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Importance of regional variation in conservation planning: a rangewide example of the Greater Sage-Grouse

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Abstract. We developed rangewide population and habitat models for Greater Sage-Grouse (*Centrocercus urophasianus*) that account for regional variation in habitat selection and relative densities of birds for use in conservation planning and risk assessments. We developed a probabilistic model of occupied breeding habitat by statistically linking habitat characteristics within 4 miles of an occupied lek using a nonlinear machine learning technique (Random Forests). Habitat characteristics used were quantified in GIS and represent standard abiotic and biotic variables related to sage-grouse biology. Statistical model fit was high (mean correctly classified = 82.0%, range = 75.4–88.0%) as were cross-validation statistics (mean = 80.9%, range = 75.1–85.8%). We also developed a spatially explicit model to quantify the relative density of breeding birds across each Greater Sage-Grouse management zone. The models demonstrate distinct clustering of relative abundance of sage-grouse populations across all management zones. On average, approximately half of the breeding population is predicted to be within 10% of the occupied range. We also found that 80% of sage-grouse populations were contained in 25–34% of the occupied range within each management zone. Our rangewide population and habitat models account for regional variation in habitat selection and the relative densities of birds, and thus, they can serve as a consistent and common currency to assess how sage-grouse habitat and populations overlap with conservation actions or threats over the entire sage-grouse range. We also quantified differences in functional habitat responses and disturbance thresholds across the Western Association of Fish and Wildlife Agencies (WAFWA) management zones using statistical relationships identified during habitat modeling. Even for a species as specialized as Greater Sage-Grouse, our results show that ecological context matters in both the strength of habitat selection (i.e., functional response curves) and response to disturbance.

Key words: breeding habitat; conservation planning; ecological variation; function habitat response; Greater Sage-Grouse; landscape context; population index; resource selection function; spatial modeling; thresholds.

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INTRODUCTION

In an increasingly anthropogenic world where funding for conservation activities is limited, effective landscape-scale conservation planning tools have been progressively embraced by resource management agencies to both maximize conservation investments and reduce impacts of anthropogenic disturbances. This has corresponded with rapid expansion of landscape-scale, spatially explicit models of species habitat, such as resource selection functions (RSF) (Boyce and McDonald 1999, Johnson et al. 2006, 2013), which simultaneously give insight into the ecology of species and can be used to produce maps to help guide where conservation actions should be most effective. Often, RSF models do not encompass the entire range of a focal species, and therefore, biological relationships are extrapolated to novel areas, not included in the development of the RSF models, when decisions must be made. Extrapolating known relationships often represents the best available information to decision makers, but should be done with caution because the accuracy of extrapolated models relies on similar habitat availability in the novel area (Mladenoff et al. 1999, Aarts et al. 2008).

A species response to particular habitat components can change as a function of the prevalence of the resource, which is referred to as the functional response of a species (Mysterud and Ims 1998). Understanding functional responses related to habitat selection through RSF modeling can elucidate threshold values for habitat quantity and quality, tolerance to perturbations, and cumulative effects (Rhodes et al. 2008). Understanding functional responses is important as conservation plans generally require targets for the amount of habitat required for specific species in order for managers to make cost-effective decisions and balance competing interests (Carwardine et al. 2008). Unfortunately, setting conservation targets based upon thresholds defined for other regions is precarious (Rhodes et al. 2008) because thresholds can vary tremendously across species and landscapes (van der Hoek et al. 2015). Landscape-scale modeling across broad extents is important in understanding how functional responses may vary for wide-ranging species, as landscapes are seldom homogeneous across large extents.

Data on the abundance of individuals are rare for most taxa, yet if available, they can provide baseline data for monitoring populations and conservation actions (Sagarin et al. 2006). Abundance is often clustered across the range of a species, typically being high in relatively few sites and low in the majority (Murphy et al. 2006). Knowledge and mapping of population centers or "hotspots" can be critically important for conservation planning as many species with broad distributions occur in densities of several orders of magnitude higher in hotspots compared with occupied habitats outside of hotspot boundaries (Brown et al. 1995). Locations of population centers of many species can be stable over several decades even while population sizes fluctuate (Brown et al. 1995). Consequently, habitat protection can affect drastically different proportions of target populations depending on overlap with population centers.

Ideally, conservation planning makes the best use of information related to population abundance and habitat requirements while accounting for regional gradients and differences in functional responses. When broad-scale population survey data exist, probabilistic surfaces of density indices and habitat selection indices can be integrated to create analytical tools across broad spatial scales (Coates et al. 2015). This type of integrative methodology can create composite, spatially explicit indices that reflect demographic and habitat information and make predictions to guide landscape-level conservation actions. Unfortunately, such data are rare in conservation planning because the broad-scale population surveys are lacking for many species and habitat modeling, by necessity, is often conducted at scales smaller than a species range.

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a wide-ranging species of conservation concern that occurs throughout the sagebrush ecosystem in the Intermountain West of the United States (Schroeder et al. 2004: see Figure 1). Sage-grouse occupy approximately one-half of their historical distribution, and populations have declined concomitantly with the loss of sagebrush since pre-European settlement of the West (Schroeder et al. 2004). Currently, sage-grouse are considered "not-warranted" for listing under the United States Endangered Species Act of 1973 (ESA; U.S. Fish and Wildlife Service [USFWS] 2015), with a 5-year review to the decision scheduled for September 2020. Because of the wide-reaching implications of an ESA listing on western lands within North America, monitoring sage-grouse populations is imperative to help inform land and wildlife management agencies responsible for regulatory actions and policies. Lek sites (traditional breeding grounds) provide opportunity to count sage-grouse annually and monitor population response. Leks are typically located in nesting habitat where males are most likely to encounter females for breeding opportunities (Gibson and Langen 1996), and several studies support this hypothesis for both

Greater Prairie chickens (*Tympanuchus cupido*) and sage-grouse (Schroeder and White 1993, Gibson 1996*b*, Holloran and Anderson 2005, Doherty et al. 2010*b*, 2011, Coates et al. 2013). Although sage-grouse leks have been counted each year since the 1950s, wildlife agencies have drastically increased their efforts in surveying known leks and searching for new lek sites since the mid-1990s, with almost exponential increases in survey effort during the last decade (WAFWA 2015). Broad-scale sage-grouse lek survey data managed by each state with sage-grouse provide a unique opportunity to identify sources of temporal and spatial variation in functional responses across the entire range of a species that inhabits most of the western United States. Furthermore, findings from such analysis could be used to target thresholds for conservation planning activities for a species of increasingly high conservation concern.

Knowledge of high-abundance population centers for priority species represents a starting point to frame regional conservation initiatives and can direct management actions to landscapes where they will have the largest benefit to regional populations (Sanderson et al. 2002, Groves 2003). We developed a model to quantify the relative density of breeding birds within each sage-grouse management zone. This was motivated by past work across the range that showed sage-grouse populations are highly clustered (Connelly et al. 2004, Stiver et al. 2006, Doherty et al. 2011). Fortunately, sage-grouse are one of the few species in which extensive data sets exist on distribution and relative abundance across their entire breeding distribution, making an analysis of this scale possible (Connelly et al. 2004, Schroeder et al. 2004). We had two primary objectives within this study: (1) To develop rangewide habitat and population models that identify regional variation in habitat selection and relative densities of sage-grouse for use in conservation planning and risk assessments and (2) to assess the importance of variability in habitat selection and thresholds of disturbance and to identify differences in functional responses across the range of sage-grouse.

STUDY AREA

Our study area includes the entire range of North American sage-grouse populations with the exception of six active leks located in Canada (Fig. 1). Canadian leks were not included in our modeling because of significant differences in available spatial data between the United States and Canada. Loss and degradation of native vegetation have affected much of the sagebrush (*Artemisia* spp.) ecosystem in western North America, and this ecosystem has become increasingly fragmented because of conifer encroachment, exotic annual grass invasion, and anthropogenic development (Knick et al. 2003). The Western Association of Fish and Wildlife Agencies (WAFWA) Conservation Strategy for Greater Sage-Grouse (Stiver et al. 2006) delineated seven sage-grouse management zones to guide conservation and management (Table 1). The boundaries of these management zones were delineated based on differences in ecological and biological attributes (i.e., floristic provinces) rather than on arbitrary political boundaries (Stiver et al. 2006) (Fig. 1). Maps representing the major ecological gradients and subsequent dominant land cover types are shown in Appendix S1. We stratified our analyses by sage-grouse management zones because spatial partitioning of data improves model fit where regional niche variation occurs (Murphy and Lovett-Doust 2007) because of fundamental differences in the ecological gradients and different functional responses at regional scales.

METHODS

Breeding habitat model

We developed a binomial probabilistic model of occupied breeding habitat by quantifying habitat characteristics, within 6.4 km (4 miles) of both occupied sage-grouse leks and pseudoabsence points using a classification instance of the nonparametric model Random Forests (Cutler et al. 2007, Olden et al. 2008, Evans et al. 2011, Baruch-Mordo et al. 2013). Model predictions produce an estimated probability of sage-grouse lek occurrence for each 120 × 120 m grid cell within each sage-grouse management zone. Components of sage-grouse habitat were compiled into a GIS database from various sources, but generally represent standard abiotic and biotic variables used in past work to represent sage-grouse habitat (Table 2). Sage-grouse habitat use has been investigated extensively across

