek size (number of individuals counted on leks) based on seasonal female habitat and mortality risk predictors: mean relative probability of brood habitat selection within 800 m of leks (**a**), mean early nonbreeding season (Sep 1–Nov 30) mortality risk within 400 m of lek (**b**), and nest mortality risk within 30 m of leks (**c**), Carbon County, Wyoming, USA, 2019. For mean relative probability of brood habitat selection within 800 m, 1 represents low probability of selection and 5 represents high probability of selection. For early nonbreeding season and nest mortality risk, 1 represents low nest mortality risk and 5 represents high mortality risk.

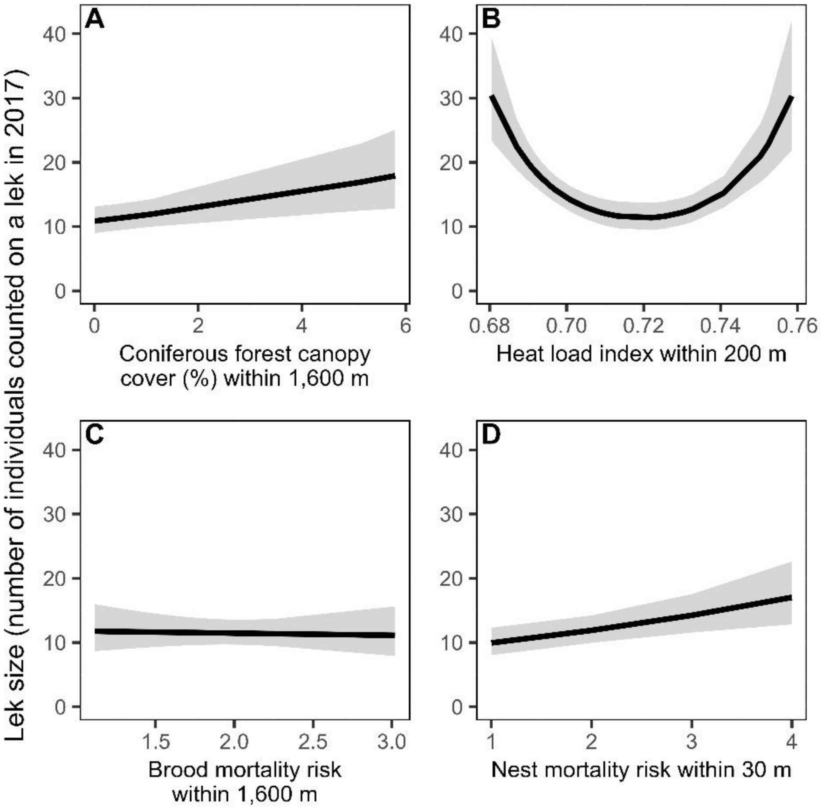

Figure C7. Partial effects plots for the top linear Poisson regression model predicting 2017 sharp-tailed grouse lek size (number of individuals counted on leks) based on landscape features and seasonal female habitat and mortality risk predictors: mean percent canopy cover of coniferous forest within 1,600 m (**a**), mean heat load index within 200 m (**b**), mean brood mortality risk within 1,600 m (**c**), and mean nest mortality risk within 30 m of lek (**d**), Carbon County, Wyoming, USA, 2019. For brood mortality risk within 1,600 m and nest mortality risk within 30 m, 1 represents low nest mortality risk and 5 represents high mortality risk.

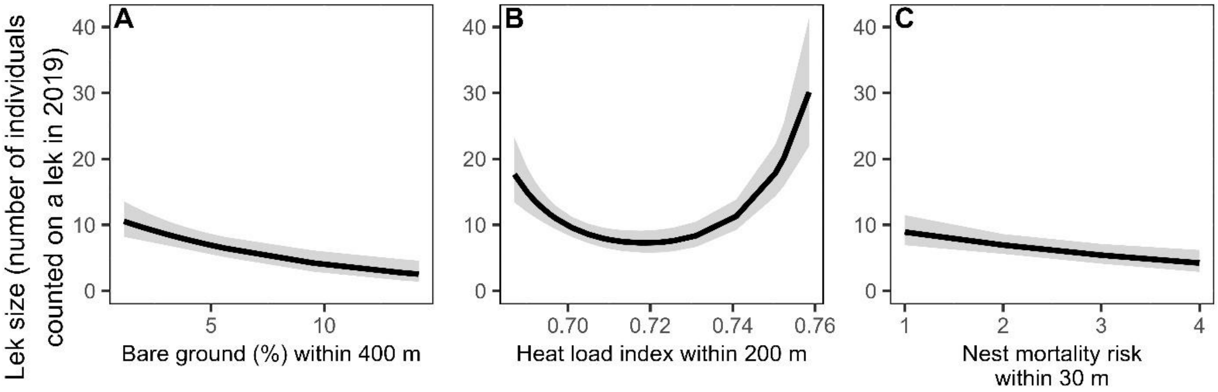

Figure C8. Partial effects plots for the top linear Poisson regression model predicting 2019 sharp-tailed grouse lek size (number of individuals counted on leks) based on environmental conditions and seasonal habitat and mortality risk predictors: percent bare ground within 400 m (**a**), mean heat load index within 200 m (**b**), and mean nest mortality risk within 30 m of lek (**c**), Carbon County, Wyoming, USA, 2019. For nest mortality risk within 30 m, 1 represents low nest mortality risk and 5 represents high mortality risk.