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REVIEW

Greater sage-grouse seasonal habitat associations: A review and considerations for interpretation and management applications

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Abstract

Habitat features needed by wildlife can change in composition throughout the year, particularly in temperate ecosystems, leading to distinct seasonal spatial-use patterns. Studies of species-habitat associations therefore often focus on understanding relationships within discrete seasonal periods with common goals of prediction (e.g., habitat mapping) and inference (e.g., interpreting model coefficients). Across the range of the greater sage-grouse (*Centrocercus urophasianus*) of western North America, the increasing use of high-frequency tracking devices has led to a surge in habitat association studies covering multiple temporal periods and spatial extents. We reviewed the literature for seasonal habitat association studies corresponding to the second and third orders of selection (Johnson 1980). Our objectives were to summarize the methodological approaches used to estimate habitat associations to

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aid understanding in cross-study comparisons and identify common habitat features reported as selected or avoided within different seasonal periods. We reviewed 71 second- and third-order studies published from 2007–2023 that evaluated covariates collected in a geographic information system (GIS) and modeled probability of selection or intensity of use. The most common study design evaluated a single level of selection (third-order) and was multi-scale (i.e., covariates were measured at varying spatial grains). The most common model approach estimated habitat associations using resource selection functions (RSFs) fit with logistic regression. Studies mostly focused on the breeding periods and winter, but all seasons throughout the annual cycle were covered. There was clear support for selection of sagebrush and avoidance of trees and rugged terrain across seasons, and strong selection of mesic conditions in summer. However, habitat associations for most covariates were mixed, with proportionally equivalent selection and avoidance reported, even within the same seasons. Different factors hampered cross-study comparisons, including variation in study design, but additional contributors likely included important context-dependent habitat associations, such as functional responses to changing habitat availability. We suggest collaborative studies leveraging multiple datasets can help improve seasonal habitat inference by removing the effects of variable study designs.

KEYWORDS

Centrocercus urophasianus, greater sage-grouse, habitat associations, habitat selection, literature review, resource selection, seasonal habitats

A critical element of wildlife conservation is the identification of habitats needed to support populations. Habitat represents sets of environmental conditions, resources, and risks (Matthiopoulos et al. 2020, Fieberg et al. 2021), and terrestrial species with iteroparous life histories often require distinct habitats during different temporal periods (Nielsen et al. 2010). Conservation planning efforts commonly consider whether environmental conditions provide habitat to support populations throughout the year (Heinrichs et al. 2017, Row et al. 2022). Understanding seasonal variations in habitat use is therefore crucial to identify all conditions needed for populations to persist. Indeed, studying seasonal habitats of wildlife populations has long been recognized as important (e.g., Wallestad and Eng 1975, Orians and Wittenberger 1991, Baines 1994), with habitat models playing a central role to help conservationists map and prioritize critical habitats (Guisan et al. 2017, Matthiopoulos et al. 2020).

Habitat associations characterize the environmental conditions in areas frequented by animals, reflecting the relationship between animal presence and their surrounding environment. Methods for estimating habitat associations have been comprehensively described, particularly in the context of habitat selection, and we refer unfamiliar readers to several recent in-depth reviews (Matthiopoulos et al. 2020, Fieberg et al. 2021, Northrup et al. 2022). Briefly, habitat associations are often evaluated in a used–available framework, where used locations represent where an animal occurs (typically collected from radio telemetry), and available locations represent a sample or census of the available habitats within some constrained area assumed to be accessible to the animal, such as an estimated home range (Manly et al. 2002; Northrup et al. 2013, 2022). Contrasting environmental characteristics among used and available locations provides a way to estimate habitat associations, which are commonly used to examine habitat associations in environmental space (Broennimann et al. 2012), or to predict where favorable environmental conditions exist in geographic space (i.e., predictive habitat mapping; Guisan et al. 2017). Habitat associations are often evaluated using resource selection functions (RSFs) estimated with logistic regression (Fieberg et al. 2021), but machine learning approaches (e.g., random forest) are becoming common (Lucas 2020, Picardi et al. 2020). When linear models like logistic regression are used, estimated slope coefficients represent the habitat associations, which are qualitatively easy to interpret (a negative slope coefficient indicates avoidance and a positive indicates selection). In contrast, machine learning approaches lack slope coefficients, and habitat associations must be inferred in other ways (e.g., by viewing partial dependence plots; Shoemaker et al. 2018). Importantly, estimation of habitat associations is amenable to a wide range of modeling approaches (Warton and Shepherd 2010), with a common goal to estimate how the relationship between a response (e.g., selection or intensity of use) changes as a function of changing habitat features.

Cross-study comparisons of habitat associations can be challenging because of methodological differences between studies (McGarigal et al. 2016, Avgar et al. 2017, Heisler et al. 2017). Johnson (1980) attempted to clarify the behavioral process of habitat selection by defining 4 nested orders of selection, which were later refined to reflect common availability sampling schemes (Meyer and Thuiller 2006). In this hierarchy, first-order selection describes selection of a regional area by a population; second-order describes selection of a home range; third order describes selection within a home range; and fourth-order describes selection within a habitat patch (Figure 1). Classifying studies to these orders helps put findings into a common currency, but

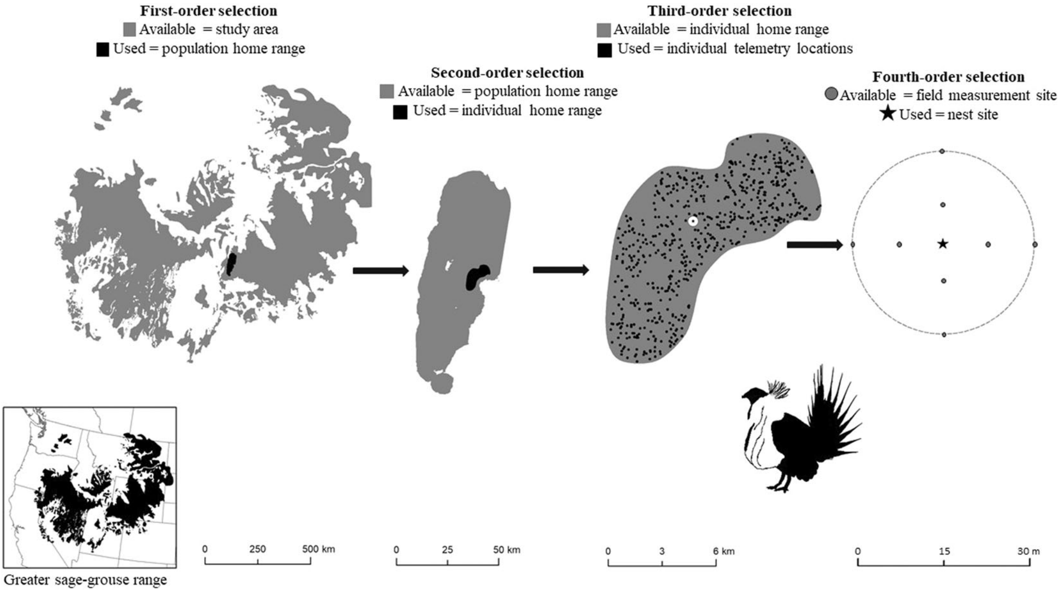

FIGURE 1 Conceptual diagram of behavioral orders of selection (following Meyer and Thuiller 2006). Greater sage-grouse (*Centrocercus urophasianus*) studies typically estimate first- through third-order selection using satellite-derived spatial data layers, whereas fourth-order selection is commonly estimated from ground-based vegetation sampling. Diagram modified with permission from N. DeCesare (Figure 1 in DeCesare et al. 2012).

comparative barriers can remain because of other differences in study design, which includes the order of selection, choice of model and covariates, grain (area surrounding a location used to measure covariates; Northrup et al. 2022), and availability extent (bounding domain defining the area available to an animal or group of animals). Different studies often use different spatial datasets to represent the same habitat feature, even though the spatial resolution, accuracy, or units may not be directly comparable (e.g., Pérez-Hoyos et al. 2017, Tarbox et al. 2022). Different habitat predictors are also frequently measured at different grains (i.e., multi-scale studies; McGarigal et al. 2016). Finally, availability can be estimated in different ways (DeCesare et al. 2012, Fieberg et al. 2021), which can have large impacts on the resulting slope coefficients that quantify habitat associations (Northrup et al. 2013). All these factors are controlled by researchers and will affect estimated habitat associations and dictate the degree to which inferences are transferable (i.e., if their results can be compared with other studies). Nevertheless, individual studies are needed to identify drivers of seasonal selection patterns and predict where seasonal habitats occur to guide management and conservation decisions (Gilchrist et al. 2005). Despite the associated challenges, efforts to synthesize findings are important because not all areas within a species' distribution are studied, and inference must commonly be applied to new areas (Connelly et al. 2004, Yates et al. 2018).

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) exhibits seasonal variation in habitat associations, has been extensively studied throughout much of its range, and provides an excellent opportunity for synthesizing existing studies to inform management guidelines. These guidelines must be extrapolated to novel areas because the species' distribution spans 11 states in the United States and 2 Canadian provinces (Schroeder et al. 2004), which makes evaluating the consistency of habitat associations from single studies crucial. Sage-grouse depend on sagebrush (*Artemisia* spp.) ecosystems (Patterson 1952), which are being lost at a high rate owing to a combination of factors, including anthropogenic land conversion (West and Young 2000), energy development (Knick et al. 2003, Walker et al. 2007), spread of invasive plants (Mack 1981, Smith et al. 2022), and drought and wildfire events (Brooks et al. 2015). Sage-grouse populations have declined by approximately 80% since the mid-1960s (Coates et al. 2021), with habitat loss being a primary driver (Braun 1995, Connelly et al. 2000).

The focus of past sage-grouse habitat studies has often fallen into 1 of 2 categories. First, studies have sought to make direct inference on habitat associations, such as quantifying selection or avoidance thresholds for targeted features of interest (e.g., oil and gas infrastructure; Aldridge and Boyce 2007, Walker 2022), or to evaluate how disturbance events like fire alter habitat associations (Brussee et al. 2022, Schuyler et al. 2022, Stevens et al. 2023). Second, studies have often been predictive in nature, creating predictive maps for land-use planning, including identifying priority seasonal habitats (Dzialak et al. 2011, Fedy et al. 2014, Walker et al. 2016), and evaluating likely spatial outcomes from different management scenarios (Ricca et al. 2018; Heinrichs et al. 2018, 2019). These goals are not mutually exclusive, and studies commonly include both objectives (Aldridge et al. 2008, Saher et al. 2022).

Sage-grouse studies frequently use the framework of Johnson (1980) to identify the order of selection evaluated (Figure 1). Fourth-order studies typically have used field-based vegetation sampling that measured conditions at resolutions finer than typical geographic information system (GIS) datasets, such as grass height and forb cover, at nest and brood sites (Holloran et al. 2005, Brussee et al. 2023). Until recently, these fine-scale studies have been most common, and 2 meta-analyses have evaluated selection of nest and brood habitats from studies using field-based vegetation sampling. Hagen et al. (2007) analyzed fine-scale habitat conditions reported at used and available nest and brood locations with a goal of understanding cover needs. Recently, Smith et al. (2020) analyzed fine-scale sagebrush, shrub, and herbaceous covers and heights at used and available nest locations, with a goal of evaluating the effectiveness of habitat guidelines for fine-scale habitat conditions (Connelly et al. 2004). Therefore, fine-scale nest and brood habitat evaluations have been described and reported, while higher-order studies (second- and third-order selection) evaluating habitat conditions at larger spatial grains during other seasonal periods, including spring, summer, and winter, have not.

Our objectives for this review were motivated by the large number of accumulating studies (Figure S1) that estimate habitat associations within discrete seasonal periods at higher orders of selection and larger spatial grains. We therefore conducted a systematic literature review that targeted GIS-based sage-grouse studies conducted at the second and third orders of selection to address 2 objectives. First, we summarized study design attributes to understand the feasibility of cross-study comparisons of seasonal habitat associations. This enabled us to better understand study design choices that can impede or aid comparisons. Second, we conducted a qualitative comparison of habitat associations within different seasonal periods to identify the most common types of covariates reported as important seasonal drivers of selection and the direction of their effects (selection or avoidance).

STUDY AREA

Greater sage-grouse occupy an area of approximately 668,412 km^2, spanning the sagebrush biome of western North America (Schroeder et al. 2004). This area encompasses diverse topography, ranging from lowlands to high mountain ranges (118 m to 4,342 m elevation), where sage-grouse favor areas with predominant sagebrush cover. Other common plant species include rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), bitterbrush (*Purshia* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), arrowleaf balsamroot (*Balsamorhiza sagittata*), and interspersed juniper (*Juniperus* spp.). Other sagebrush-associated animals include mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), pygmy rabbit (*Brachylagus idahoensis*), sage thrasher (*Oreoscoptes montanus*), and sagebrush sparrow (*Artemisiospiza nevadensis*), and common aerial and terrestrial predators include *Buteo* hawks, golden eagle (*Aquila chrysaetos*), common raven (*Corvus corax*), coyote (*Canis latrans*), American badger (*Taxidea taxus*), and bobcat (*Lynx rufus*). Major land uses are agriculture (including open rangeland livestock grazing), general human infrastructure development (roads, buildings, and powerlines), energy development (wind, solar, oil and gas extraction), and mining. The current sage-grouse range (O'Donnell et al. 2022) overlaps parts of 3 Level II ecoregions: the North American Desert, Northwestern Forested Mountains, and Great Plains (Omernik and Griffith 2014). Portions of the North American Desert ecoregion in the southwest are dominated by low-growing shrubs and grasses and are characterized by a dry, mid-latitude desert to steppe climate, with a mean annual precipitation ranging from 277 mm to 316 mm and mean annual temperature ranging from 0°C to 14°C. In the middle portion of the range, the Northwestern Forested Mountains ecoregion ranges from high alpine environments to valleys and lowlands, with sage-grouse restricted to dry lowland sagebrush environments mostly characterized by a severe, mid-latitude climate, with warm-dry summers and cold winters. Mean annual temperature ranges from -5°C to 10°C and mean annual precipitation ranges from 150 mm to 621 mm. In the northeastern portion of the range, the Great Plains ecoregion is characterized by a dry, mid-latitude steppe climate, with hot summers and cold winters, and a mean annual temperature ranging from 2.5°C to 8°C and mean annual precipitation ranging from 250 mm to 550 mm (Wiken et al. 2011).