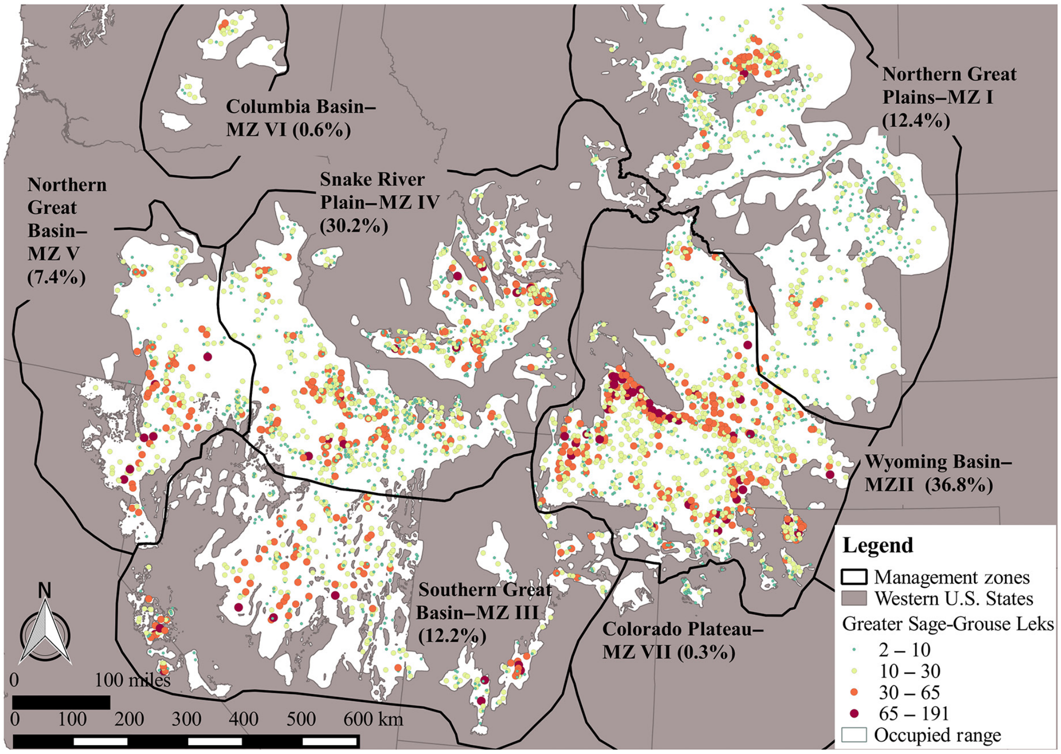

Fig. 1. Location of Greater Sage-Grouse management zones used to spatially subset analyses and the location of active Greater Sage-Grouse leks counted during 2010–2014. Percentages are derived from the sum of the mean peak count of displaying sage-grouse at individual leks during 2010–2014 within each management zone divided by the rangewide total, to give context to the amount of known populations within each management zone.

the range. For brevity, we provide the justification for variables, predicted relationships, and relevant citations in table format, rather than extensive in-text descriptions (Table 2).

Lek survey data

We compared active lek locations with pseudoabsence locations to generate models of predicted breeding sage-grouse habitat across the range. The hotspot hypothesis of lek evolution suggests that leks are typically located in close proximity to nesting habitat where males will most likely encounter prenesting females who are attracted by important habitat features (Schroeder and White 1993, Gibson 1996*a*), such as forbs required for prebreeding (Barnett and Crawford 1994) and sagebrush cover for nesting (Connelly et al. 2000). Additionally, 79–95% of sage-grouse nesting locations are located within 6.4 km of a lek (Holloran and Anderson 2005, Doherty et al. 2011, Coates et al. 2013). Further, recent studies have shown that telemetry-based models of nesting sage-grouse predicted almost two times more nesting habitat around leks than at random locations (Doherty et al. 2010*b*, Fedy et al. 2014). We therefore believe that sage-grouse lek locations are a good predictor of important breeding areas. We used lek data assembled and proofed by WAFWA to develop both our breeding habitat model and breeding population index model. For the purposes of both models, a lek was defined as active if greater than two males were counted during a single counting visit during 2010–2014 and the last count was not a zero.

Pseudoabsence data

Recent lek survey efforts have been intensive enough that although not all leks have been identified, we are confident that the spatial processes governing lek locations and sage-grouse abundance were well represented in the data. To generate pseudoabsence (i.e., background) locations, we

Table 1. Ecological descriptions of Western Association of Fish and Wildlife Agencies Greater Sage-Grouse Management Zones.

Zone	Description
Northern Great Plains (MZ I)	The Northern Great Plains includes the northeastern portions of the sage-grouse range. This management zone experiences the most precipitation, and thus, it contains larger portions of the landscape dominated by grasslands, smaller patches of sagebrush, and more silver sagebrush (Artemisia cana var. cana) than other management zones. MZ I also has the highest amount of land in private ownership, and compared with other management zones, it has the highest amount of cropland
Wyoming Basin (MZ II)	The Wyoming Basin is characterized by large expanses of Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*) with little fragmentation; however, it experiences the greatest amount of oil and gas development. Most of the precipitation in this management zone comes in the form of winter snowfall. MZ II contains the highest densities of sage-grouse across their range
Southern Great Basin (MZ III)	The Southern Great Basin includes the southern- and westernmost populations of sage-grouse. MZ III is the most arid of all the management zones and includes a mix of Wyoming big sagebrush, mountain big sagebrush (*A. tridentata* var. *vaseyana*), low sagebrush (*A. arbuscula*), and black sagebrush (*A. nova*). Topography is rugged with sagebrush on many of the valley floors transitioning to arid coniferous forests at higher elevations on the mountain slopes
Snake River Plain (MZ IV)	The Snake River Plain encompasses the north-central populations of sage-grouse. Like MZ III and MZ V, it is characterized by salt deserts in the lower elevations and conifer forests at higher elevations. Wyoming big sagebrush and basin big sagebrush (*A. tridentata* var. *tridentata*) are the dominant species, with mountain big sagebrush at higher elevations. MZ IV contains the second highest density of sage-grouse across the species range. The Snake River Plains management zone also experiences dense cropland areas; however, they are clustered at lower elevations
Northern Great Basin (MZ V)	The Northern Great Basin is similar to the Southern Great Basin, but it is less arid with precipitation occurring primarily in the winter and spring. Similar to MZ III and MZ IV, lower elevations are dominated by salt deserts and higher elevations are dominated by conifer forest
Columbia Basin (MZ VI)	The Colombia Basin is isolated from the rest of the sage-grouse range and is contained entirely within Washington state. Wyoming big sagebrush and basin big sagebrush are predominate species. MZ VI contains the lowest elevation sagebrush across the range and experiences high amounts of cropland in comparison with all other management zones with the exception of the Northern Great Plains
Colorado Plateau (MZ VII)	The Colorado Plateau is the southeastern-most management zone and contains a small fraction of the overall sage-grouse populations. It is similar to the Southern Great Basin MZ, but it receives more precipitation. Soil types within the Colorado Plateau greatly restrict the sagebrush distribution, and it contains a very small portion of the overall occupied habitat

Notes: Descriptions of management zones were originally summarized (Miller and Eddleman 2001) and adapted by WAFWA for analyses for both the 2004 Conservation Assessment of Greater Sage-Grouse and Sagebrush Habitats (Connelly et al. 2004) and 2006 Greater Sage-Grouse Comprehensive Conservation Strategy (Stiver et al. 2006). We created maps of the ecological gradients and major land cover types between Greater Sage-Grouse management zones for further reference in Appendix S1. Maps focused on the major ecological gradients and subsequent land cover (Figs. 3–9).

modeled the spatial process of known leks, using an isotropic kernel estimate (Diggle 1985), and used the inverse of the density estimate to weight samples. A gradient function allowed for a tension parameter to control the proximity of pseudoabsence locations in relation to known lek locations. We utilized the pseudoabsence model available in the spatialEco library (Evans 2015) and defined the sigma (distance smoothing for the kernel; bandwidth) as 18 km and the gradient as 1, thus providing no weighting to the pseudoabsence diffusion process. This ensured that we were sampling the range of habitat variation within each sage-grouse management zone. To avoid class imbalance (Evans and Cushman 2009) (i.e., zero inflation) issues, we generated an equal ratio of pseudoabsence to lek locations and compared resulting sample variation against population data (rasters) to evaluate whether we had an adequate sample to support model fit, spatial estimation, and inference. We chose an 18-km bandwidth because recent research has shown that this scale represents the scale at which breeding populations move across the landscape to fulfill other seasonal habitat needs (Fedy et al. 2012) and because we specifically designed our study to capture large first-order habitat selection. To accurately define first-order sage-grouse habitat availability extents, we matched the spatial scale of availability to the desired scale of inference because matching such scales is critical to obtaining reliable estimates on selection behavior (Northrup et al. 2013).

Statistical model

Nonparametric methods are becoming much more common in ecological modeling, supporting

Table 2. Description of explanatory variables used to predict the occupied Greater Sage-Grouse breeding habitat across 11 western U.S. States during 2010–2014.

Name	Source (years)	Native pixel (m)	Resampled pixel (m)	Description†	Justification (references)
General habitat predictor group					
Low sagebrush	LANDFIRE EVT 1.2 (2010)‡	30 × 30	120 × 120	% of grid cells classified as low sagebrush	Established positive relationship between sage-grouse abundance and sagebrush (Patterson 1952)
Tall sagebrush	LANDFIRE EVT 1.2 (2010)‡	30 × 30	120 × 120	% of grid cells classified as tall sagebrush	Established positive relationship between sage-grouse abundance and sagebrush (Patterson 1952)
All sagebrush	LANDFIRE EVT 1.2 (2010)‡	30 × 30	120 × 120	% of grid cells classified as all sagebrush	Established positive relationship between sage-grouse abundance and sagebrush (Patterson 1952)
Canopy cover	LANDFIRE Fuels 1.2 (2010)	30 × 30	120 × 120	% canopy cover in 10% increments from 15% to 95%	Established negative relationship between sage-grouse and conifers (Doherty et al. 2008, Baruch-Mordo et al. 2013, Fedy et al. 2014)
Grassland/herbaceous	LANDFIRE Fuels 1.2 (2010)	30 × 30	120 × 120	% of grid cells classified as grassland	Established negative relationship between sage-grouse abundance and grasslands (Patterson 1952)
Perennial water	National Hydrological Dataset NHD (2012)	Vector of Lines and Polygons	120 × 120	NHD perennial flow lines within a 6440-m moving window, multiplied by the average line length per cell (133.2 m)	Established negative relationship of riparian areas with nest site selection (Crawford et al. 2004) and established positive relationship between sage-grouse populations and riparian habitats (Blomberg et al. 2014)
Intermittent water	NHD (2012)	Vector of Lines and Polygons	120 × 120	See perennial water	See perennial water
Springs and seeps	NHD (2012)	Vector of Lines and Polygons	120 × 120	See perennial water	See perennial water
Topographic wetness index	NHD (2012) and NED elevation Data (2013)	30 × 30	120 × 120	Index of wetness	See perennial water
Climatic data predictor group§					
Gross primary production	MODIS NASA EODP (2009–2013)	1 × 1 km	120 × 120	Index of early brood-rearing habitat (mean of GPP from 5–15 through 6–15)	Forbs are important predictors of early brood survival and habitat selection (Crawford et al. 2004)
Degree days > 5°C	USFS (1961–1990) (Rehfeldt et al. 2006)	1 × 1 km	120 × 120	The number of days that reach a temperature ≥5°C	Large-scale ecological driver of land types. Hypothesized regional-scale relationship between sagebrush landscapes with higher production. Documented carryover effects (Blomberg et al. 2014)
Mean annual precipitation	USFS (1961–1990) (Rehfeldt et al. 2006)	1 × 1 km	120 × 120	Mean annual precipitation (mm)	Large-scale ecological driver of land types. Hypothesized regional-scale relationship between sagebrush landscapes with higher production. Documented carryover effects (Blomberg et al. 2014)
Annual drought index	USFS (1961–1990) (Rehfeldt et al. 2006)	1 × 1 km	120 × 120	Ratio = dd5/map	Large-scale ecological driver of land types. Hypothesized regional-scale relationship between sagebrush landscapes with higher production. Documented carryover effects (Blomberg et al. 2014)

Table 2. Continued.