METHODS

Literature review

We used Google Scholar to search published papers, theses, dissertations, and book chapters for greater sage-grouse habitat association studies that targeted second- or third-order inference and modeled probabilities of selection or intensity of use as a function of GIS-based covariates. We initially evaluated several Boolean search strings for their ability to capture a smaller set of known studies meeting our above study criteria, and we chose the following string because it returned the most relevant results: ("sage grouse" AND "centrocercus") AND ("habitat selection" OR "resource selection function" OR "step selection function") AND ("regression" OR "glm" OR "glmm"

OR “random forest” OR “maxent” OR “poisson”) AND (“used” AND “available”). We did not place any constraints on the period studies were published, and we searched the above string in Google Scholar 2 times (conducted by GTW), first on 31 August 2021 and second on 10 April 2023, to update our results with new studies published after our first search. We reviewed the search results in 2 phases to determine relevancy to our review objectives (reviews conducted by GTW and ALW). In the first phase, we reviewed each returned title and abstract for relevancy and removed publications that were not related to sage-grouse or were related but did not evaluate habitat associations. In the second phase, we fully reviewed the remaining studies to classify the order of selection evaluated and the response variable modeled, keeping only those that included GIS-based covariates that targeted second- or third-order inference on habitat associations and modeled probabilities of selection or intensity of use.

Study attributes

For model and design information, we extracted data on the type of statistical model used, how availability was defined, and order of selection (Johnson 1980, Meyer and Thuiller 2006). We classified studies as third order if availability was sampled from within a home range (either an individual or population home range). We classified studies as second order if an area larger than a typical home range was used to define availability (i.e., home ranges nested within a regional boundary or study area extent). Because not all studies clearly aligned with the definitions of Johnson (1980), we additionally classified strategies for defining availability to the following categories: seasonal population home range – locations were subset to the seasonal period of interest and pooled across individuals (and usually across years) to define the population availability extent; seasonal individual home range – locations were subset to the seasonal period of interest and pooled within individuals (and often across years) to create the individual-level availability extent; conditional per use – availability was conditionally sampled per every used location (or sets of used locations); annual population home range – the availability extent was considered to be the entire study area; seasonal migration path – used locations were pooled across individuals during seasonal migration periods; and unknown – it was unclear how availability was defined or we were unable to categorize it to one of the other types above. We additionally tracked the objectives of each study to 1 of 4 non-mutually exclusive categories: predictive mapping, general habitat evaluations, disturbance evaluations (e.g., energy infrastructure, powerlines, wind energy, wildfire), and habitat treatment assessments (e.g., conifer removal or sagebrush restoration).

For studies fitting models that estimated slope coefficients (i.e., generalized linear models), we categorized covariates into 7 broad groups for a basic summarization, and within each group, we identified several distinct covariate types (Table 1). We recorded the slope coefficient and spatial grain at which the covariate was measured. The spatial grain was often presented as the area surrounding a location, or as a radius corresponding to a circular buffered area around a location. We therefore additionally calculated the corresponding area or radius (assuming a circular area) for each covariate depending on which piece of information was provided. We could not directly compare effect sizes of slope coefficients, or conduct a formal meta-analysis on slope coefficients, because covariates were often measured at different grains, because studies did not typically report if coefficients were on a standardized scale (e.g., if coefficients were estimated in models fit to z-transformed covariates), and because studies infrequently reported coefficients for covariates that did not occur in top-ranked models. Further, differences in availability sampling among studies confound interpretation of effect sizes (i.e., coefficient estimates were likely to be larger or smaller if the availability extents differed). Therefore, we qualitatively categorized covariates as either negative or positive based on the coefficient sign and summarized them by covariate type (described below). We did not compare habitat associations from machine learning approaches because they lacked slope coefficients, and interpreting habitat effects as negative or positive was usually intractable based on the information presented.

We identified 8 types of seasonal categories: breeding (including lekking and nesting); nesting; brood rearing (including early and late brood rearing); migration; summer; fall; winter; and annual (i.e., locations were pooled across

TABLE 1 Types of covariates that were reported in top models in a literature review of greater sage-grouse (*Centrocercus urophasianus*) seasonal habitat association studies at the second or third orders of selection (2007–2023). The mean and standard deviation of the radius associated with a circular grain area (in meters) is provided for each covariate type or across all covariate types within a group. Covariate types with an asterisk (*) represent topographic conditions used to capture areas with higher soil moisture and hence mesic areas.

Covariate type	Covariate types	Grain radius ($\bar{x}$)	Grain radius (SD)
Vegetation	Bare ground	702	789
	Conifer or pinyon-juniper	486	417
	Grassland	259	228
	Herbaceous	1,035	1,109
	Litter	230	272
	Normalized difference vegetation index (NDVI)	681	655
	Riparian	935	565
	Sagebrush	735	769
	Shrub	775	668
	Shrub height	1,217	1,307
	Trees	802	742
Topography	Aspect	266	415
	Compound topographic index (CTI)*	343	538
	Elevation	103	186
	Heat load index (HLI)	1,612	1,292
	Ruggedness	340	476
	Slope	238	343
	Topographic position index (TPI)	1,208	809
Anthropogenic	Agriculture	1,114	828
	Energy	1,323	1,602
	Human development	938	1,085
	Roads	1,048	1,021
Mesic	Intermittent stream Mesic type classified cover type Springs and seeps Topographic wetness index (TWI)* Wet meadow	958	532
Water	Perennial stream Stream Water body Wetland	1,320	2,315
Invasion	Primarily cheatgrass	1,036	679
Other	Distance to lek or nest Distance to predator kill site Other cover type Viewshed	607	830

seasons). To increase sample sizes for slope coefficient comparisons, we reclassified the 8 reported categories into 4 seasonal categories that were more general: spring – combined breeding (which sometimes included early brood rearing) and nesting categories; summer – combined brood rearing (early and late) and summer categories; winter – combined fall and winter categories; and all seasons – all 8 categories combined.

To assess the direction of selection for different covariate types from linear models, we included coefficients from the main effects (i.e., excluding quadratic and interactive coefficient terms) of covariates that summarized pixel values using mean, proportion, sum, or direct intersect values (where the raster's grain matched its pixel resolution). We classified each slope coefficient as either positive or negative based on its sign. For proximity (distance) covariates, we retained the original coefficient sign if the distance was transformed with a decay function (Aldridge et al. 2012). For Euclidean distance covariates, we flipped the coefficient sign so that interpretation would be consistent across distance measures. Thus, after inverting Euclidean distance coefficients, all positive distance coefficients indicated selection for closer proximity to the feature of interest, while all negative distance coefficients indicated selection for farther proximity from the feature.

To test if the directions of covariate relationships were more frequently negative or positive (i.e., avoided or selected), we used a proportion test implemented with the prop.test function in R (R Core Team 2024). We had an *a priori* hypothesis for each covariate type in terms of the direction of the effect. For example, we expected habitat features, like sagebrush and herbaceous cover, would be selected, and disturbance features, like proximity to anthropogenic features, would be avoided. We therefore used a one-sided test with an alpha value of 0.05 to test if the proportion of positive coefficients was less or greater than 0.5 (depending on the hypothesized relationship), or no different (the null hypothesis). For covariate types with >30 coefficient samples available for comparisons (large sample group), we conducted proportion tests both across pooled seasons (i.e., all seasonal periods combined) and separately for spring, summer, and winter periods. For covariate types with 8–30 coefficient samples (small sample group), we only made comparisons across pooled seasons.

Our inference on coefficient signs was limited to covariates reported in models used for biological inference. Some studies used only a single model for inference (e.g., models fit with regularization or Bayesian approaches), but most used a model selection criteria, such as Akaike's Information Criterion (AIC), to choose a single model among a candidate set for inference. Studies that used model selection sometimes model averaged coefficients across candidate model sets to obtain a single set of coefficients for inference (Burnham and Anderson 2002). Studies that used model selection usually did not report coefficients for all candidate models (only top-ranked models), which prevented us from collecting information on all the covariates tested. Some covariates may have also been included or excluded as candidate predictors based on knowledge of conditions and spatial dataset accuracy within a study area. Therefore, our evaluation did not control for the prevalence of different types of covariates tested across studies, limiting us to focus on the direction of covariate relationships from the models used for inference (i.e., coefficients reported from single models, top-ranked models, or model averaging). We view this as a reasonable approach because covariates appearing in top models are commonly the ones used to guide management decision making. However, we acknowledge our approach likely places emphasis on the covariates that were most strongly selected or avoided because weak or neutral effects are less likely to appear in top-ranked models. We are therefore unable to make statistical statements about support for covariates based on the frequency of hypothesis tests conducted on each covariate type and their associated significance.

RESULTS

Our literature search returned 1,093 studies, of which 71 met our review criteria (Table 2). During our first phase of review, we reduced the number of studies to 104 after checking for relevancy. In the second phase, we fully reviewed the remaining 104 studies to determine the order of selection that was evaluated, keeping only those targeting second- and third-order inference on habitat associations, which reduced the number of studies to 71 (57 peer-reviewed articles, 11 theses, 2 dissertations, and 1 book chapter). Twelve studies collected data across multiple sites. Most studies evaluated populations of sage-grouse at a single site or within a single geographic region (e.g., the Bi-State area in Nevada and California), but habitat associations were also evaluated at statewide extents in Colorado, Wyoming, Nevada, California, Utah, and Washington. Studies occurred throughout most of the sage-grouse occupied range (Figure 2), including every occupied state, with the fewest studies in North and South Dakota ($n = 1$ each), and the most in Wyoming ($n = 25$). Most studies were multi-year (median study

TABLE 2 Summary information for 71 studies used in a review of greater sage-grouse (*Centrocercus urophasianus*) seasonal habitat associations at the second or third orders of selection from 2007–2023. Information includes state or province location of study in the United States or Canada, sex of marked individuals, marker type used to track individuals (very high frequency [VHF] or global positioning system [GPS]), seasons or life cycles modeled, statistical model type, definition of availability, order of selection, and main objective(s) of the study. An asterisk (*) indicates the study was from a thesis or dissertation, and a double asterisk (**) indicates we changed the order from what was reported to remain consistent with our order criteria.

Citation	Location	Sex[a]	Marker	Seasons[b]	Model[c]	Availability[d]	Order[e]	Objective[f]
Aldridge and Boyce (2007)	AB	F, U	VHF	N, R	GLM	SPHR	3	H, M
Atamian et al. (2010)	NV	F	VHF	R	Other	APHR	2	H, M
Balderson (2017)*	AB	F	GPS	S	GAM	SPHR	3	H, M, D
Baxter et al. (2017)	UT	F	VHF	R	GLMM	SPHR	3**	H, M, T
Beers and Frey (2022)	NV, UT	F, M	GPS	A, B, S, W	RF	SIHR	3	H, M
Boswell (2017)*	UT	F, M	GPS	N, R, W	GLMM	SIHR	3	H, M
Brussee et al. (2022)	CA, NV	F	VHF	R	LASSO	SPHR	2	H, M, D
Burnett (2013)*	UT	F, M	VHF	N, R, S, W	Maxent	APHR	2	H, M
Carlisle et al. (2024)	WY	F	VHF, GPS	N	RF	SPHR	3	H, M
Carpenter et al. (2010)	AB	F	VHF	W	GLM	SPHR	3	H, M, D
Casazza et al. (2011)	CA, NV	F	VHF	R	GLMM	SPHR	3	H
Coates et al. (2016*a*)	CA, NV	U	VHF, GPS	B, F, W	GLMM	SPHR	3	H, M
Coates et al. (2020)	CA, NV	U	VHF, GPS	B, S, W	GLMM	APHR	2	H, M
Doherty et al. (2008)	WY	F	VHF	W	GLM	SPHR	2	H, M, D
Doherty et al. (2010)	WY	F	VHF	N	GLM	SPHR	3	H, M, D
Dungannon (2022)*	OR, CA, NV	F	GPS	R	GLMM	SIHR	3	H
Dzialak et al. (2011)	WY	F	GPS	N, R	CLR	CPU	3	H, M
Dzialak et al. (2012)	WY	F, M	GPS	W	CLR	CPU	2, 3	H, M
Dzialak et al. (2013*a*)	WY	F	GPS	N	CLR	CPU	3	H, M, D
Dzialak et al. (2013*b*)	WY	U	GPS	W	GLM	SPHR	2	H, M, D
Dzialak et al. (2015)	WY	F	GPS	R	CLR	CPU	3	H, M, D
Fedy et al. (2014)	WY	U	VHF, GPS	N, S, W	GLM	SPHR	2	H, M
Fedy et al. (2015)	WY	F	VHF	N	GLM	SPHR	3	H, M, D
Flack (2017)*	UT	F	VHF, GPS	B, R/S, W, F	GLMM	SIHR	3	H
Foster (2016)*	OR	F	GPS	B, S, W	GLMM	SIHR	3	H, D
Freese et al. (2016)	OR	F, M	VHF	B, S	Maxent	SPHR	2	H, M
Gelling (2022)*	MT, WY	F	VHF, GPS	B, S, W	GLMM	SPHR, SIHR	3	H, M, D
Gibson et al. (2018)	NV	F	VHF	N, R	GLMM	SPHR	2	H, D
Hagen et al. (2011)	OR	F	VHF	W	GLM	SPHR	3	H
Hansen et al. (2016)	UT	F, M	GPS	W	GLMM	SPHR	3	H, M, D
Harju et al. (2013)	WY	F, M	GPS	M	CLR	CPU	3	H, M

(Continues)

TABLE 2 (Continued)

Citation	Location	Sex[a]	Marker	Seasons[b]	Model[c]	Availability[d]	Order[e]	Objective[f]
Hennig et al. (2023)	CO, WY	F	GPS	B, S, W	GLMM	APHR	2	H, M
Kirol et al. (2015)	WY	F	VHF	N, R, S	GLM	SPHR	3	H, M, D
Kohl et al. (2019)	UT, ID, WY	F	VHF	N, R	GLMM	SPHR	3	H, D
Lazenby et al. (2021)	ND	F	VHF, GPS	N, R, S	LASSO	SPHR	3**	H, M
LeBeau et al. (2017)	WY	F	VHF	N, R, S	CLR	SPHR	3	H, M, D
LeBeau et al. (2019)	WY	F	VHF	N, R, S	CLR	SPHR	3	H, M, D
Newton et al. (2017)	MT	F, M	VHF	M	CLR	SMP	3	H
O'Neil et al. (2020)	CA, NV	F	VHF, GPS	N	LASSO	SPHR	3	H, M
Olsen et al. (2021)	OR	F	VHF, GPS	N, B	GLMM	SPHR	3	H, M, T
Orning (2014)*	WY	F	VHF, GPS	B, R, M	GLMM	SIHR	3	H
Parsons et al. (2022)	SD	F, M	VHF	N, S, W	GLMM	SIHR	3	H
Parsons (2019)*	SD	F	VHF	R	CLR	CPU	3	H, M
Picardi et al. (2020)	UT	F	VHF	B, S, W	RF	Unknown	2	H, M
Poessel et al. (2022)	ID, OR	M	GPS	B, S, F, W	GLMM	SIHR	3	H, D
Pratt and Beck (2019)	WY	F	VHF, GPS	N, R, B, W	GEE	SPHR	2	H, M, D
Pratt (2017)*	MT, WY	F	GPS	B, S, W	GEE	SPHR	3	H, M
Rabon et al. (2021)	ID	F	VHF, GPS	R	GLMM	SPHR	3	H
Ricca et al. (2018)	CA, NV	F, M	VHF, GPS	A	GLMM	APHR	2	H, M, T
Rice et al. (2013)	CO	M, F, U	VHF	B, S, W	GLMM	Unknown	2	H, M
Rice et al. (2016)	CO	F	VHF	B, S, W	GLMM	APHR	2	H, M, D
Roth et al. (2022)	NV	F	VHF	N	GLMM	SPHR	3	H, M
Row et al. (2022)	WY	F	VHF	N, R, W	GLMM, BRT	SPHR	3	H, M
Sandford et al. (2017)	UT	F	VHF	R	GLMM	SPHR	3	H
Schuyler et al. (2022)	NV, OR	F	GPS	B, S, W	GLMM	SPHR	3	H, M, D
Severson et al. (2017*b*)	CA, OR, NV	F	VHF	N	GAM	SPHR	3	H, T
Severson et al. (2022)	CA	F	VHF	R	GAMM	SPHR	3	H, M
Shirk et al. (2017)	WA	F, M	VHF	B, N, R, W	Maxent	Unknown	3	H
Smith et al. (2014)	CO, WY	F	VHF	W	GLM	SPHR	3	H, M, D
Smith et al. (2016)	WY	F	GPS	W	GEE	SPHR	3	H, M
Smith et al. (2019)	WY	F, M	Unmarked	W	GLM	SPHR	2	H, M
Smith et al. (2021)	ID	F, M	VHF, GPS, unmarked	B, R, W	Maxent	SPHR	2	H, M
Stevens et al. (2023)	ID	F	GPS	N, R	LASSO	SPHR	2, 3	H, M, D
Stonehouse et al. (2015)	WA	F, M	VHF	B-S	Other	SPHR	3	H
Walker (2022)	CO	F	VHF	B, S-F, W	CLR	SIHR	3	H, D
Walker et al. (2016)	CO	F, M	VHF	B, S-F, W	GEE	APHR	2	H, M