Name	Source (years)	Native pixel (m)	Resampled pixel (m)	Description†	Justification (references)
Landform variables predictor group					
Roughness	National Elevation Data NED (2013)	30 × 30	120 × 120	SD in elevation within a 6440-m buffer of a grid cell	Established negative relationship between sage-grouse and rough terrain (Doherty et al. 2008, Fedy et al. 2014)
Elevation	NED (2013)	30 × 30	120 × 120	Average elevation within a 6440-m buffer of the grid cell	Hypothesized relationship between grouse populations and areas with higher productivity because of elevation
Steep	NED (2013)	30 × 30	120 × 120	% of landscape classified as steep using Theobald LCAP tool	Established negative relationship between sage-grouse and rough terrain (Doherty et al. 2008, Fedy et al. 2014)
Disturbance variables predictor group					
Human disturbance index	NLCD Disturbed Classes¶ (2011)	30 × 30	120 × 120	Land cover types associated with human presence	Established negative relationship between sage-grouse and human activity (Tack 2009, Naugle et al. 2011*a*)
Oil and gas wells	IHS oil and gas database (1920’s–2014)	Point	120 × 120	Density of oil and gas well locations†	Established negative relationship between sage-grouse and oil and gas development (Naugle et al. 2011*b*, Gregory and Beck 2014)
Burned landscapes	WFDSS-GeoMac Fire Perimeters (2000–2008, 2009–2013, 1984–2013)	Vector of Polygons	120 × 120	Proportion of grid cells that are burned within a 6440-m area	Established negative relationship between fire and sagebrush habitat (Nelle et al. 2000, Hess and Beck 2012)
Agriculture lands	NASS (2008–2014)	30 × 30	120 × 120	Proportion of grid cells that have been tilled since 2008 within a 6440-m area	Established negative relationship between sage-grouse and cropland (Knick et al. 2013, Fedy et al. 2014)

Note: All variables with the exception of the climate date predictor group were quantified using a 6.4-km buffer moving window (130.1 km^2).

† All variables were resampled to a 120 × 120 m pixel. All moving windows were calculated at a 6440-m (4-mile) buffer. Oil and gas layers were also calculated at a 2-mile moving window because of variations in the distance the impact was detected (Naugle et al. 2011*a*). We did not use the 120 × 120 m pixels for modeling because leks are a surrogate of habitat at a larger scale.

‡ Landfire vegetation groupings defined in Johnson et al. (2011) SAB.

§ Because climate grids of native resolution change at a 1-km scale and are highly spatially correlated, we did not resample the grids using a 6440-m moving window.

¶ NLCD urban development classes: developed, high intensity; developed low intensity; developed medium intensity; developed, open space; and NLCD impervious surfaces. The index also included roads (TIGER), oil and gas wells (compiled by each state), wind turbines (FCC obstruction database), transmission lines (Ventyx), and pipelines (Ventyx).

inference of nonlinear and spatial dynamics (Cutler et al. 2007, Olden et al. 2008, Evans et al. 2011, Baruch-Mordo et al. 2013). Random Forests uses multiple realizations of the data, with no distributional assumptions, that effectively converge on a stable estimate in very high-dimensional statistical spaces (Murphy et al. 2010, Evans et al. 2011). Model interpretation and inference were supported following the methods presented in Cutler et al. (2007), Murphy et al. (2010), and Evans et al. (2011). The expected complexity in interaction effects, potential latent variables, high spatial variability representing both global and local effects, and nonlinear relationships all support a nonlinear model such as Random Forests as an appropriate choice.

We modeled selection of breeding season habitat within the species range (Johnson 1980, Meyer and Thuiller 2006) using Random Forests, which is a bootstrapped classification and regression tree (CART) approach (Hastie et al. 2008). Random Forests is based on the principle of weak learning, where a set of weak subsample models converge on a stable global model. This method has been shown to provide stable estimates while being robust to many of the issues associated with spatial data (Cutler et al. 2007, Evans et al. 2011) such as autocorrelation and nonstationarity (i.e., nonconstant mean and variance). It also fits complex, nonlinear relationships, accounts for high-dimensional interaction effects, and accounts for hierarchically structured data inherent in nonstationary processes (Cutler et al. 2007, Evans et al. 2011). We expected both global trends in sage-grouse habitat selection and localized variation in habitat selection within each of the seven sage-grouse management zones. First- and second-order variations are addressed in the hierarchical nature of the iterative node partitioning, making this a good model to implement when global trend and local variations (Cressie 1991) are expected to occur in the same model (Evans et al. 2011). Analysis was conducted in program R (R Core Team 2012) using the rgdal (Bivand et al. 2013), sp (Bivand et al. 2008), and raster (Hijmans and Etten 2013) libraries to read spatial data, assign values from spatial covariates to the point observations of our dependent variable, and make spatial predictions. We used the implementation of Random Forests (Breiman 2001) in the R library Random Forest (Liaw and Wiener 2002) and followed the model selection method introduced in Murphy et al. (2010) using the rfUtilities library (Evans and Murphy 2014). Parsimony in Random Forests is important not only for producing a more interpretable model but also for reducing any fitting of the model to statistical noise, thus providing a better model fit (Murphy et al. 2010, Evans et al. 2011).

Evaluation of model fit and spatial predictions

To assess model fit, we used OOB (out-of-bag) error and confusion matrixes (Liaw and Wiener 2002). The OOB error represents the internal evaluation of global and class error against the withheld data from the bootstrap and represents an error distribution across all bootstrap replicates in the ensemble where the median error is used to represent the OOB error. We evaluated model stability and performance using cross-validation methods (Evans et al. 2011), where 10% of data were withheld from training the model and used as a validation data set. Overfitting was assessed by comparing error rates between OOB and cross-validation.

We also tested the sensitivity of the fitted model to errors in classification between used vs. available locations in the rfUtilities library (Evans and Murphy 2014) by randomly changing known lek locations to pseudoabsence points and evaluating cross-classification errors. We systematically changed known lek locations to zeros in 5% increments to understand the influence of pseudoabsence errors on overall error rates and model stability. This was performed because an unknown portion of our pseudoabsence locations were expected to fall within suitable sage-grouse breeding habitat. The primary motivation behind implementing a sensitivity test was to address model sensitivity to any lack of independence. A pseudoreplication problem would also affect the independence (correlation) of the bootstraps and potentially overfit the model. Because ensemble models are based on the premise of weak learning and variation in the bootstrap, if the data are homogenous, the bootstraps would not be independent and the ensemble would exhibit considerable correlation and effectively overfit the model. In evaluating model fit and convergence, we did not observe any indication of ensemble correlation. The sensitivity test allowed better understanding of overall error rates within our model, and more importantly, it allowed the assessment of model stability and prediction congruency across a range of lek locations that are misclassified as pseudoabsence.

Regional variation in habitat selection and disturbance thresholds

We used probability partial plots to elucidate habitat relationships of the modeled covariates after partialing out (holding constant) the other variables in the model. To improve interpretability, we plotted each given covariate for all management zones on the same plot. The probability partial plots were derived using the rfUtilities library (Evans and Murphy 2014).

Management zone VII

Management zone VII, while modeled, has a very small sample size (~0.3% of counted birds between 2010 and 2014) and only contains

652 km^2 of the 192,381 km^2 modeled breeding habitat (Table 5). Therefore, we did not focus on these results in the general manuscript or include MZ VII in figures highlighting functional habitat responses.

Breeding population index model

To map high-abundance population centers, we followed the methods and logic very similar to the models developed by the U.S. Geological Survey (USGS) for the Bi-State Distinct Population Segment of sage-grouse (Coates et al. 2015). Distribution models that combine information about habitat quality and abundance of sage-grouse from multiple data sources are valuable given recent intensification of sage-grouse management and policymaking (Coates et al. 2015). We modified their methods (Coates et al. 2015) to better represent a sage-grouse population index, because their original technique was developed to highlight management priority areas. Our final population index model incorporated two standardized kernel-based point density models, representing local and regional scales and our breeding habitat model described earlier. The results of our models are grids that represent an index to the relative amount of breeding birds for each 120 × 120 m area within each management zone. Our final population index model incorporates spatial patterns of sage-grouse habitat selection with contemporary information of abundance allowing the use of the available data, as proxies for management (Stephens et al. 2015). Population indices, such as ours, allow conservation actions to be targeted to the right landscapes, and help identify threats to a species that are occurring in areas that could impact large proportions of sage-grouse populations.

Kernel density function.—Kernel density functions have been commonly used in ecology to delineate home ranges of individual animals and to map concentrated areas of use by populations (Silverman 1986, Worton 1989). Within our study, we used the kernel density function to group cells of concentrated use by attributing count data to a grid placed over top of a sage-grouse management zone (Silverman 1986, Worton 1989). Using kernels to define population concentrations is consistent with past work defining core areas for sage-grouse (Doherty et al. 2011). We created two kernel models based on two separate bandwidth values (i.e., 6.4 and 18 km), which reflect published information on sage-grouse movement and seasonal space-use patterns. The 6.4-km bandwidth was chosen to correspond with utilization distribution of areas conducive for reproduction in relation to lek sites (e.g., breeding, nesting, brood-rearing), as demonstrated in populations at multiple sites (Holloran and Anderson 2005, Doherty et al. 2011, Coates et al. 2013). Although leking areas generally serve as hubs for nesting and are usually centered across seasonal areas (Coates et al. 2013), some sage-grouse move relatively long distances to access wintering areas (Fedy et al. 2012, Coates et al. 2013). Thus, we incorporated the larger spatial scale of 18 km to reflect these life history patterns (Fedy et al. 2012). Combining the scales appropriately placed greater emphasis on adjacent areas, thus preventing oversmoothing, but still allowed for the representation of sage-grouse occurrence at further distances. We used SAGA-GIS version 2.1.0 (SAGA-GIS 2015) to create two Gaussian kernel density functions. The same set of active lek locations from our habitat model defined the point density for our kernel models, and each point was weighted by the mean peak count of displaying sage-grouse from 2010 to 2014. Following the logic of Coates et al. (2014), we standardized each kernel using a row standardization. We then added each grid together and divided by 2, using the raster library (Hijmans and Etten 2013) in R. The output is a 120 × 120 m raster that represents a multiscale density process of sage-grouse lek counts across two biologically meaningful scales (Eq. 1).

$$\text{Kernel Index} = (\text{standardized 6.4-km kernel} + \text{standardized 18-km kernel})/2 \tag{1}$$

Population index.—Our Kernel Index summarizes the best available information on the relative density of birds across the entire sage-grouse range. We selected bandwidths to correspond with linear movement distance of sage-grouse within the breeding season (Doherty et al. 2011), as well as movements between breeding and other seasonal habitats (Fedy et al. 2012). We believe that the combination of both kernels into a single Kernel Index represents ecologically meaningful areas for sage-grouse. However, kernel functions are inherently an estimator of the spatial point density process, and thus, they are not explicitly linked to habitat features.