TABLE 2 (Continued)

Citation	Location	Sex[a]	Marker	Seasons[b]	Model[c]	Availability[d]	Order[e]	Objective[f]
Wanner (2022)*	WY	F	GPS	W	GLMM	SPHR	3	H
Wayment (2022)*	UT	F	VHF, GPS	R	CLR	SIHR	3	H
Westover et al. (2016)	UT	F	VHF	R	GLMM	SPHR	3**	H, M
Wood (2019)*	UT	F, M	GPS	W	GLMM	SIHR	3	H, M
Yost et al. (2008)	OR	F	VHF	N	Maxent	SPHR	2	H, M

[a] Sex classifications: female (F), male (M), unknown (U).

[b] Seasons or life cycles: nest (N), brood (R), breeding (B), migration (M), summer (S), fall (F), winter (W), annual (A).

[c] Model type: boosted regression trees (BRT), conditional logistic regression (CLR), generalized additive model (GAM), generalized additive mixed model (GAMM), general estimating equations (GEE), generalized linear model (GLM), generalized linear mixed model (GLMM), lasso binomial regression (LASSO), random forest (RF), other (not readily categorized).

[d] Availability: annual population home range (APHR), conditional per use (CPU), seasonal population home range (SPHR), seasonal individual home range (SIHR), seasonal migration path (SMP), unknown.

[e] Order of selection: second (2), third (3).

[f] Objective: general habitat evaluations (H), predictive mapping (M), assessing disturbance (D), assessing habitat treatments (T).

duration = 4 years, range = 1–22 years), and data were collected from 1989–2022. All studies evaluated habitat associations, 73% of studies conducted predictive mapping (*n* = 52), 34% of studies evaluated responses to disturbance (*n* = 24), and 6% of studies evaluated habitat treatment effects (*n* = 4).

Model types

All studies fit models in a used–available framework, and most models were used to estimate an RSF, where the exponential forms of the coefficients were used for understanding covariate relationships or mapping. Logistic regression was the most common statistical model used to estimate coefficients in RSFs, with generalized linear models and generalized linear mixed models accounting for 56% of models (*n* = 40). Random effects were commonly fit as random intercepts to individual birds in mixed models, while random slopes were rarely fit (3 out of 29 studies using mixed models). Conditional logistic regression was the next most frequent model used (15%, *n* = 11), and generalized estimating equations, generalized additive models, Maxent, random forest, and least absolute shrinkage and selection operator (LASSO) were used at lesser frequencies and collectively represented 24% (*n* = 17) of model types (Figure 3A).

Availability and seasons

Availability was most commonly defined using a seasonal population home range (64% of studies), followed by seasonal individual home range (17% of studies), conditional per use (8% of studies), annual population home range (6% of studies), unknown methods (4% of studies), and seasonal migration path (1% of studies). Availability boundaries were delineated using kernel density estimators (30% of studies), minimum convex polygons (28% of studies), dissolved fixed-radius buffers around points (or transect lines in one instance; 24% of studies), study area boundaries (13% of studies), unreported delineation methods (4% of studies), and availability matched to used locations within a constrained distance (1% of studies).

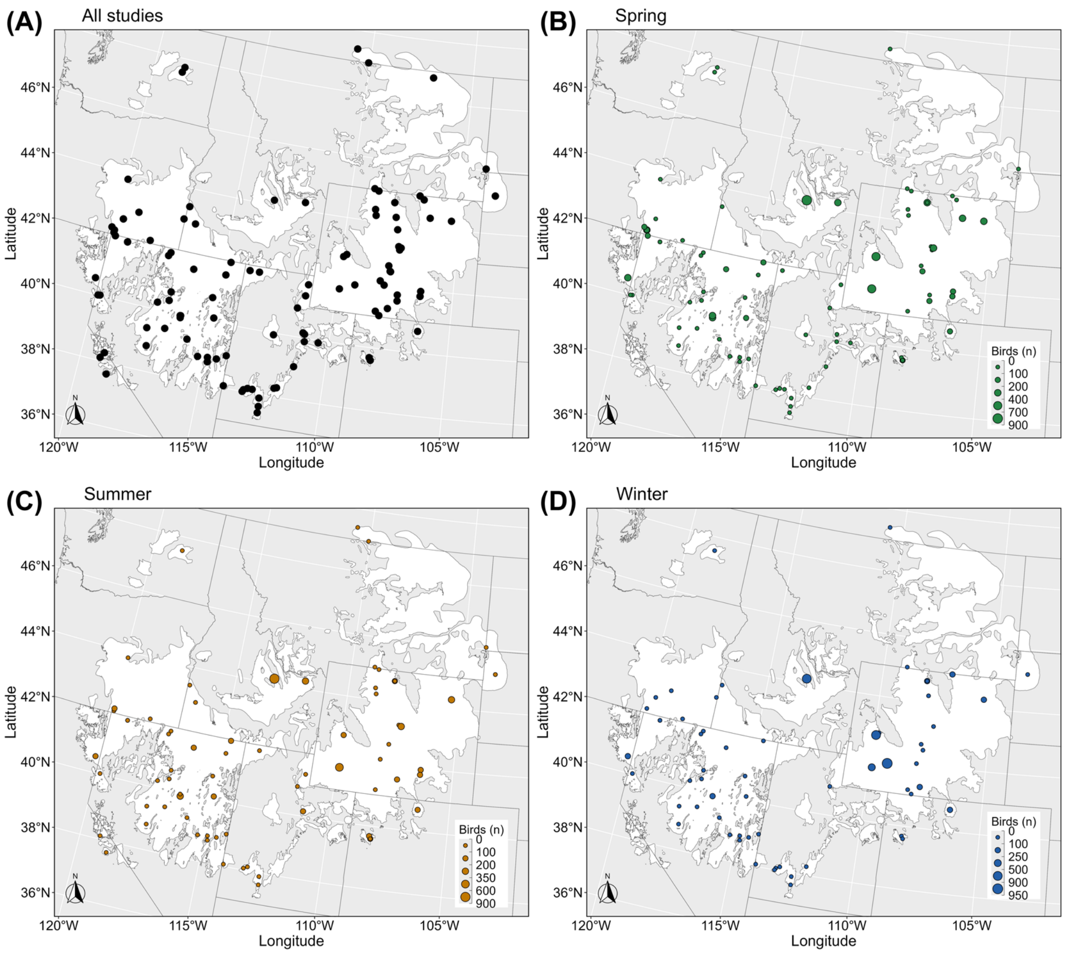

FIGURE 2 Study locations (*n* = 71 publications but many evaluated multiple study sites) summarized in a review of modeled greater sage-grouse (*Centrocercus urophasianus*) seasonal habitat associations in the United States and Canada at the second or third orders of selection from 2007–2023 (panel A represents all locations across seasons; panels B–D represent discrete seasons). The current distribution for greater sage-grouse is shown (white). Circle size reflects the number of marked birds used in studies that evaluated habitat selection in B) spring, C) summer, and D) winter temporal periods.

The way seasons were defined, and the terms used to describe them, were variable. Some studies defined seasons using previously published data on life-history events (Fedy et al. 2014, Parsons 2019, Parsons et al. 2022), others used the location dataset from the study to determine seasonal shifts based on movement patterns (Atamian et al. 2010, Burnett 2013, Stonehouse et al. 2015, Hansen et al. 2016, Schuyler et al. 2022), and many used data to determine the timing of life-history events (e.g., brood-rearing season defined as observed hatch date to 14–56 days or more post hatch; Walker et al. 2016; Westover et al. 2016; Gibson et al. 2018; Kohl et al. 2019; LeBeau et al. 2017, 2019). The remaining studies provided no information on seasonal definitions. Brood-rearing seasons were frequently broken into distinct periods (e.g., early and late; Brussee et al. 2022), and 2 studies compared brooding and non-brooding selection separately (Kirol et al. 2015, Rabon et al. 2021). Studies also made distinctions between incubation and recess periods during nesting (Dzialak et al. 2013*a*) and foraging and loafing periods of broods (Dungannon 2022). Seasons that

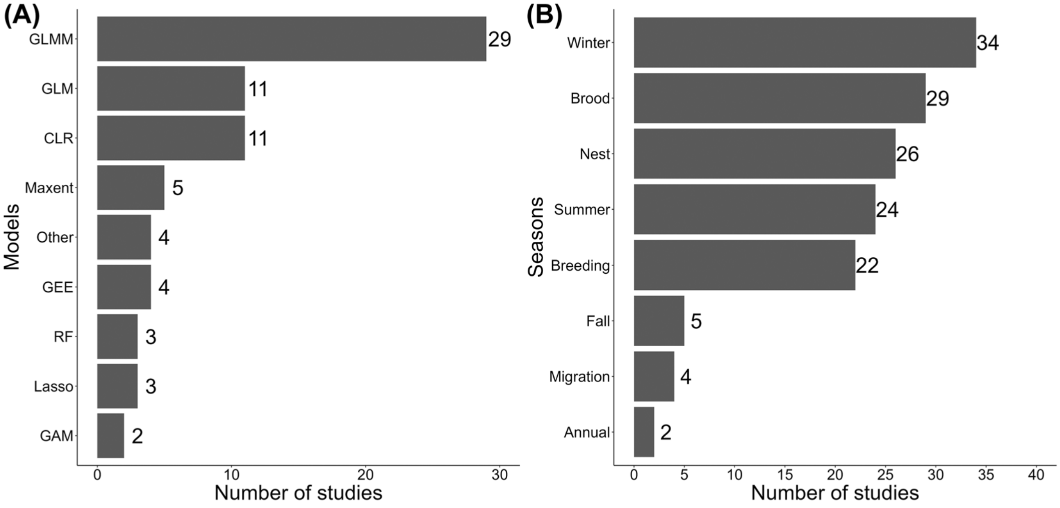

FIGURE 3 Summary of modeled greater sage-grouse (*Centrocercus urophasianus*) seasonal habitat associations in the United States and Canada from reviewed studies at the second or third orders of selection in 2007–2023. We present the frequency of studies ($n = 71$ but 1 study used multiple model types) using different types of statistical models (A). From top to bottom, model types were generalized linear mixed model (GLMM), generalized linear model (GLM), conditional logistic regression (CLR), maximum entropy (Maxent), other (model types limited to a single study such as boosted regression trees), general estimating equations (GEE), random forest (RF), least absolute shrinkage and selection operator (LASSO), and generalized additive model (GAM). We also present the number of studies ($n = 71$) using temporal life-stage and seasonal classified periods (B). Many studies evaluated several seasons.

occurred during some portion of the sage-grouse reproduction cycle (i.e., breeding, nesting, brood rearing) were most common, followed by winter, and brood and summer periods (Figure 3B). The 3 general categories of spring, summer, and winter spanned most of the calendar year (Figure 4).

Covariates and coefficients

Fifty-four of 71 studies (76%) reported slope coefficients for modeled covariates. Covariates associated with vegetation characteristics were most common, followed by measures of topography and landform, anthropogenic features, mesic features, water, invasive vegetation (like cheatgrass), and other types of covariates that could not be easily classified (Figure 5A). Studies summarized covariates extracted at used and available points using a variety of statistics. Covariates were measured using means, proportions, distances (Euclidean and decay-transformed distances), direct intersects, standard deviations, sums, and densities. Additionally, covariates were infrequently treated as quadratic or interactive in models (Figure 5B). The grain sizes at which covariates were summarized were highly variable, and the standard deviation was greater than the means for most covariate types (Table 1). The mean of most grain radii was <1 km. Covariate types associated with disturbance and water features had the largest grains, while vegetation and topographic features tended to have the smallest grains.