We wanted to create a population index to further refine our Kernel Index. First, we wanted a method that would reduce the importance of lands with low probabilities of being habitat based upon known sage-grouse habitat relationships. Secondly, we wanted to increase the value of lands with high probabilities of being occupied habitat, but further away from known leks, thus having lower value in the Kernel Index. We did this by multiplying the Kernel Index by the probability of our breeding habitat model (Eq. 2).

$$\text{Population index} = (\text{Kernel Index} \times \text{breeding habitat model}) \quad (2)$$

Highest population index values arise where high breeding habitat probabilities co-occur with landscapes having higher lek counts. The use of this equation also effectively reduces the value of landscapes near larger sage-grouse leks, which are effectively nonhabitat based upon the prediction of the breeding habitat model. Lastly, multiplying the Kernel Index by the breeding habitat model increases the value of lands further from known sage-grouse leks that have high probabilities of containing breeding sage-grouse. We thought that this was important because our data set utilized all known sage-grouse population survey data across their range; however, our survey data do not represent all leks.

Aggregation using population index volumes

We ordered all population index values from each grid cell within a management zone from the highest to lowest density. We selected the highest density cells in order until they summed to 10% of the total population index within a management zone. We repeated the selection process in 10% increments selecting the highest remaining grid cell densities first until we had 10 bins (i.e., highest density bin represented the top 10% of the population, 100% bin representing all breeding areas identified in modeling). Results are cumulative, such that all bins contain all preceding bins of 10% increments. We then calculated the percentage of the occupied distribution within each incremental 10% population bin.

RESULTS

Breeding habitat model

On average, our breeding habitat model correctly classified 82.0% (range: 75.4–88.0%) of hold-out data from OOB samples (Table 3). Our models also correctly classified independent *K*-fold hold-out data (mean across management zones = 80.9%; range: 75.0–85.8%) (Table 3). General agreement between OOB error rates and *K*-fold cross-validation indicates stability in our model to predict independent data and lack of overfitting (Table 3). We documented higher error rates within pseudoabsence classes compared with our active lek class (Table 4); however, simulations indicated that estimates were stable across a wide range of pseudoabsence errors (0–30% simulated errors in 5% increments). For example, the mean SE across the seven management zones with 20% simulated pseudoabsence errors is 0.032. Low SE indicates model stability and the ability of the Random Forests to predict through statistical noise arising from points that were modeled as absences, which in fact supports lek formation (i.e., false absence). We documented a ~3% error increase for every 5% increase in false absences.

Table 3. Percentage of *K*-fold cross-validation hold-out data set locations (10%) that were correctly classified by a model built with 90% of the data set.

Management zone	1—out-of-bag error	*K*-fold cross-validation % correctly classified
MZ I—Northern Great Plains	76.3	75.9
MZ II—Wyoming Basin	75.4	75.0
MZ III—Southern Great Basin	85.9	85.3
MZ IV—Snake River Plain	83.9	83.6
MZ V—Northern Great Basin	76.3	75.1
MZ VI—Columbia Basin	88.0	85.8
MZ VII—Colorado Plateau	88.0	85.4
Average	82.0	80.9

Note: These results are compared with internal model fit statistics generated via bootstrap resampling (1—out-of-bag error bootstrap error rates).

Table 4. Classification confusion error rates for leks and pseudoabsence locations.

Management zone	Pseudoabsence (%)	Leks (%)
MZ I—Northern Great Plains	29.8	16.9
MZ II—Wyoming Basin	32.7	16.5
MZ III—Southern Great Basin	18.0	9.9
MZ IV—Snake River Plain	21.0	11.3
MZ V—Northern Great Basin	29.4	19.7
MZ VI—Columbia Basin	12.0	12.0
MZ VII—Colorado Plateau	12.0	10.0

Notes: Error rates were generated from bootstrap resampling. Across management zones, there was a general pattern of higher errors in the pseudoabsence class, with the exception of the two smallest management zones, the Columbia Basin and the Colorado Plateau.

Models demonstrate that breeding habitat is highly condensed within the current occupied range of sage-grouse (Fig. 2). All currently active leks occurred on probabilities >0.65; we therefore used this threshold to quantify the amount of breeding habitat. When we use this threshold value, 26% of the current occupied range is predicted to be breeding habitat (Table 5, Fig. 2). Across the range of sage-grouse, general habitat variables and climatic gradient variables had greater importance than disturbance variables in predicting occupied breeding habitat (Table 6; Appendix S2). Not surprisingly, a positive association with the percentage of a landscape dominated by sagebrush within 130.1 km^2 (50.24 mile^2; 32,153 acres) was the top variable in four of the seven models and was in the top five variables for all models (Table 6). We documented variation in habitat selection for sagebrush but also show similar patterns across the range (Fig. 3). However, functional habitat selection for sagebrush modeled for the Northern Great Plains and Columbia Basin management zones diverged from results for the rest of the management zones, because sage-grouse were modeled to occupy habitats

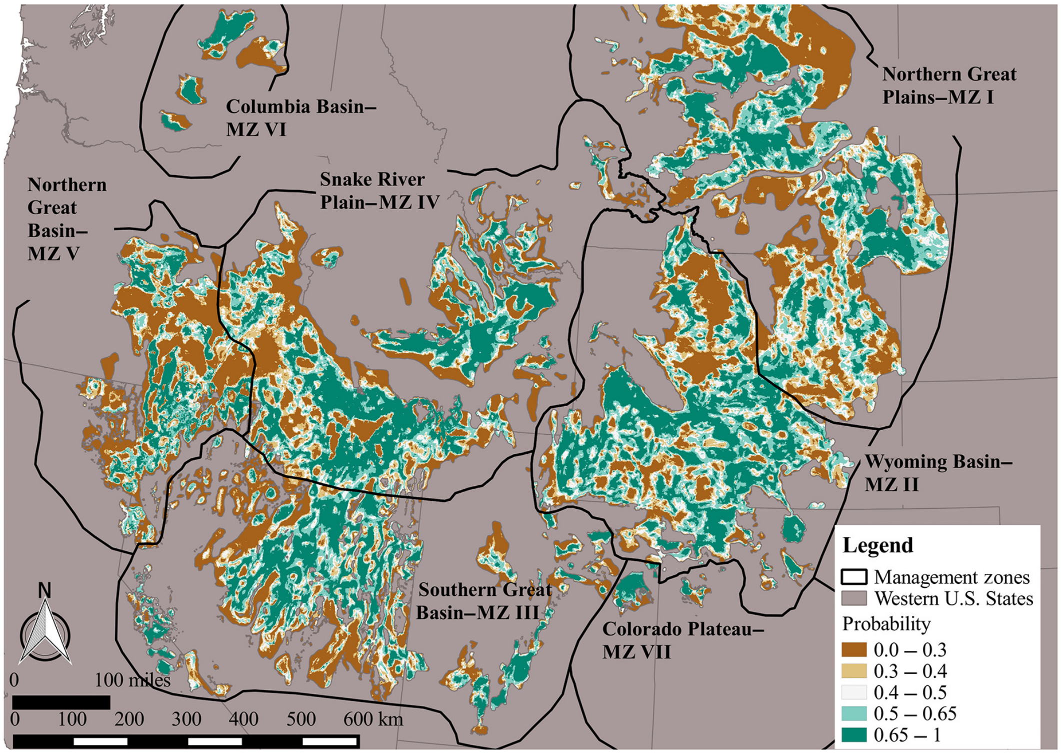

Fig. 2. Breeding habitat model of Greater Sage-Grouse developed within each of the seven management zones. The breeding habitat model is a spatially explicit probability prediction that the surrounding landscape will contain enough breeding habitat to support Greater Sage-Grouse lek formation. All active leks within the sage-grouse range (2010–2014) occurred on probabilities >0.65.

Table 5. Area (km^2) of occupied range (Schroeder et al. 2004) and modeled breeding habitat across the Greater Sage-Grouse range in North America.

Management zone	Occupied range	Modeled breeding habitat	Percentage of occupied range
MZ I—Northern Great Plains†	186,480	41,731	22
MZ II—Wyoming Basin	149,820	48,189	32
MZ III—Southern Great Basin	124,057	36,629	30
MZ IV—Snake River Plain	156,360	46,700	30
MZ V—Northern Great Basin	78,293	14,018	18
MZ VI—Columbia Basin	11,161	4462	40
MZ VII—Colorado Plateau	4777	652	14
Rangewide†	710,948	192,381	26

Note: Breeding habitat probabilities were calculated using a 0.65 threshold, because all current active leks had a probability >0.65.

† Does not include the Canadian portion of the range.

with lower proportions of sagebrush in zones I and VI (Fig. 3). All sage-grouse breeding habitats showed strong avoidance of tree cover; however, strength of avoidance varied between management zones (Fig. 4). The human disturbance index was selected within models for all management zones except the Northern Great Basin with a variable importance range (0.48 for Colorado Plateau to 0.09 for Southern Great Basin, Table 6; Appendix S2). While threshold values between management zones varied similar to tree canopy cover, models documented clear thresholds in amount of landscape-level disturbance tolerated and exhibited the sharpest declines in probability distributions once thresholds were crossed (Fig. 5). Models showed that Northern Great Plains management zone had the lowest threshold for the human disturbance index (2.9% when P ~ 0.65, Fig. 5). Models also documented variability and

Table 6. Top five variables and their importance values selected for each management zone from 2010 to 2014.