The proportion of positive-signed coefficients differed significantly from 0.5 for many covariate types, indicating strong evidence of selection for or avoidance of features across studies (Figure 6). Across pooled seasons, we found the covariates that were mostly avoided (90% CIs for proportion with a positive sign

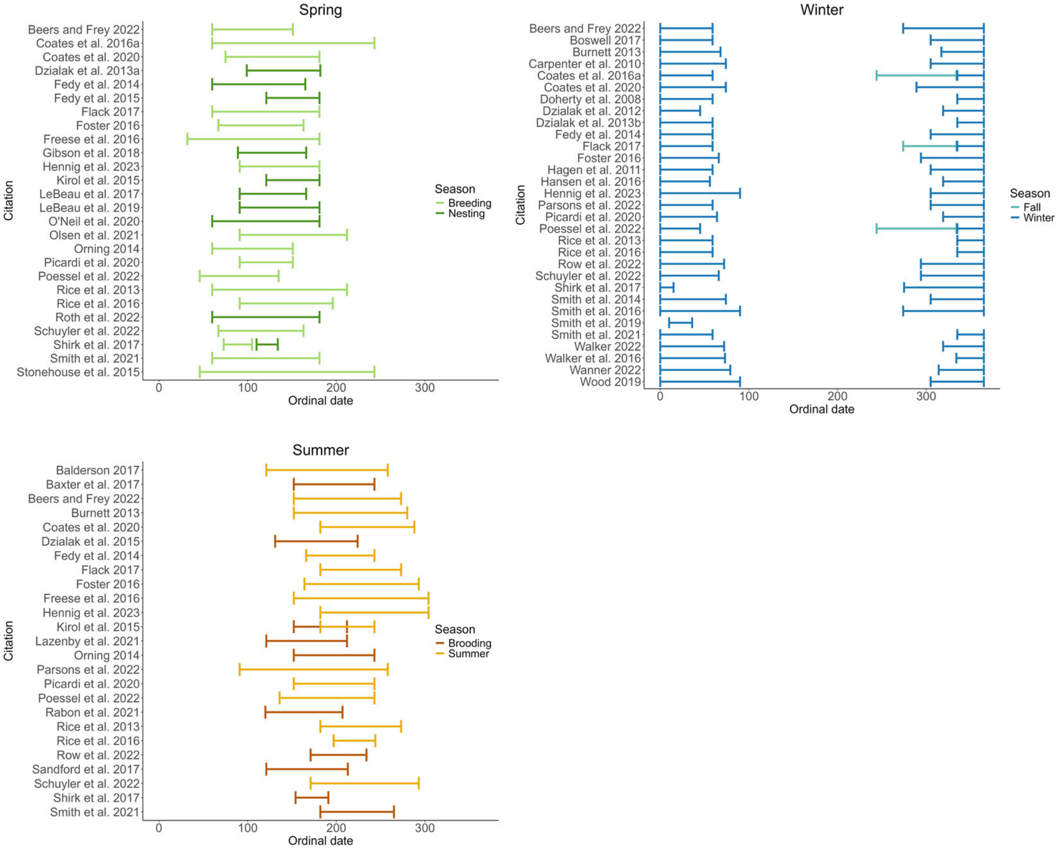

FIGURE 4 Ordinal dates used to define seasonal periods for greater sage-grouse (*Centrocercus urophasianus*) habitat association studies (second- or third-order selection) in the United States and Canada reviewed from 2007–2023. Seasonal ranges are provided for studies that provided information on seasonal cutoff dates. We grouped variable nomenclature and temporal definitions to produce 3 general seasonal periods (spring, summer, and winter). Spring often overlapped with nesting periods, summer often included brood periods, and winter is presented with fall because the fall season was only modeled separately in 3 studies and overlapped periods defined as winter.

were <0.5) were slope, pinyon-juniper cover, tree cover, topographic roughness, riparian cover, and road (proximity to). In contrast, mesic cover (proximity to), elevation, water features (proximity to), herbaceous cover, and sagebrush cover were all mostly selected. Proportions were equivalent to 0.5 (mixed) for other covariate types across pooled seasons but still followed our hypothesized directions. Within discrete seasons, proportions of different covariate types were generally similar across spring, summer, and winter seasons, but there was reduced statistical power due to fewer coefficients per group, resulting in fewer significant tests. Notable findings within the discrete seasons included strong evidence for selection for water features (proximity to) during summer but mixed responses to water in spring and winter and weak evidence for selection of topographic position index in spring and winter but mixed responses in summer. In the small sample covariate group (pooled across all seasons only), we found strong evidence for avoidance of trees (proximity to) and weak evidence for avoidance of energy disturbance (proximity to) and human disturbance (Figures S2). In contrast, we found strong evidence for selection of grassland and litter cover. There were mixed results for energy disturbance (density), human disturbance (proximity to), transmission lines (proximity to), agriculture (proximity to), large water features, road density, shrub height, and compound

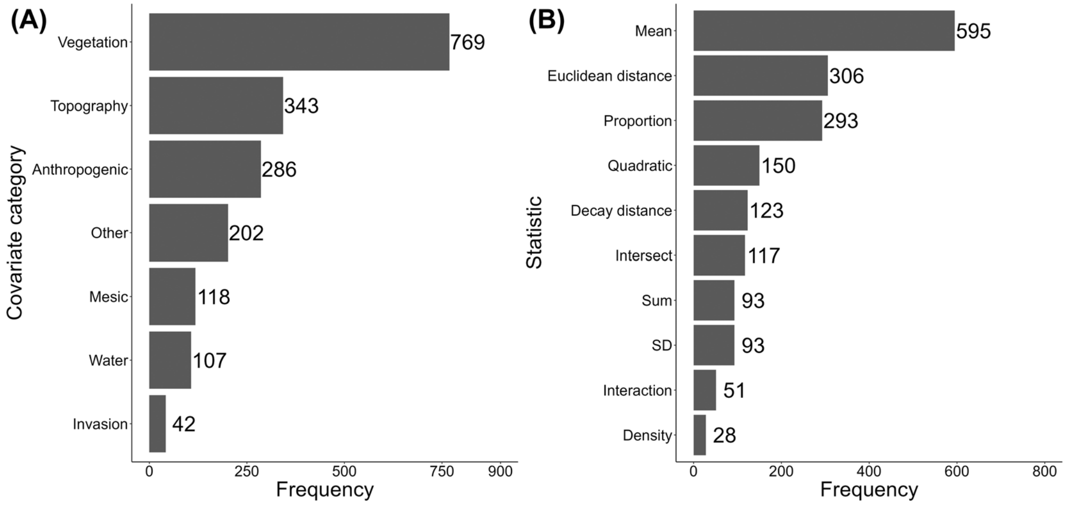

FIGURE 5 Summary of modeled greater sage-grouse (*Centrocercus urophasianus*) seasonal habitat association attributes in the United States and Canada from reviewed studies at the second or third orders of selection from 2007–2023 showing the frequency of covariate categories reported in top models (A) and the frequency of statistics (standard deviation = SD) and functional forms used to summarize or model covariates in top models (B).

topographic index, but the proportion of positive coefficients mostly trended toward the hypothesized directions (Figure S2).

DISCUSSION

Study design

Logistic regression was the most common modeling approach used to estimate seasonal habitat associations. Prior work has demonstrated that when availability samples are sufficiently large and uniform over the availability space, coefficients estimated with logistic regression asymptotically approach those obtained under an inhomogeneous point-process model, which models the true underlying process from which use distributions arise (Warton and Shepherd 2010). Therefore, logistic regression was appropriate when these conditions were met (after discarding the intercepts; Fieberg et al. 2021), but other models, including machine learning models like MaxEnt (Elith et al. 2011), were also appropriate (Warton and Shepherd 2010). Nearly all the studies we reviewed used datasets that were collected from tracking devices, which can lead to autocorrelations from repeated measures on the same individuals and induce bias in model coefficients (Gillies et al. 2006). Random intercept structures or down weighting were commonly used in an attempt to control for sample imbalance among individuals or autocorrelations induced from non-independence of observations (Gillies et al. 2006). However, recent work has highlighted that bias can still exist in fixed effects slope coefficients when random slopes are missing from models (Muff et al. 2020). Few studies fit random slopes, even though they may reduce bias when sample sizes are sufficiently large to support their inclusion, which is particularly important when parameter inference is the goal. Modeling approaches that excel at predictive performance like regularization (e.g., LASSO; Tibshirani 1996, Gerber and Northrup 2020) and machine learning (e.g., random forest; Breiman 2001, Shoemaker et al. 2018) were less common than linear models, even though predictive habitat mapping appeared to be an important goal of most studies. This

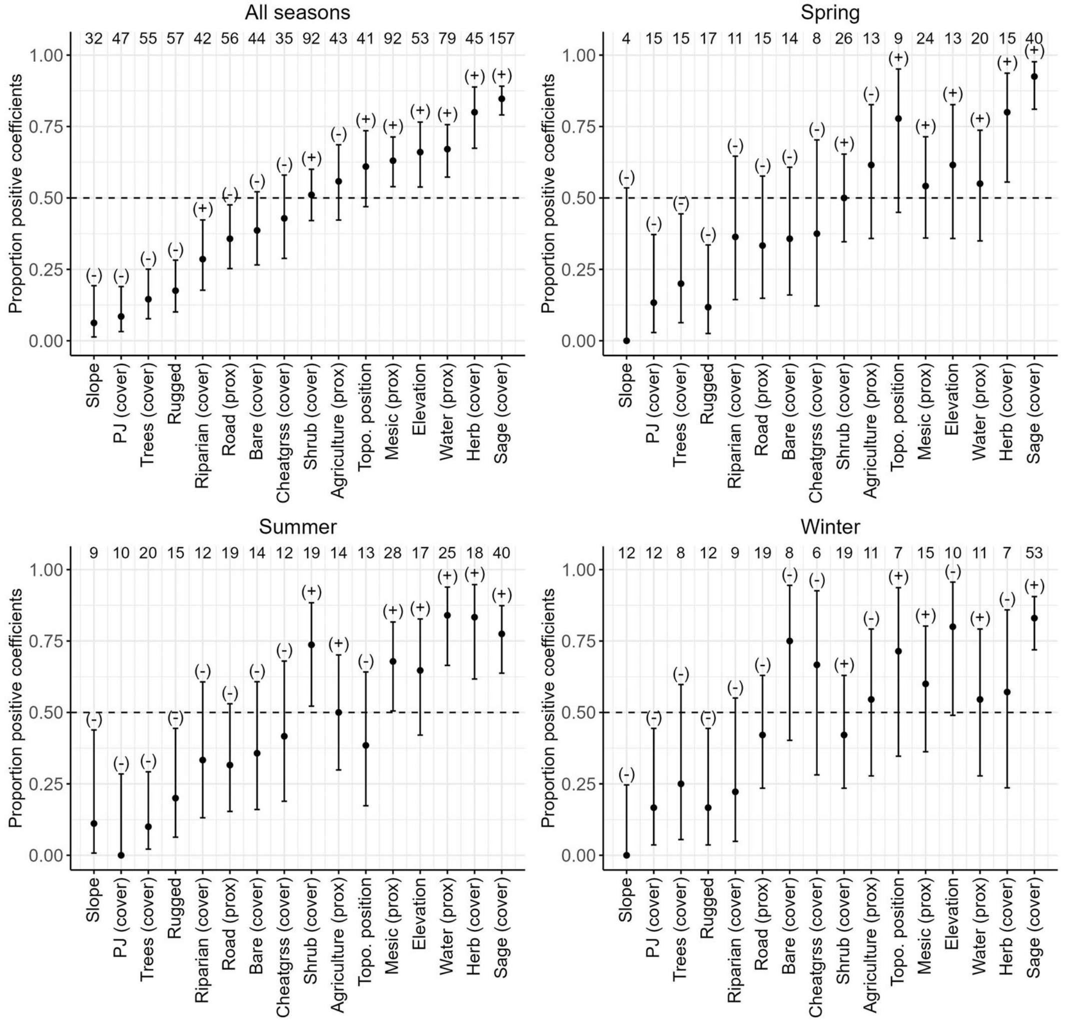

FIGURE 6 Qualitative habitat associations from greater sage-grouse (*Centrocercus urophasianus*) seasonal habitat studies in the United States and Canada at the second or third orders of selection conducted from 2007–2023. Relationships are shown pooled across all seasons (top left) or separately for spring, summer, and winter (remaining panels). The proportions of covariates reported as positive (selected) are shown for each covariate type. The 90% confidence intervals of the proportions are displayed along with the hypothesized 1-sided direction of the effect in parentheses and sample sizes are shown along the top of plots. Covariate types included those measured as a proportion of land cover (cover) or as proximity to a feature (prox; positive coefficients indicate selection for being closer to feature). Other covariate notations include pinyon-juniper (PJ), topographic (topo.) position, and herbaceous (herb).

suggests regularization and machine learning models may be underused in sage-grouse studies oriented towards predictive inference, although the improved predictive performance of machine learning comes at the loss of parameter inference (i.e., slope coefficients).

Habitat associations were estimated using a variety of sampling designs. Studies frequently targeted selection of habitats within a home range (i.e., third-order), which was commonly estimated from pooled locations across multiple individual sage-grouse (i.e., a population-level home range). We considered these studies to be assessments of third-order selection because used and available locations were evaluated within a home range extent, but the approach of pooling used locations across individuals will produce inference akin to an estimated mean individual-level response. We classified many studies as evaluating second-order selection because the availability domains were much larger than a typical home range (e.g., availability domains created from 20-km buffers placed around used points; Fedy et al. 2014). However, this does not follow the stricter definition of second-order selection, which contrasts a nested home range within a larger availability area, such as a regional population extent (Meyer and Thuiller 2006). Therefore, it was not possible to precisely match the observed orders of selection for all the studies reviewed (Johnson 1980, Meyer and Thuiller 2006), and many studies reflected a gradient of inference that fell somewhere between second-order and third-order selection. The magnitude of coefficients can be affected by the availability domain (Northrup et al. 2013), which was widely variable among studies. A larger availability domain means that available samples can be farther from use locations, and corresponding habitat characteristics are likely to diverge as a function of distance, leading to potentially stronger or weaker contrasts between used and available locations as the available boundary changes (Jarnevich et al. 2017).

Few studies evaluated habitat associations using methods that account for the influence of changing availability. Functional responses occur when selection changes as a function of availability (Mysterud and Ims 1998). For example, if sagebrush cover is homogenous and widely available to sage-grouse, its associated slope coefficient from a logistic regression model may be zero or even negative, indicating no selection or avoidance of sagebrush cover. In contrast, low availability of sagebrush is expected to produce a positive coefficient for sagebrush cover because the close association between sage-grouse and sagebrush is firmly established. Functional responses in habitat associations can therefore be a source of coefficient sign flipping (e.g., Figure 2 in Holbrook et al. 2019). Only 2 of the studies reviewed evaluated functional responses (O'Neil et al. 2020, Stevens et al. 2023), but support for their presence in some covariates was found in both cases. More work is needed to understand the prevalence of functional responses across different land cover types in sage-grouse.

Studies measured habitats over a wide range of grain sizes. For example, during the winter period, sagebrush covariates were reported at grain radii ranging from 90 m (Dzialak et al. 2012, Smith et al. 2016) up to 6,440 m (Fedy et al. 2014). The importance of multi-scale (i.e., multi-grain) covariate evaluations has been stressed in wildlife ecology repeatedly (Meyer and Thuiller 2006, McGarigal et al. 2016), including evaluating a wide range of grains to ensure the optimal scale is captured (Jackson and Fahrig 2015). Nearly all reviewed studies evaluated multiple candidate grains for each covariate. However, while variation in optimal grains may represent biological realism (optimal grains can presumably vary spatially) and may be reasonable within the analysis of a single study, it creates obvious challenges for cross-study comparisons. Indeed, issues related to grain often make cross-study comparisons intractable (Wheatley and Johnson 2009). We argue that controlling for these effects will generally need to occur under a standardized study design. We also note the relevance of Taylor and Tibshirani (2015) to multi-scale selection, as they highlight the problem of mining data to identify optimal fits, which comes at the cost of inflated Type I errors.

We focused on study design attributes in this review when considering factors affecting cross-study comparisons because that information was available. However, context-dependent habitat associations undoubtedly contributed to the mixed responses observed. Beyond categorizing habitat associations by season (seasonal variation is a form of context-dependent selection; Nielsen et al. 2010), we were unable to directly evaluate the contribution of ecological factors to mixed responses. Context-dependent selection is a process likely of interest to managers because the underlying ecological causes can potentially be manipulated. The causes are numerous, but for sage-grouse they can include habitat and life-stage interactions (e.g., selection of risky habitats can change by life stage; Dinkins et al. 2014*b*), nonlinear selection and avoidance responses to habitat (Balderson 2017, Severson et al. 2017*b*, Beers and Frey 2022), and functional responses from variation in habitat availability (O'Neil et al. 2020, Schuyler et al. 2022, Stevens et al. 2023). Habitat selection is also hypothesized to be density dependent (Northrup et al. 2022), although we are unaware of this ever being evaluated in sage-grouse. Disturbance features could also lead to mixed habitat associations through context-dependent interactions, such as sage-grouse avoiding road infrastructure during sensitive life stages but selecting it during other times of year (Walker 2022), or through functional responses caused from direct loss of habitat such as exotic annual grass invasion (Brussee et al. 2022) or sagebrush loss after wildfire (Schuyler et al. 2022). The sage-grouse studies we reviewed were frequently conducted to understand effects of disturbance (Doherty et al. 2008, 2010; Dzialak et al. 2011, 2012, 2013*a*; Walker 2022) and to map habitat in disturbed landscapes (Stevens et al. 2023), which raises the question of how representative sage-grouse study areas are compared to average habitat conditions within the sage-grouse distribution.

Our review highlights several components of study design that varied across studies. Overall, the studies reviewed made appropriate model choices to estimate habitat associations and were mostly multi-scale, as recommended by others (McGarigal et al. 2016). The appropriateness of the availability sampling schemes was hard to assess because this component of study design is sensitive to choices made by the modeler (Northrup et al. 2013). Fortunately, most studies used cross-validation to verify that their models made predictions proportional to the probability of selection when evaluated with out-of-sample data (Boyce et al. 2002, Johnson et al. 2006), suggesting their availability choices were likely reasonable from a predictive standpoint. While variable study designs have important implications for the comparability of seasonal habitat studies, which might seem prohibitive, we think summarizing these study design components could help managers and researchers align each study to those most closely related within the larger body of literature (i.e., Table 2). We suggest that future habitat association studies may benefit by framing the purpose of the study following the distinctly different goals of data exploration, prediction, and parameter inference (Tredennick et al. 2021). Doing so could not only help researchers choose an appropriate modeling strategy but also help readers classify how the study best translates to management applications (i.e., models that are optimal for the purpose of predictive mapping will generally not be optimal for coefficient inference; Gerber and Northrup 2020).

Habitat associations

Our review uncovered many types of covariates appearing in top-ranked habitat models. We discuss these covariates in broader categories, providing our interpretation of the reported relationships and exploring potential reasons for any mixed findings, particularly when the finding was counter to our expectation. We reiterate here that reporting of habitat associations is not informative regarding the number of statistical tests carried out for each type of covariate or their statistical significance. Rather, our summaries of qualitative coefficient signs focus on the consistency of estimated relationships reported from final models used for inference.

Sagebrush

The reliance of sage-grouse on sagebrush has been firmly established, and the preponderance of studies reporting selection for this resource was expected. Sagebrush provides food and cover for sage-grouse in spring and winter but is less important in summer when they also feed on insects and herbaceous plants (Barnett and Crawford 1994, Drut et al. 1994). The summarized coefficients reflected this pattern with strongest evidence for selection occurring in spring and winter and the lowest in summer (Figure 6). The main effect coefficients of sagebrush were frequently positive but included a negative quadratic effect (18% of observations), suggesting selection for intermediate levels of sagebrush. Although infrequent, instances of sagebrush avoidance did occur. For example, Coates et al. (2020) developed site-level models for several Great Basin study areas. They obtained negative coefficients for a subset of sites (spring: 1 out of 12; summer: 3 out of 14; and winter: 3 out of 12) under a controlled study design (all site-level models were built using the same availability scheme, grains, and covariates). The few cases of avoidance therefore suggest context dependence (e.g., functional responses or unmodeled interactions) at the site level rather than contradictory relationships induced from variable study designs.

Study design choices may have contributed to apparent sagebrush avoidance in other studies. For example, the choice of spatial dataset used to represent sagebrush can vary in accuracy. Apa et al. (2021) estimated negative associations with sagebrush in the closely related Gunnison sage-grouse (*Centrocercus minimus*) for some populations. They attributed apparent avoidance to several potential factors, including variable accuracy of sagebrush-classified pixels in some areas where sagebrush was intermixed with other shrub species. Indeed, the spatial datasets used to represent sagebrush or other shrub covers varied across the reviewed studies; many used fractional cover datasets produced by the United States Geological Survey (Rangeland Condition Monitoring Assessment and Projection; Rigge 2023) and United States Department of Agriculture (Rangeland Analysis Platform; Jones et al. 2018, Allred et al. 2021), or classified vegetation type datasets produced by the United States Geological Survey (LANDFIRE, www.landfire.gov). Fractional cover accuracy can vary substantially when tested against field-based samples (Applestein and Germino 2022), and one study found this agreement was lowest below 12 km^2 in an evaluation conducted at sites in Oregon and Idaho (corresponding to a grain radius of 1,955 m; Applestein and Germino 2023). Raster pixels were typically summarized at a much smaller grain radius than this threshold (Table 1). We highlight these potential factors not to discourage the use of spatial datasets but rather to raise awareness that spatial datasets are imperfect and will influence models and maps. On-the-ground knowledge is therefore critical to understand how this might affect the application of model outputs.

Trees

The mostly negative associations with trees likely represented the combination of unsuitable resources and predation risks (Dinkins et al. 2014*b*). Forested areas are unsuitable because of reductions or absence of sagebrush communities (but sagebrush understories may still exist in some conifer areas; Coates et al. 2017, Severson et al. 2017*a*), while they represent predation risks because trees provide perching and nesting structures for aerial predators (Casazza et al. 2011, Dinkins et al. 2014*b*, Coates et al. 2017). Conifer and non-conifer trees are presumably avoided by sage-grouse for the same reasons, although conifer presence can additionally lead to desiccation of herbaceous plant communities (Kormos et al. 2017) and commonly interfaces with sagebrush in early successional stages (Lundblad et al. 2022). Therefore, conifer cover has received special attention from a sage-grouse management perspective, and attempts are commonly made to isolate its effects from general tree cover (Severson et al. 2017*b*, Picardi et al. 2020). The infrequent cases where studies reported selection for tree cover may have been due to selection for other features near trees, such as riparian areas (Dinkins et al. 2014*b*), selection for thermal refugia in the afternoon by broods in summer (Dungannon 2022), or other moderating factors like correlated topography that breaks sight lines between birds and trees thereby allowing closer proximity with reduced risk (Beers and Frey 2022).

Herbaceous covers including invasive grasses

Vegetation in the form of forbs and grasses provides important food and cover for sage-grouse from spring through fall, and the mostly positive associations reported were expected. The study by Coates et al. (2020)

in the Great Basin is again particularly insightful owing to its controlled study design and multi-site models, which help to isolate potential context dependence. In this study, negative herbaceous coefficients were infrequently reported at sites in spring (1 out of 10) and summer (2 out of 11). These results are similar to the proportion of avoidance across all the reviewed studies (Figure 6), suggesting variable study design was unlikely a major driver of the infrequent negative selection responses in other studies. Surprisingly, we found several studies evaluated associations with herbaceous covers in winter (Hagen et al. 2011, Pratt 2017, Coates et al. 2020, Schuyler et al. 2022). Given herbaceous cover is senesced during this period throughout the sage-grouse range, we suspect it likely was supported in final models because it acted as a proxy for other conditions, for example, soil moisture, which correlates with taller forms of sagebrush (Carpenter et al. 2010). Alternatively, the mixed results during the winter (as opposed to mostly positive responses in spring and summer) might simply reflect the degree of overlap between seasonal ranges.

We made an important distinction between herbaceous and invasive annual covers (e.g., cheatgrass [*Bromus tectorum*]; Figure 6). We isolated coefficients associated with the latter because of their known detrimental effects to sagebrush ecosystems. The mixed responses to cheatgrass reported may therefore seem odd given the role invasive annual grasses play in wildfire cycles and sagebrush destruction (Pellant 1990, Pilliod et al. 2017). However, sage-grouse were reported to select areas invaded by invasive annual grasses during different seasons, including selection of post-burn invaded areas by late broods in summer (Brussee et al. 2022), and mixed selection and avoidance for other seasons (Hagen et al. 2011; Coates et al. 2016*a*, 2020; Brussee et al. 2022). Apparent selection can therefore occur despite the overall risk invaded annual grass areas pose to sage-grouse (O'Neil et al. 2020, Brussee et al. 2022) and sagebrush ecosystems (Blomberg et al. 2014, Coates et al. 2016*b*). Additionally, mixed selection responses might be attributed at least in part to the study design choice of spatial dataset. Like sagebrush, herbaceous fractional datasets can vary significantly in their accuracy (Applestein and Germino 2022, 2023), and methodologies used to develop fractional covers of annual invasive grasses are highly variable and may target different species of annual grasses (Tarbox et al. 2022). Therefore, we suggest careful attention to studies reporting selection of this cover type when conducting cross-study comparisons, including the specific conditions the datasets are purporting to capture. While invasive annual grasses degrade habitats and are ultimately detrimental to sage-grouse and sagebrush ecosystems, the studies we reviewed do not support consistent avoidance of these areas by sage-grouse.

Agriculture

Responses to agricultural features were among the most mixed. We think this reflects the varied ways with which sage-grouse interact with agriculture. Agriculture is a poorly defined term and can include distinctly different categories, such as irrigated versus non-irrigated, tilled (e.g., plowing or other forms of soil disruption) versus non-tilled, cropland versus non-cropland (e.g., non-tilled hayfields and alfalfa pivots can be selected; Peterson 1970), and livestock rangelands. In addition, selection or avoidance of various subcategories of agriculture by sage-grouse may depend on interactions with other features or conditions, such as proximity to sagebrush cover (Shirk et al. 2017) and seasonal climate conditions like drought, the latter of which can intensify the use of some types of agriculture (Donnelly et al. 2018). Brussee et al. (2022) posited that irrigated lands can create quasi-riparian areas in the Great Basin. However, they were unable to accurately distinguish potentially favorable agricultural areas, such as grasslands and idle pasture lands, from less favorable types because of limitations in spatial dataset accuracy (again, highlighting the important role of spatial datasets in estimated habitat associations).

Unfortunately, we were unable to draw any firm conclusions regarding seasonal selection patterns to agricultural features because of unclear terminology, but studies indicated selection for closer proximity to hayfields and alfalfa in summer (Burnett 2013, Gelling 2022), presumably because these areas were moister and insect-rich (Aldridge and Boyce 2007, Burnett 2013, Gelling 2022). Therefore, most datasets used to represent agriculture were not described clearly enough to make finer distinctions of the various categories described above, yet more descriptive categories are critical to facilitate the transfer of findings across studies. We therefore view the lack of detail provided for various categories of agriculture as a limitation when reporting habitat associations. Although evaluating demographic responses to agriculture is distinctly different than evaluating selection patterns, it is worth highlighting that Pratt and Beck (2021) emphasized the importance of understanding how these features affect sage-grouse survival during various life stages, as agricultural areas are commonly proposed to act as sink habitats (Aldridge and Boyce 2007, Kirol et al. 2015). Thus, selection patterns between sage-grouse and different types of agriculture features are very much an open area of research, and we suggest the mixed results reported largely occur because the umbrella term of agriculture covers a diverse range of land covers.

Riparian and mesic

We expected selection for mesic (areas with moister soil conditions) and riparian (corridors along streams and other water bodies) landscapes in the summer and avoidance in the spring and winter when sage-grouse switch to a sagebrush-dominant diet. The proportion of positive selection coefficients largely followed this pattern for proximity to mesic areas, but selection responses to riparian cover did not. Riparian landscapes were represented primarily as proportions of land covers classified from LANDFIRE existing vegetation types, and 2 studies in the Great Basin represented over half of these coefficients (Coates et al. 2016*a*, 2020). These same studies reported that sage-grouse selected strongly for proximity to water features (streams and other water bodies) during the summer across sites. Therefore, the proximity to water covariate type might better reflect riparian landscapes in the studies we reviewed compared to land cover categories derived from satellite imagery, which may not have distinguished riparian areas comprised of shrubs and herbaceous covers from those with trees. Fedy et al. (2014) highlighted challenges of accurately capturing hydrological features and riparian cover types in spatial datasets throughout Wyoming. While we generally expected sage-grouse to select for riparian cover types in summer, they can contain risky habitat features, such as taller vegetation structures like trees that offer perches for raptors. Dinkins et al. (2014*b*) found that responses of females with broods to riparian cover types differed by the age of chicks, with avoidance during the period chicks were young and most susceptible to predation, but selection by older broods. This trade-off between resources and risks may explain some of the avoidance responses observed.

Elevation

Interpreting selection and avoidance responses to elevation requires careful attention to both study design and context dependence. Sage-grouse tended to select for higher elevations across seasons, but avoidance of higher elevations was not infrequent. Proposed mechanisms for sage-grouse selecting higher elevation habitats in summer include better herbaceous cover provided by cooler and moister environments (Foster 2016, Flack 2017, O'Neil et al. 2020, Smith et al. 2021, Brussee et al. 2022, Schuyler et al. 2022) and reduced land disturbance from human activities, such as human development like roads and croplands, and invasive annual grasses that commonly occur in basins and valley bottoms (Lockyer et al. 2015, Picardi et al. 2020, Schuyler et al. 2022). However, several studies reported that sage-grouse selected for lower elevation summer habitats or different elevational bands. For example, Burnett (2013) found a bimodal use distribution, with some birds selecting post-burn herbaceous areas at higher elevations, while others favored agricultural fields at lower elevations. Indeed, selection for proximity to some agriculture features may be an important driver of seasonal use patterns, as discussed in the preceding section, and therefore correlated with elevation. Elevation main effects frequently included an associated quadratic effect (21% of main effects), indicating nonlinearity in the response.

We found no suggested mechanisms for sage-grouse elevational selection in winter in the reviewed studies, but others have proposed the importance of snow-free areas – occurring in both basins and wind-exposed plateaus and ridges – may be plausible reasons (Connelly et al. 2011). Elevation selection patterns can therefore be highly context dependent. We further suggest elevation effects can be strongly influenced by the available sampling domain. For example, Rice et al. (2016) used a fixed study area boundary (the North Park Basin in Colorado) to sample availability for the 3 seasonal periods modeled (akin to second-order selection). The elevation distributions at used locations across all 3 seasons were lower than the available sample locations (Rice et al. 2016). Unsurprisingly, sage-grouse were found to select lower elevations in each season. In contrast, Foster (2016) defined availability for sage-grouse in Oregon within individual seasonal home ranges (third-order selection), the boundaries of which varied by season, and found that sage-grouse selected for intermediate levels of elevation within each season. Therefore, careful attention to the sampling domain is especially warranted when interpreting elevation-based habitat associations. Ideally, elevation would be replaced with the actual environmental conditions driving habitat use distributions when parameter inference is the goal, although identifying these conditions may be challenging in practice. We further suggest this claim extends to other topographic landform covariates, such as the topographic position and compound topographic indices.