Management zone	First variable	Second variable	Third variable	Fourth variable	Fifth variable
Northern Great Plains	Canopy cover	All sagebrush	Roughness	Topographic wetness index	Gross primary production
(I)	1.00	0.63	0.57	0.55	0.45
Wyoming Basin	All sagebrush	Canopy cover	Annual drought index	Degree days > 5°C	Mean annual precipitation
(II)	1.00	0.73	0.68	0.59	0.49
Southern Great Basin	All sagebrush	Degree days > 5°C	Elevation	Annual drought index	Canopy cover
(III)	1.00	0.79	0.70	0.54	0.48
Snake River Plain	Canopy cover	Annual drought index	All sagebrush	Degree days > 5°C	Gross primary production
(IV)	1.00	0.60	0.59	0.51	0.50
Northern Great Basin	All sagebrush	Annual drought index	Low sagebrush	Mean annual precipitation	Degree days > 5°C
(V)	1.00	0.96	0.91	0.79	0.65
Columbia Basin	Elevation	Degree days > 5°C	Grassland/ herbaceous	Annual drought index	All sagebrush
(VI)	1.00	0.42	0.41	0.27	0.22
Colorado Plateau	All sagebrush	Low sagebrush	Human disturbance index	Oil and gas wells	
(VII)	1.00	0.67	0.48	0.40	

Notes: Importance values are scaled by management zone, so that the top variable equals 1 and the remaining variables are a proportion derived by dividing by the top variable, and are derived from probability-scaled partial plots in the Random Forest package in R. Variable importance values for the remaining retained variables (6th to 10th) are in Appendix S2 and, in some cases, explain similar amounts of variation as the fifth variable.

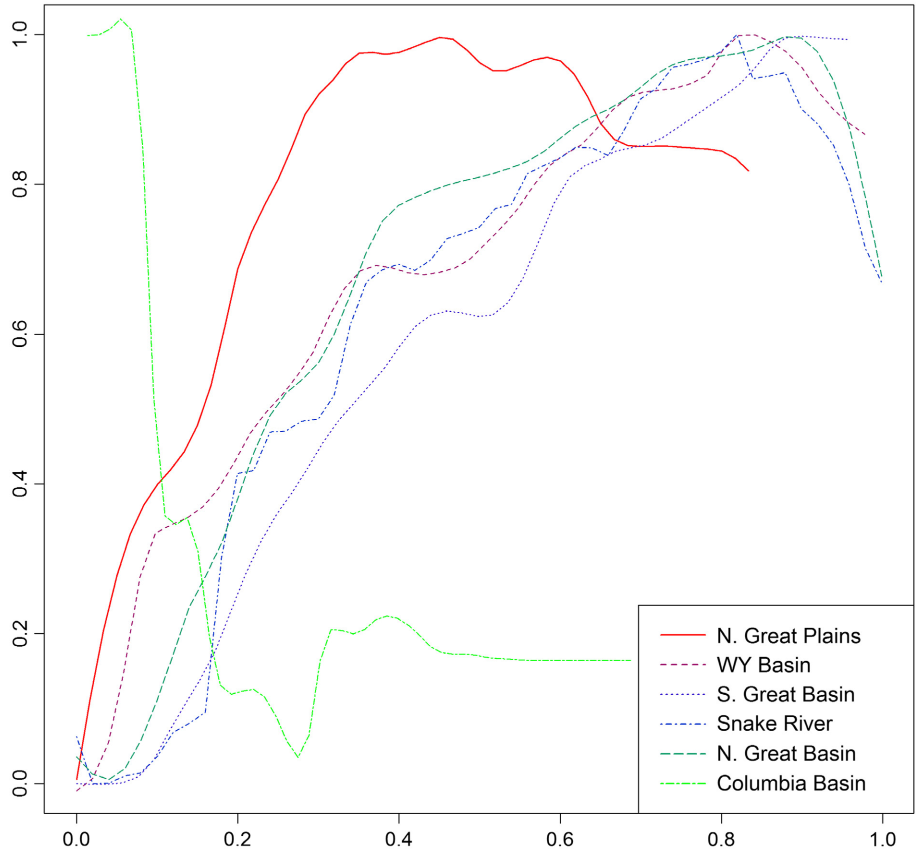

Fig. 3. Functional habitat response between the percentage of all sagebrush cover types (x-axis) within a 6.4-km buffer (130.1 km^2) and the probability (y-axis) a landscape will contain enough breeding habitat to support Greater Sage-Grouse lek formation within each management zone (2010–2014). Functional response curves were generated using partial probability plots to explore the influence of a given variable on the probability of occurrence while partialing out the average effects of all other variables in the final model.

differences in threshold values for the amount of tillage in the landscape, with sage-grouse in management zone I showing the least tolerance for tilled landscapes (Fig. 6). Despite variability in disturbance and nonhabitat thresholds, we found similar patterns in the peaks of probability distributions ($P > 0.8$) for our two strongest historic climatic predictors (annual drought index [Fig. 7] and degree days > 5°C [Fig. 8]). A current measure of climate as measured by gross primary production had lower variable importance than our historic climate envelopes in model selection (Table 6). We documented similar patterns of selection for gross primary production, although peaks varied across the range with the lowest selected range of gross primary production in the Northern Great Basin and the highest in the Northern Great Plains (Fig. 9).

Breeding population index model

We demonstrate distinct clustering in the relative abundance of sage-grouse populations within each management zone (Figs. 10 and 11). On average, approximately half of the breeding population is predicted to be within 10% of the occupied range. Across all management zones, all populations visually demonstrated asymptotic properties between each additional 10% of the population and the area required to contain those populations (Fig. 11). For example, to go from 80% of the population index to 90%, increased the area required by 44% on average (range: 41% MZ II to 50% MZ I; Fig. 11).

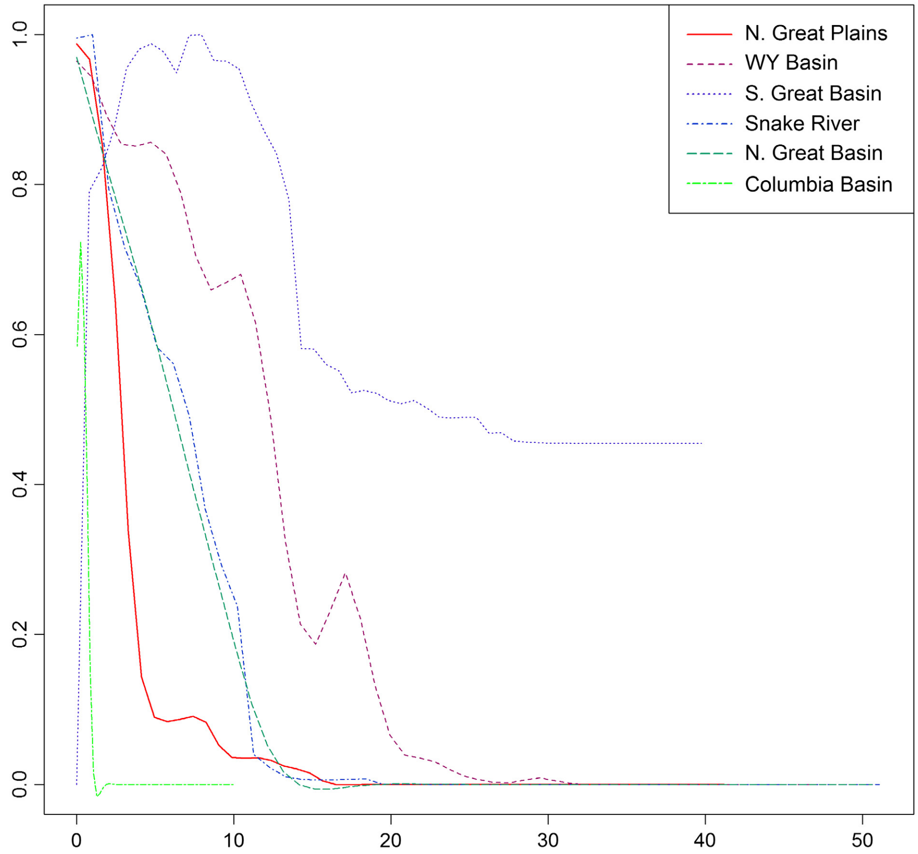

Fig. 4. Functional habitat response between tree canopy cover (*x*-axis) within a 6.4-km buffer (130.1 km^2) and the probability (*y*-axis) a landscape will contain enough breeding habitat to support Greater Sage-Grouse lek formation within each management zone (2010–2014). Functional response curves were generated using partial probability plots to explore the influence of a given variable on the probability of occurrence while partialing out the average effects of all other variables in the final model.

DISCUSSION

Clustering of populations is a common ecological phenomenon (e.g., Brown et al. 1995, Murphy et al. 2006). Knowledge of these high-value areas can direct management actions to landscapes where they will have the largest benefit to regional populations (Sanderson et al. 2002, Groves 2003). We documented pronounced clustering in the relative abundance of sage-grouse populations within each management zone (Figs. 10 and 11), consistent with past work at regional (Doherty et al. 2010*a*, Coates et al. 2014), state (Fedy et al. 2014), and local scales (Aldridge and Boyce 2007, Doherty et al. 2010*b*). Our results indicate that approximately half of the breeding population is within ~10% of the range. We also found that 80% of sage-grouse populations were contained in 25–34% of the occupied range within each management zone. Across all management zones, all populations showed an exponential increase in the area required to contain each additional 10% of the population (Fig. 11). Because sage-grouse exhibit markedly clustered populations, if landscape-level risks occur in high-density areas they could negatively affect large proportions of the populations. Conversely, focusing conservation efforts into landscapes that contain higher proportions of birds may demonstrate substantially higher biological returns for conservation investments of similar acreages. Therefore we suggest that, birds, not acres or dollars spent, would be the best currency in conservation plans, because identical acreages of

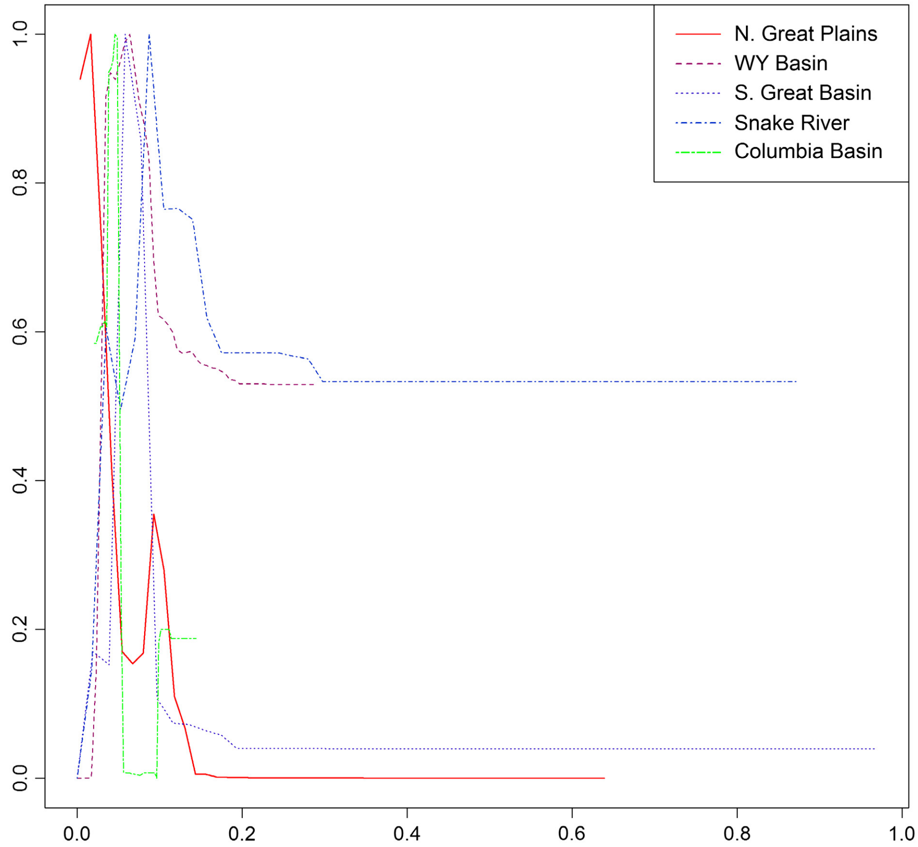

Fig. 5. Functional habitat response between the amount of human disturbance index (*x*-axis) within a 6.4-km buffer (130.1 km^2) and the probability (*y*-axis) a landscape will contain enough breeding habitat to support Greater Sage-Grouse lek formation within each management zone (2010–2014). Functional response curves were generated using partial probability plots to explore the influence of a given variable on the probability of occurrence while partialing out the average effects of all other variables in the final model.