Slope and rugged terrain

While slope and ruggedness are not synonymous, they are often highly correlated (Flack 2017, Lazenby et al. 2021). Most studies supported strong avoidance of steep and rugged terrain by sage-grouse across seasons. However, the reasons for the estimated coefficients were usually not provided. Dinkins et al. (2014*b*) proposed that sage-grouse avoided rugged terrain because it provided more perching habitat for avian predators. In a separate study, they additionally found lower female mortality rates in less rugged areas (Dinkins et al. 2014). Further supporting a predation-risk hypothesis, Kirol et al. (2015) found higher mortality rates in sage-grouse selecting rugged areas in summer, and Pratt (2017) reported nests located in rugged areas were lost to predators at higher rates. Steep and rugged areas may have also been avoided because of their associations with specific vegetation characteristics, including conifer, which frequently occurs in steep and rugged areas (Boswell 2017, Severson et al. 2017*a*, Apa et al. 2021). Rugged terrain was also proposed to constrain brood movements, forcing birds into undesirable corridors closer to conifer as they moved to mesic areas from nest areas (Olsen et al. 2021). Despite the widespread avoidance of these conditions across studies, rugged terrain may provide important habitat under certain conditions. For example, other studies point to the importance of shelter provided by rugged terrain during extreme winter storms (Beck 1977, Hupp and Braun 1989). We therefore suggest the underlying drivers of avoidance (or, much less frequently, selection) for steep and rugged terrain are context-dependent, and here we have highlighted only a few plausible mechanisms.

Disturbance (energy infrastructure)

As expected, responses to oil and gas infrastructure (well pads, pump stations, pipelines, and service roads) were mostly negative for both density and proximity measures (Figure S2), but sample sizes prohibited summarizing responses separately by season. Contrary to our expectations, sage-grouse were occasionally reported to select for some energy disturbance features (or intermediate levels of disturbance) during brood rearing and summer (Aldridge and Boyce 2007; Harju et al. 2013; Orning 2014; Fedy et al. 2014, 2015; Kirol et al. 2015; Flack 2017; Gelling 2022;

Walker 2022) and spring (Gelling 2022), but proposed reasons for selection were not always provided. However, more than one feature representing energy infrastructure was sometimes present in the same model in these studies. For example, Aldridge and Boyce (2007) found that broods selected areas closer to well sites but avoided areas with greater density of visible wells, a level of nuance our coefficient summaries clearly missed. Walker (2022) reported avoidance of all types of energy infrastructure (well pads, roads, and pipelines) in spring and winter but selection for areas with intermediate levels of infrastructure and areas closer to pipelines and roads in summer and fall in western Colorado. While the selection mechanism underlying that pattern was unknown, it was proposed that pipelines and roadsides had greater forb and insect resources important for females and broods in summer and fall and infrastructure with disturbed surface (active well pads and roads) are typically nearby (Walker 2022). The rugged topography of the study area (high-elevation ridges surrounded by steep terrain) also constrained both where sage-grouse occurred and where energy infrastructure was built (Walker et al. 2020).

We suggest study design attributes for both covariate grain and the availability sample are particularly important when evaluating energy infrastructure. In the case of availability, not all individuals in a population will be exposed to the same levels of disturbance features. Study designs targeting third-order selection and individual home ranges are well suited for this type of problem due to the varying level of disturbance each bird will encounter (Walker 2022). In the case of grain, variable grains impede comparisons between studies for quantitative assessments, which are critically needed to guide policy as the energy footprint continues to expand (LeBeau et al. 2023). We also emphasize that sage-grouse habitat associations with energy features is not informative to sage-grouse fitness; energy infrastructure is known to negatively affect sage-grouse population growth (Walker et al. 2007, Green et al. 2017), survival (Kirol et al. 2015, Kirol et al. 2020), and reproduction (Kirol et al. 2020). Therefore, like any other detrimental habitat features selected or avoided, habitat association studies conducted in disturbed areas will benefit from paired demographic analyses (Aldridge and Boyce 2007, Kirol et al. 2015, O'Neil et al. 2020, Pratt and Beck 2021, Brussee et al. 2022).

Disturbance (roads)

We anticipated avoidance of roads, which mostly occurred across seasons, but responses were mixed. Roads represented a range of conditions within the studies examined, including 2-tracks and gravel roads with low traffic volumes, intermediate surface roads (e.g., state highways), and high traffic highways and interstates. We were unable to categorize road conditions into finer groups for most studies, but responses are likely to vary based on road attributes like traffic volume (Johnson et al. 2011). Roads often occur disproportionately in mesic areas (valley bottoms) and flat areas (ridges) within sage-grouse habitat (Walker et al. 2020), potentially leading to apparent selection or avoidance due to these correlations (Dean et al. 2019). For example, Kirol et al. (2015) reported that roads were located in less rugged areas in their southcentral Wyoming study area (rugged terrain was strongly avoided), leading to intermediate levels of apparent selection to areas near haul roads in summer by late-brooding females (but see Harju et al. 2013 for an example of apparent selection for haul roads after controlling for rugged terrain effects). Therefore, multicollinearity between disturbance predictors like roads and other desirable habitat features likely contributes to the mixed results we report. We suggest future habitat association studies that fit road effects will facilitate understanding by distinguishing the types of road features tested; Kirol et al. (2015) provides a good example of distinguishing road categories in a habitat association analysis.

Inference from habitat association studies

Inference at both smaller and larger scales are needed to guide landscape management for sage-grouse. Smith et al. (2020) recently called into question the focus on fine-scale habitat characteristics in habitat management guidelines (Connelly et al. 2000), highlighting the need to consider habitat conditions at scales aligning with management units (e.g., grazing allotments). While we agree that broader spatial scales are important, the Bureau of Land Management and several state agencies recognize the relevance of managing habitats across a range of orders and scales in habitat evaluations (Connelly et al. 2003, 2004; Stiver et al. 2015). The large number of higher-order studies reviewed here lends credence to this understood need. While our habitat association summaries are likely unsurprising for several well-known variables, they also highlighted the reality of our initial confusion and perception of habitat study uncertainty – sage-grouse studies frequently report contradictory associations for the same types of covariates, even when comparisons are made within the same season. These mixed associations likely arise from a combination of variable study designs and context-dependent selection, and while it is important to control for the former, we suspect study design effects from higher-order studies are likely to remain a challenge, even in the presence of increased study design standardization.

The difficulties of reporting comparable coefficients from RSF models are well known (Avgar et al. 2017, Fieberg et al. 2021). Avgar et al. (2017) suggested that coefficients from RSFs should be reported as relative risk ratios (which they termed relative selection strength ratios) to aid cross-study comparisons. This measure provides a way to interpret habitat associations as a change in the magnitude of selection per unit change in habitat, conditional on other covariates in the model being fixed at their mean. Very few studies reported coefficients in this way, and while we think the recommendation is a useful way to understand habitat selection responses, it would not mitigate all the effects introduced from the variable study designs encountered. As discussed, model choice and other study design attributes affect the coefficients and potentially the signs of coefficients. Indeed, this led us to focus on qualitative summaries of coefficient signs. Smith et al. (2020) were able to quantitatively evaluate findings from fine-scale studies because means and variances of used and available habitat measurements were provided (they did not analyze coefficients). These statistics were rarely reported in the studies reviewed here, presumably because slope coefficients are of interest in higher-order studies versus covariate values obtained from spatial datasets (in contrast to habitat estimates obtained through labor-intensive field-based sampling in fine-scale studies; Hagen et al. 2007). However, having this information could allow the methodology of Smith et al. (2020) to be applied to higher-order selection studies, although comparability issues between covariate datasets might reduce its effectiveness.

While quantitative values of coefficients are clearly critical for predictive mapping and to understand habitat selection relationships, such as testing for treatment effects (Severson et al. 2017*b*) or thresholds of disturbance (Walker 2022), their comparative value is limited by study design. A recent meta-analysis evaluating sage-grouse selection responses to energy infrastructure features further highlights the challenges of comparing RSF coefficients across studies (LeBeau et al. 2023), including missing statistics presented for used and available habitats, different transformations on features measured as distances, and variation in areas over which disturbance densities were calculated (i.e., grain). These authors suggested a standard set of grains and transformations could be evaluated as supplemental information in future disturbance studies, which would aid cross-study comparisons. For example, we observed that 100-, 564-, and 1,000-m grain radii were fairly common when summarizing energy feature densities around used and available locations and might offer useful benchmarks at which to report supplemental coefficient estimates, even if these are not the optimal grain radii at which final models are produced. Thus, reporting multiple metrics is helpful for those attempting meta-analyses (LeBeau et al. 2023).

Although study design can complicate cross-study comparisons of habitat associations, we suggest the following considerations when evaluating reported selection and avoidance by sage-grouse to specific environmental features (Table 2 will likely be a useful resource). First, identifying studies that model habitat associations within the same season and at the same order of selection is helpful. DeCesare et al. (2012) elegantly demonstrated the significant impact that the level of selection can have on models and predictive maps (see Figure 4 in DeCesare et al. 2012). Second, we suggest checking that the temporal periods (i.e., seasons) or behavioral states align. In this review, we pooled finer temporal periods for summarizing selection coefficients, such as late brood habitat with a general summer season, and we did not distinguish between males and females. While our summaries admittedly gloss over this level of detail, it is important to be aware of it. Third, careful examination of the spatial datasets is helpful to understand what the covariates are explicitly attempting to capture, in addition to the grain at which they are measured. In our experience, smaller grains tend to lead to smaller estimated coefficients for selected habitat features, like sagebrush fractional cover, but the relationship between grain and coefficient size can vary by covariate type and may be largest (or smallest) at intermediate grains. Finally, it is important to understand if the study included any additional factors that might impede or aid comparisons, such as habitat treatment effects or disturbance factors like wildfire, which can potentially lead to unexpected selection patterns (Schuyler et al. 2022).

For those developing new studies, we suggest helping to clarify mixed habitat associations by developing and testing hypotheses on how sage-grouse interact with these habitat features and proposing the mechanisms leading to the estimated coefficients. Additionally, we strongly encourage reporting coefficients and their standard errors when linear models are fit, and whether models were fit to standardized covariates (nearly half of the reviewed studies did not report this vital piece of information). Reporting statistics on used and available distributions of covariates, such as means and variances, will further help characterize habitat features selected and avoided at the order and grains of the study and may open the door for cross-study quantitative assessments (Smith et al. 2020). Finally, sage-grouse field studies have accumulated sufficient telemetry data to conduct larger joint analyses across multiple datasets (Fedy et al. 2014; Ricca et al. 2018; Coates et al. 2016*a*, 2020). Leveraging existing datasets by combining them can help address some of the habitat association uncertainties highlighted here and elsewhere (Smith et al. 2020). Fitting models under common study designs is beneficial as an approach that controls for study design effects and allows researchers to focus directly on habitat ecology. Thus, reaching out to other researchers and combining data is likely to lead to fruitful collaborative work.

RESEARCH IMPLICATIONS

The consistent habitat associations reported across the higher-order studies we reviewed are important and will likely improve the predictive performance of models for habitat mapping applications. In contrast, mixed habitat associations can benefit from special attention when considering their role in shaping observed space-use patterns, which may be caused by important context-dependent selection as availability of resources varies across the species' range, or variable study designs. In particular, clear descriptions of features representing roads, agriculture, and riparian areas can help resource managers interpret findings. Some of the mixed habitat association covariates are additionally important because they include disturbance features, which natural resource managers commonly plan for and integrate into wildlife management guidelines (Manier et al. 2014, Stiver et al. 2015). Evaluating and presenting these associations at a range of scales previously evaluated can help aid comparability with other studies.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This review was based solely on data reported in published studies (Table 2) and did not involve the capture, handling, or direct observation of animals. As such, Institutional Animal Care and Use Committee (IACUC) approval was not required.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created in this study.

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REFERENCES

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508-526.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983-994.

Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: a spatially explicit hierarchical approach. Journal of Wildlife Management 76:391-406.

Allred, B. W., B. T. Bestelmeyer, C. S. Boyd, C. Brown, K. W. Davies, M. C. Duniway, L. M. Ellsworth, T. A. Erickson, S. D. Fuhlendorf, and T. V. Griffiths. 2021. Improving Landsat predictions of rangeland fractional cover with multitask learning and uncertainty. Methods in Ecology and Evolution 12:841-849.

Apa, A. D., K. Aagaard, M. B. Rice, E. Phillips, D. J. Neubaum, N. Seward, J. R. Stiver, and S. Wait. 2021. Seasonal habitat suitability models for a threatened species: the Gunnison sage-grouse. Wildlife Research 48:609-624.

Applestein, C., and M. J. Germino. 2022. How do accuracy and model agreement vary with versioning, scale, and landscape heterogeneity for satellite-derived vegetation maps in sagebrush steppe? Ecological Indicators 139:108935.

Applestein, C., and M. J. Germino. 2023. Satellite-derived plant cover maps vary in performance depending on version and product. Ecological Indicators 155:110950.

Atamian, M. T., J. S. Sedinger, J. S. Heaton, and E. J. Blomberg. 2010. Landscape-level assessment of brood rearing habitat for greater sage-grouse in Nevada. Journal of Wildlife Management 74:1533-1543.

Avgar, T., S. R. Lele, J. L. Keim, and M. S. Boyce. 2017. Relative selection strength: Quantifying effect size in habitat-and step-selection inference. Ecology and Evolution 7:5322-5330.

Baines, D. 1994. Seasonal differences in habitat selection by black grouse *Tetrao tetrix* in the northern Pennines, England. Ibis 136:39-43.

Balderson, K. L. 2017. Habitat selection and nesting ecology of translocated greater sage-grouse. Thesis, University of Regina, Regina, Canada.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. Journal of Range Management 47:114-118.

Baxter, J. J., R. J. Baxter, D. K. Dahlgren, and R. T. Larsen. 2017. Resource selection by greater sage-grouse reveals preference for mechanically-altered habitats. Rangeland Ecology & Management 70:493-503.

Beck, T. D. 1977. Sage grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41:18-26.

Beers, A. T., and S. N. Frey. 2022. Greater sage-grouse habitat selection varies across the marginal habitat of its lagging range margin. Ecosphere 13:e4146.

Blomberg, E. J., J. S. Sedinger, D. V. Nonne, and M. T. Atamian. 2014. Annual male lek attendance influences count-based population indices of greater sage-grouse. Journal of Wildlife Management 78:179.

Boswell, R. 2017. Seasonal resource selection and habitat treatment use by a fringe population of greater sage-grouse. Thesis, Utah State University, Logan, USA.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281-300.

Braun, C. E. 1995. Distribution and status of sage grouse in Colorado. Prairie Naturalist 27:1.

Breiman, L. 2001. Random forests. Machine Learning 45:5-32.

Broennimann, O., M. C. Fitzpatrick, P. B. Pearman, B. Petitpierre, L. Pellissier, N. G. Yoccoz, W. Thuiller, M. J. Fortin, C. Randin, and N. E. Zimmermann. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography 21:481-497.

Brooks, M. L., J. R. Matchett, D. J. Shinneman, and P. S. Coates. 2015. Fire patterns in the range of the greater sage-grouse, 1984-2013—implications for conservation and management. Report 2015-1167. U.S. Geological Survey, Reston, Virginia, USA.

Brussee, B. E., P. S. Coates, S. T. O'Neil, M. L. Casazza, S. P. Espinosa, J. D. Boone, E. M. Ammon, S. C. Gardner, and D. J. Delehanty. 2022. Invasion of annual grasses following wildfire corresponds to maladaptive habitat selection by a sagebrush ecosystem indicator species. Global Ecology and Conservation 37:e02147.

Brussee, B. E., P. S. Coates, S. T. O'Neil, M. A. Ricca, J. E. Dudko, S. P. Espinosa, S. C. Gardner, M. L. Casazza, and D. J. Delehanty. 2023. Influence of fine-scale habitat characteristics on sage-grouse nest site selection and nest survival varies by mesic and xeric site conditions. Ornithological Applications 125:1-15.

Burnett, A. C. 2013. Modeling habitat use of a fringe greater sage-grouse population at multiple spatial scales. Thesis, Utah State University, Logan, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Carlisle, J., K. Smith, J. Beck, M. Murphy, and A. D. Chalfoun. 2024. Beyond overlap: considering habitat preference and fitness outcomes in the umbrella species concept. Animal Conservation 27:212-225.

Carpenter, J., C. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806-1814.

Casazza, M. L., P. S. Coates, and C. T. Overton. 2011. Linking habitat selection and brood success in greater sage-grouse. Pages 151-167 *in* B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. University of California Press, Berkeley, USA.

Coates, P. S., B. E. Brussee, M. A. Ricca, J. P. Severson, M. L. Casazza, K. B. Gustafson, S. P. Espinosa, S. C. Gardner, and D. J. Delehanty. 2020. Spatially explicit models of seasonal habitat for greater sage-grouse at broad spatial scales: informing areas for management in Nevada and northeastern California. Ecology and Evolution 10: 104-118.

Coates, P. S., M. L. Casazza, M. A. Ricca, B. E. Brussee, E. J. Blomberg, K. B. Gustafson, C. T. Overton, D. M. Davis, L. E. Niell, and S. P. Espinosa. 2016*a*. Integrating spatially explicit indices of abundance and habitat quality: an applied example for greater sage-grouse management. Journal of Applied Ecology 53:83-95.

Coates, P. S., B. G. Prochazka, M. S. O'Donnell, C. L. Aldridge, D. R. Edmunds, A. P. Monroe, M. A. Ricca, G. T. Wann, S. E. Hanser, and L. A. Wiechman. 2021. Range-wide greater sage-grouse hierarchical monitoring framework—implications for defining population boundaries, trend estimation, and a targeted annual warning system. Report 2331-1258. U.S. Geological Survey, Reston, Virginia, USA.

Coates, P. S., B. G. Prochazka, M. A. Ricca, K. B. Gustafson, P. Ziegler, and M. L. Casazza. 2017. Pinyon and juniper encroachment into sagebrush ecosystems impacts distribution and survival of greater sage-grouse. Rangeland Ecology & Management 70:25-38.

Coates, P. S., M. A. Ricca, B. G. Prochazka, M. L. Brooks, K. E. Doherty, T. Kroger, E. J. Blomberg, C. A. Hagen, and M. L. Casazza. 2016*b*. Wildfire, climate, and invasive grass interactions negatively impact an indicator species by reshaping sagebrush ecosystems. Proceedings of the National Academy of Sciences 113: 12745-12750.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. Station Bulletin 80. University of Idaho, College of Natural Resources Experiment Station, Moscow, USA.

Connelly, J. W., E. T. Rinkes, and C. E. Braun. 2011. Characteristics of greater sage-grouse habitats: a landscape species at micro and macro scales. Studies in Avian Biology 38:69-83.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.

Dean, W. R. J., C. L. Seymour, G. S. Joseph, and S. H. Foord. 2019. A review of the impacts of roads on wildlife in semi-arid regions. Diversity 11:81.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, and L. E. Morgantini. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1068-1083.

Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey. 2014*a*. Greater sage-grouse (*Centrocercus urophasianus*) hen survival: effects of raptors, anthropogenic and landscape features, and hen behavior. Canadian Journal of Zoology 92:319-330.

Dinkins, J. B., M. R. Conover, C. P. Kirol, J. L. Beck, and S. N. Frey. 2014*b*. Greater sage-grouse (*Centrocercus urophasianus*) select habitat based on avian predators, landscape composition, and anthropogenic features. Condor 116:629-642.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74:1544-1553.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Donnelly, J. P., B. W. Allred, D. Perret, N. L. Silverman, J. D. Tack, V. J. Dreitz, J. D. Maestas, and D. E. Naugle. 2018. Seasonal drought in North America's sagebrush biome structures dynamic mesic resources for sage-grouse. Ecology and Evolution 8:12492-12505.

Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994. Brood habitat use by sage grouse in Oregon. Great Basin Naturalist 54: 170-176.

Dungannon, T. D. 2022. The role of trees and thermal refugia in greater sage-grouse brood habitat selection. Thesis, Oregon State University, Corvallis, USA.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, J. P. Mudd, J. B. Winstead, and L. Hayden-Wing. 2011. Identifying and prioritizing greater sage-grouse nesting and brood-rearing habitat for conservation in human-modified landscapes. PloS ONE 6:e26273.

Dzialak, M. R., C. V. Olson, S. M. Harju, S. L. Webb, and J. B. Winstead. 2012. Temporal and hierarchical spatial components of animal occurrence: conserving seasonal habitat for greater sage-grouse. Ecosphere 3:1-17.

Dzialak, M. R., C. V. Olson, S. M. Harju, and J. B. Winstead. 2013*a*. Spatial generality of predicted occurrence models of nesting habitat for the greater sage-grouse. Ecosphere 4:1-20.

Dzialak, M. R., C. V. Olson, S. L. Webb, S. M. Harju, and J. B. Winstead. 2015. Incorporating within-and between-patch resource selection in identification of critical habitat for brood-rearing greater sage-grouse. Ecological Processes 4: 1-15.

Dzialak, M. R., S. L. Webb, S. M. Harju, C. V. Olson, J. B. Winstead, and L. D. Hayden-Wing. 2013*b*. Greater sage-grouse and severe winter conditions: identifying habitat for conservation. Rangeland Ecology & Management 66:10-18.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43-57.

Fedy, B. C., K. E. Doherty, C. L. Aldridge, M. O'Donnell, J. L. Beck, B. Bedrosian, D. Gummer, M. J. Holloran, G. D. Johnson, and N. W. Kaczor. 2014. Habitat prioritization across large landscapes, multiple seasons, and novel areas: an example using greater sage-grouse in Wyoming. Wildlife Monographs 190:1-39.

Fedy, B. C., C. P. Kirol, A. L. Sutphin, and T. L. Maechtle. 2015. The influence of mitigation on sage-grouse habitat selection within an energy development field. PloS ONE 10:e0121603.

Fieberg, J., J. Signer, B. Smith, and T. Avgar. 2021. A 'How to'guide for interpreting parameters in habitat-selection analyses. Journal of Animal Ecology 90:1027-1043.

Flack, M. B. 2017. Ecology of greater sage-grouse inhabiting the southern portion of the Rich-Morgan-Summit Sage-Grouse Management Area. Thesis, Utah State University, Logan, USA.

Foster, L. J. 2016. Resource selection, and demographic rates of female greater sage-grouse following large-scale wildfire. Thesis, Oregon State University, Corvallis, USA.

Freese, M. T., S. L. Petersen, R. F. Miller, A. C. Yost, and W. D. Robinson. 2016. Spatial analysis of greater sage-grouse habitat use in relation to landscape level habitat structure. Journal of Ecosystem & Ecography 6:205.

Gelling, E. L. 2022. Seasonal habitat selection and breeding ecology of greater sage-grouse in Carbon County, Montana. Thesis, University of Wyoming, Laramie, USA.

Gerber, B. D., and J. M. Northrup. 2020. Improving spatial predictions of animal resource selection to guide conservation decision making. Ecology 101:e02953.

Gibson, D., E. J. Blomberg, M. T. Atamian, S. P. Espinosa, and J. S. Sedinger. 2018. Effects of power lines on habitat use and demography of greater sage-grouse (*Centrocercus urophasianus*). Wildlife Monographs 200:1-41.

Gilchrist, G., M. Mallory, and F. Merkel. 2005. Can local ecological knowledge contribute to wildlife management? Case studies of migratory birds. Ecology and Society 10:20.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887-898.

Green, A. W., C. L. Aldridge, and M. S. O'donnell. 2017. Investigating impacts of oil and gas development on greater sage-grouse. Journal of Wildlife Management 81:46-57.

Guisan, A., W. Thuiller, and N. E. Zimmermann. 2017. Habitat suitability and distribution models: with applications in R. Cambridge University Press, Cambridge, United Kingdom.

Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. Wildlife Biology 13:42-50.

Hagen, C. A., M. J. Willis, E. M. Glenn, and R. G. Anthony. 2011. Habitat selection by greater sage-grouse during winter in southeastern Oregon. Western North American Naturalist 71:529-538.

Hansen, E. P., A. Stewart, and S. N. Frey. 2016. Influence of transmission line construction on winter sage-grouse habitat use in southern Utah. Human–Wildlife Interactions 10:169-187.

Harju, S. M., C. V. Olson, M. R. Dzialak, J. P. Mudd, and J. B. Winstead. 2013. A flexible approach for assessing functional landscape connectivity, with application to greater sage-grouse (*Centrocercus urophasianus*). PLoS ONE 8:e82271.

Heinrichs, J. A., C. L. Aldridge, D. L. Gummer, A. P. Monroe, and N. H. Schumaker. 2018. Prioritizing actions for the recovery of endangered species: emergent insights from greater sage-grouse simulation modeling. Biological Conservation 218: 134-143.

Heinrichs, J. A., C. L. Aldridge, M. S. O'Donnell, and N. H. Schumaker. 2017. Using dynamic population simulations to extend resource selection analyses and prioritize habitats for conservation. Ecological Modelling 359:449-459.

Heinrichs, J. A., L. E. Walker, J. J. Lawler, N. H. Schumaker, K. C. Monroe, and A. D. Bleisch. 2019. Recent advances and current challenges in applying source-sink theory to species conservation. Current Landscape Ecology Reports 4: 51-60.

Heisler, L. M., R. G. Poulin, and C. M. Somers. 2017. Stop using dichotomous terms to reference observations of scale-dependent habitat selection. Landscape Ecology 32:1531-1542.

Hennig, J. D., J. Scasta, A. C. Pratt, C. P. Wanner, and J. L. Beck. 2023. Habitat selection and space use overlap between feral horses, pronghorn, and greater sage-grouse in cold arid steppe. Journal of Wildlife Management 87:e22329.

Holbrook, J. D., L. E. Olson, N. J. DeCesare, M. Hebblewhite, J. R. Squires, and R. Steenweg. 2019. Functional responses in habitat selection: clarifying hypotheses and interpretations. Ecological Applications 29:e01852.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638-649.

Hupp, J. W., and C. E. Braun. 1989. Topographic distribution of sage grouse foraging in winter. Journal of Wildlife Management 53:823-829.

Jackson, H. B., and L. Fahrig. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24:52-63.

Jarnevich, C. S., M. Talbert, J. Morisette, C. Aldridge, C. S. Brown, S. Kumar, D. Manier, C. Talbert, and T. Holcombe. 2017. Minimizing effects of methodological decisions on interpretation and prediction in species distribution studies: an example with background selection. Ecological Modelling 363:48-56.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70: 347-357.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997–2007. Pages 407-450 *in* B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. University of California Press, Berkeley, California, USA.

Jones, M. O., B. W. Allred, D. E. Naugle, J. D. Maestas, P. Donnelly, L. J. Metz, J. Karl, R. Smith, B. Bestelmeyer, and C. Boyd. 2018. Innovation in rangeland monitoring: annual, 30 m, plant functional type percent cover maps for US rangelands, 1984–2017. Ecosphere 9:e02430.

Kirol, C. P., J. L. Beck, S. V. Huzurbazar, M. J. Holloran, and S. N. Miller. 2015. Identifying greater sage-grouse source and sink habitats for conservation planning in an energy development landscape. Ecological Applications 25:968-990.

Kirol, C. P., K. T. Smith, N. E. Graf, J. B. Dinkins, C. W. LeBeau, T. L. Maechtle, A. L. Sutphin, and J. L. Beck. 2020. Greater sage-grouse response to the physical footprint of energy development. Journal of Wildlife Management 84:989-1001.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Kohl, M. T., T. A. Messmer, B. A. Crabb, M. R. Guttery, D. K. Dahlgren, R. T. Larsen, S. N. Frey, S. Liguori, and R. J. Baxter. 2019. The effects of electric power lines on the breeding ecology of greater sage-grouse. PloS ONE 14:e0209968.

Kormos, P. R., D. Marks, F. B. Pierson, C. J. Williams, S. P. Hardegree, S. Havens, A. Hedrick, J. D. Bates, and T. J. Svejcar. 2017. Ecosystem water availability in juniper versus sagebrush snow-dominated rangelands. Rangeland Ecology & Management 70:116-128.

Lazenby, K. D., P. S. Coates, S. T. O'Neil, M. T. Kohl, and D. K. Dahlgren. 2021. Nesting, brood rearing, and summer habitat selection by translocated greater sage-grouse in North Dakota, USA. Ecology and Evolution 11: 2741-2760.

LeBeau, C., K. Smith, S. Howlin, A. Tredennick, and K. Kosciuch. 2023. A meta-analysis investigating the effects of energy infrastructure proximity on grouse demography and space use. Wildlife Biology 2023:e01087.

LeBeau, C. W., G. D. Johnson, M. J. Holloran, J. L. Beck, R. M. Nielson, M. E. Kauffman, E. J. Rodemaker, and T. L. McDonald. 2017. Greater sage-grouse habitat selection, survival, and wind energy infrastructure. Journal of Wildlife Management 81:690-711.

LeBeau, C. W., K. T. Smith, M. J. Holloran, J. L. Beck, M. E. Kauffman, and G. D. Johnson. 2019. Greater sage-grouse habitat function relative to 230-kV transmission lines. Journal of Wildlife Management 83:1773-1786.

Lockyer, Z. B., P. S. Coates, M. L. Casazza, S. Espinosa, and D. J. Delehanty. 2015. Nest-site selection and reproductive success of greater sage-grouse in a fire-affected habitat of northwestern Nevada. Journal of Wildlife Management 79: 785-797.

Lucas, T. C. 2020. A translucent box: interpretable machine learning in ecology. Ecological Monographs 90:e01422.

Lundblad, C. G., C. A. Hagen, J. P. Donnelly, S. T. Vold, A. M. Moser, and S. P. Espinosa. 2022. Sensitivity to weather drives Great Basin mesic resources and greater sage-grouse productivity. Ecological Indicators 142:109231.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7: 145-165.