conservation actions can overlap with vastly different numbers of sage-grouse. Our population index models can be used to quantify the relative percentage of sage-grouse populations that overlap management areas, providing regional population context to decisions and the relative ranking of landscape importance for sage-grouse. Simple spatial overlap analyses using our model are a first step in bringing context to the potential population-level effects of both deleterious and beneficial management decisions.

A trade-off exists between model prediction and generalized biological understanding when selecting the appropriate spatial extent for the development of RSF models (Elith and Leathwick 2009). Reducing extent can increase model accuracy (Fedy et al. 2014), but at the cost of generalizability as the models explain variation over a smaller parameter space. Careful thought must be given to study objectives. Sage-grouse management zones are based on unique floristic provinces (Stiver et al. 2006, Appendix S1). The management zone extent represents a good trade-off for our goals because this extent allowed generalized broad-scale biological understanding across far-reaching extents and still retained high spatial predictive capabilities within management zones.

The desired geographic scale of understanding is paramount in studies aimed at obtaining inference on selection behavior. Our study was specifically designed to assess first-order selection of sage-grouse seasonal home ranges (Johnson 1980, Meyer and Thuiller 2006). The rationale for

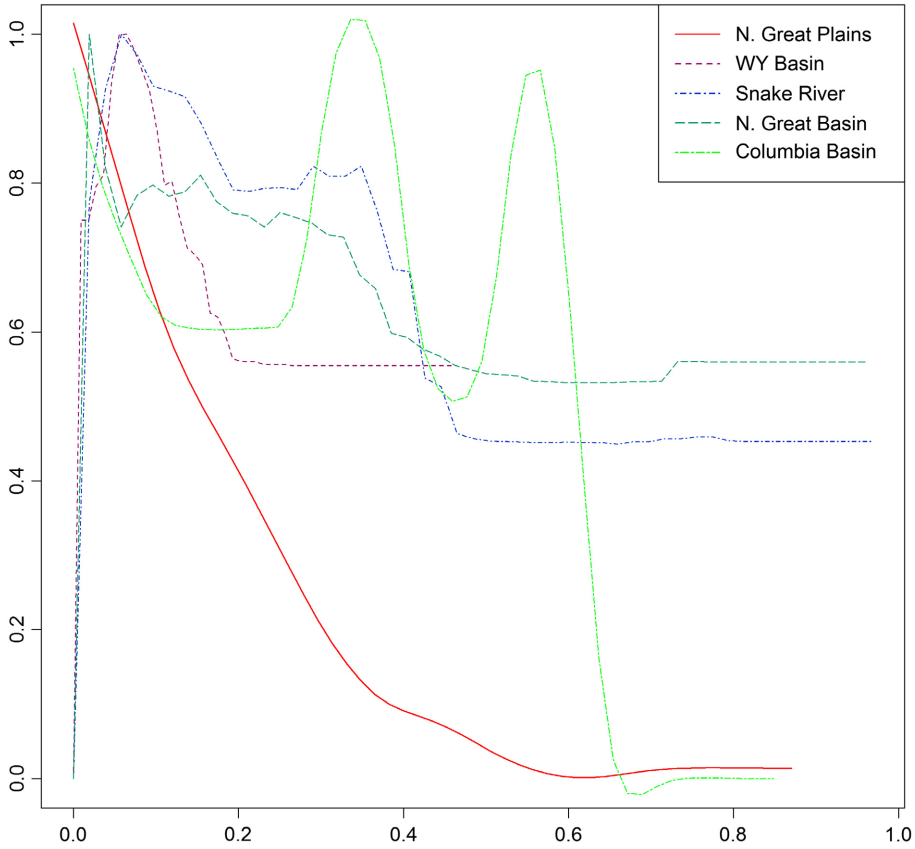

Fig. 6. Functional habitat response between the amount of tilled cropland (*x*-axis) within a 6.4-km buffer (130.1 km^2) and the probability (*y*-axis) a landscape will contain enough breeding habitat to support Greater Sage-Grouse lek formation within each management zone (2010–2014). Functional response curves were generated using partial probability plots to explore the influence of a given variable on the probability of occurrence while partialing out the average effects of all other variables in the final model.

using the first-order scale was twofold: (1) The primary objective was to develop population and habitat models that account for regional variation within each sage-grouse management zone and (2) broad-scale lek data represent locations of populations and are not adequate to appropriately model second- or third-order habitat selection (Johnson 1980, Meyer and Thuiller 2006). Lower orders of habitat selection are generally derived from finer-scale telemetry data at the individual level. Using first-order assessments here that produce a relative probability for each 120 × 120 m grid cell across the range of the species allows for later integration with other research at finer scales (e.g., second to fourth orders). We believe that investigating first-order habitat selection across the entire sage-grouse range is important, because understanding landscape context can elucidate why the results of second- and third-order habitat selection studies can seemingly give conflicting results and varying thresholds, even for well-studied topics (Donovan et al. 1997).

While generating biological insight into species habitat selection is obviously important, one can argue that measures of model prediction and stability are even more important for conservation planning and risk analyses, especially when they may be utilized by agencies to spatially assess species risk, delineate priority areas, or direct resource allocation (see review in Elith and Leathwick 2009). Our models demonstrated high statistical model fit and demonstrated stability to withheld data (Tables 3 and 4). On average, our

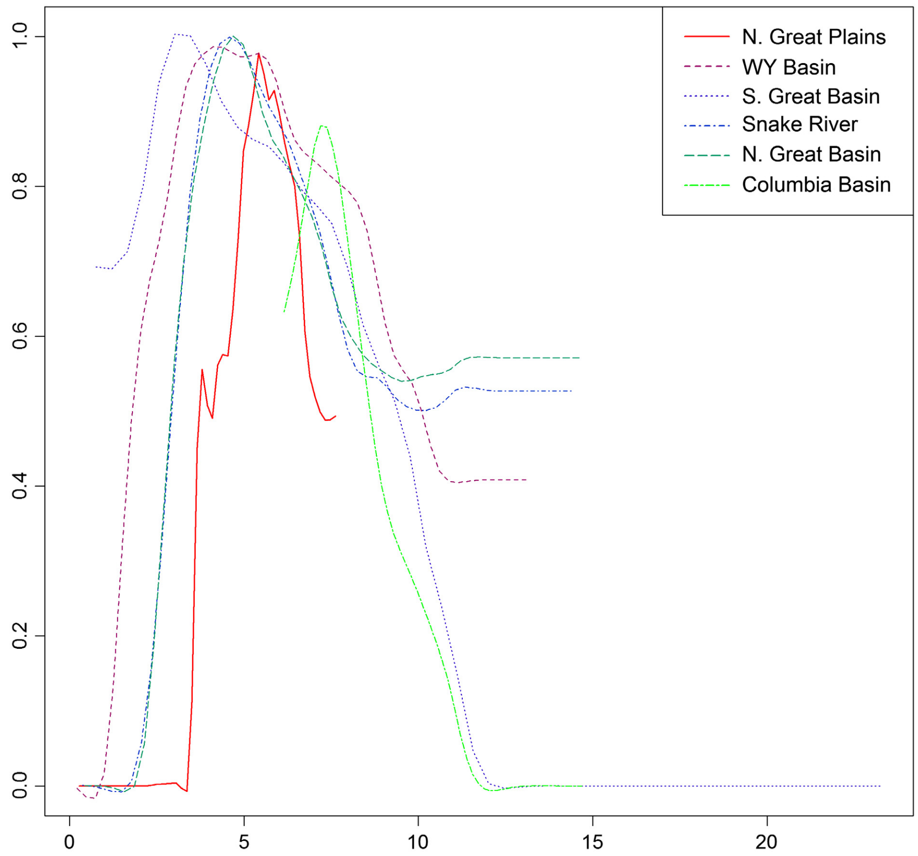

Fig. 7. Functional habitat response between the average annual drought index (*x*-axis) within a 6.4-km buffer (130.1 km^2) and the probability (*y*-axis) a landscape will contain enough breeding habitat to support Greater Sage-Grouse lek formation within each management zone (2010–2014). Functional response curves were generated using partial probability plots to explore the influence of a given variable on the probability of occurrence while partialing out the average effects of all other variables in the final model.

breeding habitat model correctly classified 82.0% (range: 75.4–88.0%) of hold-out data from OOB bootstrap samples and also correctly classified independent *K*-fold hold-out data (mean across management zones = 80.9%; range: 75.0–85.8%, Table 3). General agreement between OOB error rates and *K*-fold cross-validation indicates stability in our model to predict independent data and lack of overfitting (Shmueli 2010). Demonstrated model fit and validations were important, as this modeling effort was directly intended to assess sage-grouse spatial overlap with landscape-level risks.