Manier, D. J., Z. H. Bowen, M. L. Brooks, M. L. Casazza, P. S. Coates, P. A. Deibert, S. E. Hanser, and D. H. Johnson. 2014. Conservation buffer distance estimates for greater sage-grouse: a review. U.S. Department of the Interior, U.S. Geological Survey, Reston, Virginia, USA.

Manly, B., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Springer, New York, New York, USA.

Matthiopoulos, J., J. R. Fieberg, and G. Aarts. 2020. Species-habitat associations: spatial data, predictive models, and ecological insights. University of Minnesota Libraries Publishing, Minneapolis, USA.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161-1175.

Meyer, C. B., and W. Thuiller. 2006. Accuracy of resource selection functions across spatial scales. Diversity and Distributions 12:288-297.

Muff, S., J. Signer, and J. Fieberg. 2020. Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects models using Bayesian or frequentist computation. Journal of Animal Ecology 89:80-92.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology 79:1435-1441.

Newton, R. E., J. D. Tack, J. C. Carlson, M. R. Matchett, P. J. Fargey, and D. E. Naugle. 2017. Longest sage-grouse migratory behavior sustained by intact pathways. Journal of Wildlife Management 81:962-972.

Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biological Conservation 143: 1623-1634.

Northrup, J. M., M. B. Hooten, C. R. Anderson Jr., and G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use–availability design. Ecology 94:1456-1463.

Northrup, J. M., E. Vander Wal, M. Bonar, J. Fieberg, M. P. Laforge, M. Leclerc, C. M. Prokopenko, and B. D. Gerber. 2022. Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. Ecological Applications 32:e02470.

O'Donnell, M. S., D. R. Edmunds, C. L. Aldridge, J. A. Heinrichs, A. P. Monroe, P. S. Coates, B. G. Prochazka, S. E. Hanser, and L. A. Wiechman. 2022. Defining biologically relevant and hierarchically nested population units to inform wildlife management. Ecology and Evolution 12:e9565.

O'Neil, S. T., P. S. Coates, B. E. Brussee, M. A. Ricca, S. P. Espinosa, S. C. Gardner, and D. J. Delehanty. 2020. Wildfire and the ecological niche: diminishing habitat suitability for an indicator species within semi-arid ecosystems. Global Change Biology 26:6296-6312.

Olsen, A. C., J. P. Severson, B. W. Allred, M. O. Jones, J. D. Maestas, D. E. Naugle, K. H. Yates, and C. A. Hagen. 2021. Reversing tree encroachment increases usable space for sage-grouse during the breeding season. Wildlife Society Bulletin 45:488-497.

Omernik, J. M., and G. E. Griffith. 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management 54:1249-1266.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137: S29-S49.

Orning, E. K. 2014. Effect of predator removal on greater sage-grouse (*Centrocercus urophasianus*) ecology in the Bighorn Basin conservation area of Wyoming. Thesis, Utah State University, Logan, USA.

Parsons, L., J. Jenks, T. Runia, and A. Gregory. 2022. Comparing methods of defining priority areas for greater sage-grouse. Frontiers in Ecology and Evolution 10:896023.

Parsons, L. A. 2019. Greater sage-grouse survival, breeding ecology, resource selection, and West Nile virus prevalence on the eastern fringe of their range (Chapter 5). Dissertation, South Dakota State University, Brookings, USA.

Patterson, R. L. 1952. The sage grouse in Wyoming. First edition. Sage Books for Wyoming Game and Fish Commission, Denver, Colorado, USA.

Pellant, M. 1990. The cheatgrass-wildfire cycle—are there any solutions. Pages 11–18 *in* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller, compilers. Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management. Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Ogden, Utah, USA.

Pérez-Hoyos, A., F. Rembold, H. Kerdiles, and J. Gallego. 2017. Comparison of global land cover datasets for cropland monitoring. Remote Sensing 9:1118.

Peterson, J. G. 1970. The food habits and summer distribution of juvenile sage grouse in central Montana. Journal of Wildlife Management 34:147-155.

Picardi, S., T. Messmer, B. Crabb, M. Kohl, D. Dahlgren, N. Frey, R. Larsen, and R. Baxter. 2020. Predicting greater sage-grouse habitat selection at the southern periphery of their range. Ecology and Evolution 10:13451-13463.

Pilliod, D. S., J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass–fire cycle in the Great Basin: precipitation timing and fine fuel composition predict wildfire trends. Ecology and Evolution 7:8126-8151.

Poessel, S. A., D. M. Barnard, C. Applestein, M. J. Germino, E. A. Ellsworth, D. Major, A. Moser, and T. E. Katzner. 2022. Greater sage-grouse respond positively to intensive post-fire restoration treatments. Ecology and Evolution 12:e8671.

Pratt, A. C. 2017. Partial migration, habitat selection, and the conservation of greater sage-grouse in the Bighorn Basin of Montana and Wyoming. Dissertation, University of Wyoming, Laramie, USA.

Pratt, A. C., and J. L. Beck. 2019. Greater sage-grouse response to bentonite mining. Journal of Wildlife Management 83:866-878.

Pratt, A. C., and J. L. Beck. 2021. Do greater sage-grouse exhibit maladaptive habitat selection? Ecosphere 12:e03354.

R Core Team. 2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rabon, J. C., P. S. Coates, M. A. Ricca, and T. N. Johnson. 2021. Does reproductive status influence habitat selection by female greater sage-grouse in a sagebrush-juniper landscape? Rangeland Ecology & Management 79:150-163.

Ricca, M. A., P. S. Coates, K. B. Gustafson, B. E. Brussee, J. C. Chambers, S. P. Espinosa, S. C. Gardner, S. Lisius, P. Ziegler, and D. J. Delehanty. 2018. A conservation planning tool for greater sage-grouse using indices of species distribution, resilience, and resistance. Ecological Applications 28:878-896.

Rice, M. B., A. D. Apa, M. L. Phillips, J. H. Gammonley, B. B. Petch, and K. Eichhoff. 2013. Analysis of regional species distribution models based on radio-telemetry datasets from multiple small-scale studies. Journal of Wildlife Management 77:821-831.

Rice, M. B., L. G. Rossi, and A. D. Apa. 2016. Seasonal habitat use by greater sage-grouse (*Centrocercus urophasianus*) on a landscape with low density oil and gas development. PloS ONE 11:e0165399.

Rigge, M. B. 2023. Rangeland condition monitoring assessment and projection, 1985–2021. U.S. Geological Survey, Earth Resources Observation and Science Center, Sioux Falls, South Dakota, USA.

Roth, C. L., S. T. O'Neil, P. S. Coates, M. A. Ricca, D. A. Pyke, C. L. Aldridge, J. A. Heinrichs, S. P. Espinosa, and D. J. Delehanty. 2022. Targeting sagebrush (*Artemisia* spp.) restoration following wildfire with greater sage-grouse (*Centrocercus urophasianus*) nest selection and survival models. Environmental Management 70:288-306.

Row, J. R., M. J. Holloran, and B. C. Fedy. 2022. Quantifying the temporal stability in seasonal habitat for sage-grouse using regression and ensemble tree approaches. Ecosphere 13:e4034.

Saher, D. J., M. S. O'Donnell, C. L. Aldridge, and J. A. Heinrichs. 2022. Balancing model generality and specificity in management-focused habitat selection models for Gunnison sage-grouse. Global Ecology and Conservation 35:e01935.

Sandford, C. P., M. T. Kohl, T. A. Messmer, D. K. Dahlgren, A. Cook, and B. R. Wing. 2017. Greater sage-grouse resource selection drives reproductive fitness under a conifer removal strategy. Rangeland Ecology & Management 70:59-67.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, and M. A. Hilliard. 2004. Distribution of sage-grouse in North America. Condor 106:363-376.

Schuyler, E. M., C. A. Hagen, C. R. Anthony, L. J. Foster, and K. M. Dugger. 2022. Temporal mismatch in space use by a sagebrush obligate species after large-scale wildfire. Ecosphere 13:e4179.

Severson, J. P., P. S. Coates, M. C. Milligan, S. T. O'Neil, M. A. Ricca, S. C. Abele, J. D. Boone, and M. L. Casazza. 2022. Moisture abundance and proximity mediate seasonal use of mesic areas and survival of greater sage-grouse broods. Ecological Solutions and Evidence 3:e12194.

Severson, J. P., C. A. Hagen, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017*a*. Effects of conifer expansion on greater sage-grouse nesting habitat selection. Journal of Wildlife Management 81:86-95.

Severson, J. P., C. A. Hagen, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017*b*. Short-term response of sage-grouse nesting to conifer removal in the northern Great Basin. Rangeland Ecology & Management 70:50-58.

Shirk, A. J., M. A. Schroeder, L. A. Robb, and S. A. Cushman. 2017. Persistence of greater sage-grouse in agricultural landscapes. Journal of Wildlife Management 81:905-918.

Shoemaker, K. T., L. J. Heffelfinger, N. J. Jackson, M. E. Blum, T. Wasley, and K. M. Stewart. 2018. A machine-learning approach for extending classical wildlife resource selection analyses. Ecology and Evolution 8:3556-3569.

Smith, I. T., S. J. Knetter, L. K. Svancara, J. W. Karl, T. R. Johnson, and J. L. Rachlow. 2021. Overlap between sagebrush habitat specialists differs among seasons: implications for umbrella species conservation. Rangeland Ecology & Management 78:142-154.

Smith, J. T., B. W. Allred, C. S. Boyd, J. C. Carlson, K. W. Davies, C. A. Hagen, D. E. Naugle, A. C. Olsen, and J. D. Tack. 2020. Are sage-grouse fine-scale specialists or shrub-steppe generalists? Journal of Wildlife Management 84:759-774.

Smith, J. T., B. W. Allred, C. S. Boyd, K. W. Davies, M. O. Jones, A. R. Kleinhesselink, J. D. Maestas, S. L. Morford, and D. E. Naugle. 2022. The elevational ascent and spread of exotic annual grass dominance in the Great Basin, USA. Diversity and Distributions 28:83-96.

Smith, K. T., J. L. Beck, and A. C. Pratt. 2016. Does Wyoming's core area policy protect winter habitats for greater sage-grouse? Environmental Management 58:585-596.

Smith, K. T., J. B. Dinkins, and J. L. Beck. 2019. Approaches to delineate greater sage-grouse winter concentration areas. Journal of Wildlife Management 83:1495-1507.

Smith, K. T., C. P. Kirol, J. L. Beck, and F. C. Blomquist. 2014. Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. Ecosphere 5:1-20.

Stevens, B. S., S. B. Roberts, C. J. Conway, and D. K. Englestead. 2023. Effects of large-scale disturbance on animal space use: functional responses by greater sage-grouse after megafire. Ecology and Evolution 13:e9933.

Stiver, S., E. Rinkes, D. Naugle, P. Makela, D. Nance, and J. Karl, editors. 2015. Sage-grouse habitat assessment framework: multiscale habitat assessment tool. Technical Reference 6710-1. Bureau of Land Management and Western Association of Fish and Wildlife Agencies, Denver, Colorado, USA.

Stonehouse, K. F., L. A. Shipley, J. Lowe, M. T. Atamian, M. E. Swanson, and M. A. Schroeder. 2015. Habitat selection and use by sympatric, translocated greater sage-grouse and Columbian sharp-tailed grouse. Journal of Wildlife Management 79:1308-1326.

Tarbox, B. C., N. D. Van Schmidt, J. E. Shyvers, D. J. Saher, J. A. Heinrichs, and C. L. Aldridge. 2022. Bridging the gap between spatial modeling and management of invasive annual grasses in the imperiled sagebrush biome. Rangeland Ecology & Management 82:104–115.

Taylor, J., and R. J. Tibshirani. 2015. Statistical learning and selective inference. Proceedings of the National Academy of Sciences 112:7629-7634.

Tibshirani, R. 1996. Regression shrinkage and selection via the lasso. Journal of the Royal Statistical Society Series B: Statistical Methodology 58:267-288.

Tredennick, A. T., G. Hooker, S. P. Ellner, and P. B. Adler. 2021. A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology 102:e03336.

Walker, B. L. 2022. Resource selection by greater sage-grouse varies by season and infrastructure type in a Colorado oil and gas field. Ecosphere 13:e4018.

Walker, B. L., A. D. Apa, and K. Eichhoff. 2016. Mapping and prioritizing seasonal habitats for greater sage-grouse in Northwestern Colorado. Journal of Wildlife Management 80:63-77.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644-2654.

Walker, B. L., M. A. Neubaum, S. R. Goforth, and M. M. Flenner. 2020. Quantifying habitat loss and modification from recent expansion of energy infrastructure in an isolated, peripheral greater sage-grouse population. Journal of Environmental Management 255:109819.

Wallestad, R., and R. L. Eng. 1975. Foods of adult sage grouse in central Montana. Journal of Wildlife Management 39: 628-630.

Wanner, C. P. 2022. Validation of winter concentration area guidelines and winter habitat ecology for greater sage-grouse in the Red Desert, Wyoming. Thesis, University of Wyoming, Laramie, USA.

Warton, D. I., and L. C. Shepherd. 2010. Poisson point process models solve the" pseudo-absence problem" for presence-only data in ecology. Annals of Applied Statistics 4:1383-1402.

Wayment, H. P. 2022. Greater sage-grouse brood responses to livestock grazing in sagebrush rangelands. Thesis, Utah State University, Logan, USA.

West, N. E., and J. A. Young. 2000. Intermountain valleys and lower mountain slopes. North American Terrestrial Vegetation 2:255-284.

Westover, M., J. Baxter, R. Baxter, C. Day, R. Jensen, S. Petersen, and R. Larsen. 2016. Assessing greater sage-grouse selection of brood-rearing habitat using remotely-sensed imagery: can readily available high-resolution imagery be used to identify brood-rearing habitat across a broad landscape? PloS ONE 11:e0156290.

Wheatley, M., and C. Johnson. 2009. Factors limiting our understanding of ecological scale. Ecological Complexity 6: 150-159.

Wiken, E., F. J. Nava, and G. Griffith. 2011. North American terrestrial ecoregions—level III. Commission for Environmental Cooperation, Montreal, Canada.

Wood, J. A. 2019. The effects of dixie harrow treatments on greater sage-grouse resource selection and the nutritional value of sagebrush during winter. Thesis, Brigham Young University, Provo, Utah, USA.

Yates, K. L., P. J. Bouchet, M. J. Caley, K. Mengersen, C. F. Randin, S. Parnell, A. H. Fielding, A. J. Bamford, S. Ban, and A. M. Barbosa. 2018. Outstanding challenges in the transferability of ecological models. Trends in Ecology & Evolution 33:790-802.

Yost, A. C., S. L. Petersen, M. Gregg, and R. Miller. 2008. Predictive modeling and mapping sage grouse (*Centrocercus urophasianus*) nesting habitat using Maximum Entropy and a long-term dataset from Southern Oregon. Ecological Informatics 3:375-386.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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