Sage-grouse are a unique species in wildlife management as we have broad-scale population surveys across the species range that follow a common survey protocol (i.e., lek counts, Connelly et al. 2000). Additionally, although birds require unique habitat components throughout their annual cycle, they do not migrate long distances and, with the exception of peripheral populations in Alberta and Saskatchewan, do not cross international borders. These characteristics simplify many management strategies and facilitate consistency in survey protocols that allowed research into regional variation in functional responses. Additionally, broad-scale population data facilitate the development of integrative methodologies to create composite spatially explicit indices that reflect demographic and habitat information within this study and others (Coates et al. 2014). Indices such as these—particularly those that can be predicted spatially—can help guide

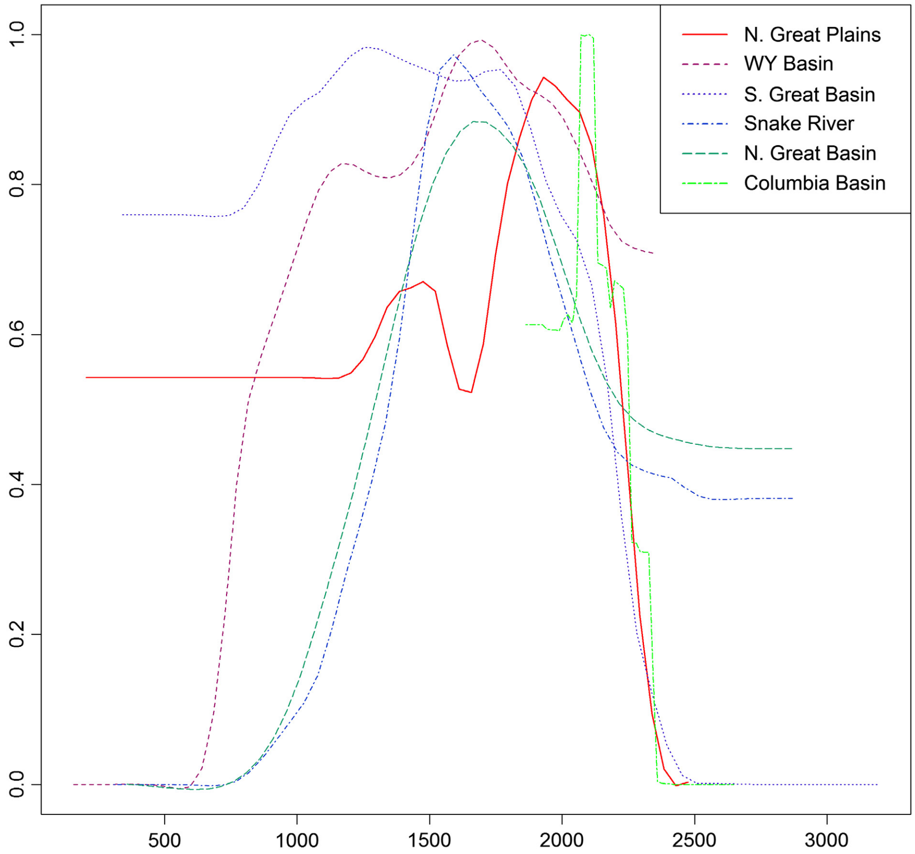

Fig. 8. Functional habitat response between the average degree day 5°C (*x*-axis) within a 6.4-km buffer (130.1 km^2) and the probability (*y*-axis) a landscape will contain enough breeding habitat to support Greater Sage-Grouse lek formation within each management zone (2010–2014). Functional response curves were generated using partial probability plots to explore the influence of a given variable on the probability of occurrence while partialing out the average effects of all other variables in the final model.

landscape-level conservation actions (Stephens et al. 2015). However, in the context of our models, broad-scale lek data are inadequate for modeling second- or third-order habitat selection (Johnson 1980, Meyer and Thuiller 2006), which are known to be important determinants of sage-grouse habitat selection (Connelly et al. 2000). Past research has used lek data as an independent data source to validate landscape-level spatial predictions of second- and third-order habitat selection models generated from telemetry data in both Greater Sage-Grouse (Doherty et al. 2010*b*, Fedy et al. 2014) and Gunnison Sage-Grouse (Aldridge et al. 2012). Thus, first-order habitat selection models will give regional context to priority breeding areas, but should not be viewed as prescriptive at the site level. It should be expected that some priority areas identified at the first-order scale will lack appropriate habitats at the second- or third-order scale and therefore may be unoccupied. Site-scale recommendations will require input from local biologist as well as finer-resolution data (e.g., telemetry data, GPS movements, soil types, local vegetation).

Lek data seem to represent the overall spatial process of relative abundance for sage-grouse, particularly in recent years due to the dramatic increases in survey effort over the last decade (WAFWA 2015). However, sage-grouse lek surveys follow a common survey protocol; they do not follow a statistical design. A design-based survey with a dual-frame sampling protocol (Haines and Pollock 1998, Royle et al. 2005) would strengthen analyses allowing estimation

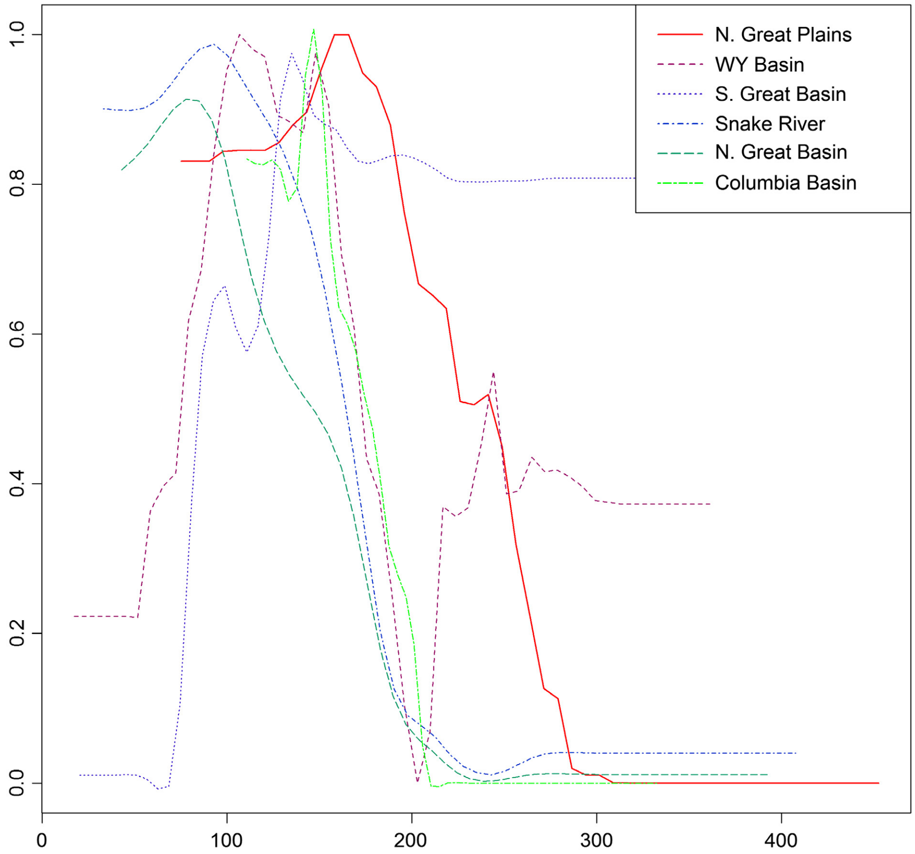

Fig. 9. Functional habitat response between the gross primary production (x-axis) within a 6.4-km buffer (130.1 km^2) and the probability (y-axis) a landscape will contain enough breeding habitat to support Greater Sage-Grouse lek formation within each management zone (2010–2014). Functional response curves were generated using partial probability plots to explore the influence of a given variable on the probability of occurrence while partialing out the average effects of all other variables in the final model.

and understanding of implications of currently inestimable parameters, such as the effects of sampling variation and detection probabilities on count estimates, or the proportion of leks surveyed each year (Blomberg et al. 2013*a*). The latter parameter is one of the most important breakthroughs, because it could allow more robust estimates of population size with associated variances, vs. the reasonable, but ad hoc approaches used to generate current minimum population estimates (WAFWA 2015). A recent example of a statistically rigorous framework for estimating populations in a similar species, lesser prairie chickens (*Tympanuchus pallidicinctus*), could provide guidance for such an approach in sage-grouse (McDonald et al. 2014). Ultimately, the above limitations affect the scale of inference. Models developed using these data should be viewed as regional indices for conservation planning and risk assessment. Because our goal was to provide regional context and relative ranking of landscape importance for sage-grouse, the use of lek count data was appropriate.

Landscapes are seldom homogeneous across large extents. Thus, landscape-scale modeling is important to understand how functional responses vary for wide-ranging species. Variation in functional response to particular habitat components has been documented in ungulates (Godvik et al. 2009, Herfindal et al. 2009, Moreau et al. 2012, Beyer et al. 2013), wolves (Hebblewhite and Merrill 2008, Houle et al. 2010, Matthiopoulos et al. 2011), and other large mammals (Gillies et al. 2006, Roever et al. 2012).

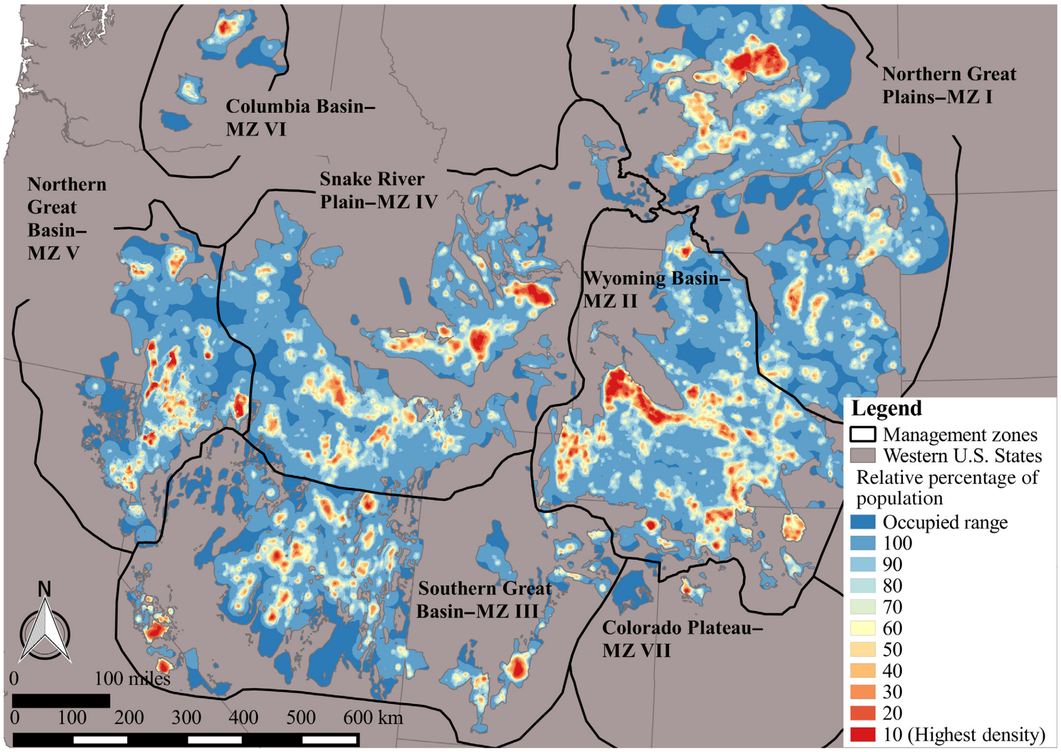

Fig. 10. Breeding population index model of Greater Sage-Grouse within each of the seven management zones. Our population index model provides spatial insight into the relative importance of specific areas to the overall management zonewide breeding abundance of Greater Sage-Grouse during 2010–2014. Population index values are relative within each management zone. Sage-grouse population index areas represent spatial locations of the known breeding population in 10% bins differentiated by color. The darkest red areas contain 10% of the breeding population in the smallest area. Because bins are additive, red and orange hue areas combined capture 50% of the population, etc.

Typically, these studies focused on the spatial scales of inter-home range variation within one to several subpopulations (Mysterud and Ims 1998, Gillies et al. 2006, Hebblewhite and Merrill 2008, Herfindal et al. 2009, Houle et al. 2010). Some studies have moved further along the hierarchical order of habitat selection (Johnson 1980) and focused on within-home range variation in functional response (Houle et al. 2010, Moreau et al. 2012). However, almost all these studies were driven by high-input and high-detail Global Positioning System (GPS) radiotelemetry data, with few exceptions (Mysterud and Ims 1998, Herfindal et al. 2009). We demonstrate that less detailed data (i.e., lek survey data), collected across large extents (i.e., the entire species range), can also highlight the regional variation in functional responses. Our analyses clearly highlight that understanding regional variation in habitat selection is critical to designing effective conservation plans for sage-grouse.

We documented variability in sage-grouse functional response to sagebrush across the range (Fig. 3). Not surprisingly, sage-grouse showed strong selection for landscape-level sagebrush with the exception of the Columbia Basin (see variable justification in Table 2 and Fig. 3). While landscape-scale extents differed, our sagebrush functional response curves broadly agreed with other landscape-level assessments, which recommended >50% sagebrush cover (Wisdom et al. 2011) and >65% sagebrush cover (Aldridge et al. 2008). More recent analyses documented that 90% of the active leks in the western range of sage-grouse occurred in landscapes with at least 40% sagebrush (Knick et al. 2013). All active

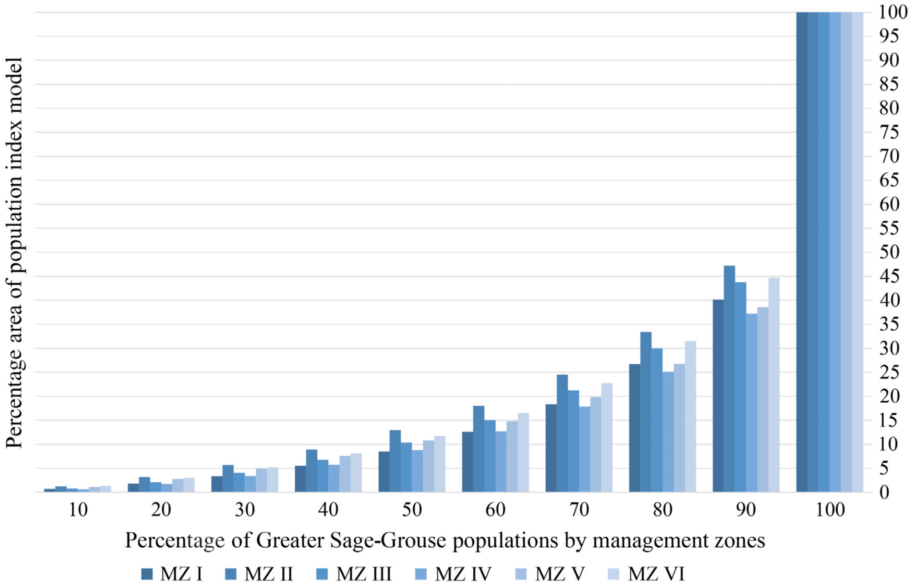

Fig. 11. The percentage of the population index model and resulting percentage area of the entire population index model by management zones during 2010–2014.

leks within our habitat selection model had predicted occupancy probabilities >0.65. When the probability of occurrence crossed this threshold, we documented sagebrush cover ranging from ~35% (Wyoming Basin) to ~55% (Southern Great Basin) (Fig. 3). These threshold values are lower than previously documented; however, contemporary thresholds of occurrence could be lower than recommendations for rangewide averaged responses for long-term persistence (Aldridge et al. 2008, Wisdom et al. 2011). Additionally, our threshold estimates are similar to estimates of ecological minimum requirements (Knick et al. 2013). These past analyses averaged habitat or population responses of sage-grouse at rangewide (Aldridge et al. 2008, Wisdom et al. 2011) or the entire western-range (MZ III–VI) extents (Knick et al. 2013). Generating averaged functional habitat response across very large extents clearly furthers biological understanding, yet by design they cannot elucidate regional differences in functional responses if they exist. We also documented divergence in the Northern Great Plains, which crossed the probability of occurrence threshold at ~20% sagebrush cover (Fig. 3). We showed variation in functional responses across a wide range of variables within all management zones; however, the Columbia Basin and Northern Great Plains consistently showed the greatest divergence in functional habitat selection. Spatial interpolation or extrapolation of habitat selection models is most accurate when the availability of habitats is approximately the same in the novel areas (Mladenoff et al. 1999, Aarts et al. 2008) because of the functional response in habitat use (Mysterud and Ims 1998). Similarly, models averaging habitat responses across the range of sage-grouse are likely to misclassify important habitats when landscape context diverges from rangewide averaged habitat conditions such as the Columbia Basin and Northern Great Plains management zones.

Parallel to many other recent studies at landscape scales (Aldridge and Boyce 2007, Doherty et al. 2008, Knick et al. 2013, Coates et al. 2014, Fedy et al. 2014), our research also suggests that sage-grouse occupancy is more complicated than just sagebrush abundance; other core environmental conditions must be met for sage-grouse landscape occupancy. We also documented variability in thresholds of disturbance factors (i.e., tillage, conifer, human disturbance index) across the range of sage-grouse (Figs. 4–6). Sage-grouse are well known to avoid human disturbances (e.g., Naugle et al. 2011*b*) and other nonhabitat features such as conifers encroaching into sagebrush-dominated landscapes (Baruch-Mordo et al. 2013). We showed strong negative relationships between sage-grouse occurrence and tree canopy cover across each management zone, which was consistent with the highest resolution and definitive study on the effects of conifer encroachment (Baruch-Mordo et al. 2013). Yet, our results indicate that caution should be used when extrapolating results from small portions of the Northern Great Basin to other sage-grouse population across the range, because of regional variation in functional responses to tree cover. Sage-grouse populations in the Northern Great Plains and the Columbia Basin exhibited more pronounced avoidance of tree canopy cover than in the Northern Great Basin, while the more contiguous habitats of the Wyoming Basin and Southern Great Basin demonstrated more tolerance (Fig. 4). The human disturbance index was included in every management zone but one; however, human disturbance was less important in explaining occurrence than landscape-level sagebrush or climatic envelope variables (Table 6; Appendix S2). However, the human disturbance index exhibited the sharpest declines in probability distributions once thresholds were crossed, suggesting important tipping points for human disturbance in proximity to leks (Fig. 5). The variation in the functional response to human disturbance was substantial among management zones, demonstrating that a one-size-fits-all approach to acceptable disturbance thresholds around leks should exercise precaution and target the lowest threshold, or potentially adjust regionally. Avoidance of areas with relatively small amounts of human disturbance is consistent with past research (Knick et al. 2013); however, direct comparison of rates across studies is not possible as the suite of variables and the scale at which they were quantified differed between studies.

If habitat fragmentation is a key determinant of where thresholds occur, we would expect to see habitat thresholds occurring earliest in landscapes with the highest levels of fragmentation (Hill and Caswell 1999, Fahrig 2003). Consistently across the range, the two most fragmented populations with the highest amounts of agriculture (Northern Great Plains and Columbian Basin; Appendix S1) had the lowest tolerance to human disturbance (Fig. 5). Increased impact of disturbance within fragmented habitats was also documented in relation to oil and gas development across the state of Wyoming. Sage-grouse within the more fragmented habitats of northern Wyoming (Great Plains management zone) showed increased population-level impacts within the same oil and gas development density categories, compared with the more contiguous habitats of southern Wyoming (Wyoming Basin management zone) (Doherty et al. 2010*a*). Variation in disturbance thresholds is also known to vary with habitat quality. For example, wolves (*Canis lupis*) in the boreal forest avoided anthropogenic development as disturbance densities increased (Lesmerises et al. 2012, Ehlers et al. 2014), but showed more tolerance of disturbance in high-quality prey habitats (Lesmerises et al. 2012). Further, habitat quality is more than simply food availability. For example, mule deer (*Odocoileus hemionus*) within the Piceance and Upper Green River Basins showed avoidance of oil and gas development; however, effect sizes were larger in the Upper Green River Basin (Sawyer et al. 2006, Northrup et al. 2015). The authors hypothesized that the more rugged areas of the Piceance Basin provided more security cover than the flatter areas of Upper Green River Basin (Northrup et al. 2015). This hypothesis was generated by observing behavior differences in which mule deer showed less avoidance of infrastructure when they had the security cover of darkness at night (Northrup et al. 2015). It is likely that the variation in sage-grouse response to disturbance observed in this study is influenced by mechanisms related to fragmentation, habitat quality, or others. However, the finer-scale data to test each of these hypotheses are not available rangewide. Regardless, the relevant point is that understanding variation in habitat selection and disturbance thresholds across large spatial extents is necessary to inform land-use management decisions that try to balance trade-offs among competing interests.

Management implications

Our work is an improvement over past rangewide population models (Doherty et al. 2011) because it represents a comprehensive integration of both habitat and population information at a rangewide scale for sage-grouse while accounting for regional variation in habitat selection and bird densities. Our models can serve as a consistent currency to assess the overlap of sage-grouse habitats (Fig. 2) and populations (Fig. 10) with conservation actions or threats.

We also document the importance of regional variation in habitat selection and varying thresholds in response to disturbance across the range. Partial probability plots highlight how ecological gradients (Appendix S1) across the range (Table 5) can change functional habitat responses and ultimately predictions of breeding habitat. Our work highlights the need for careful consideration when extrapolating results of studies in one management zone into others, especially if they have vastly different ecological context. Our study extent was rangewide and addressed first-order selection of habitats within management zones. Thus, our results should apply to questions and management at that scale. However, management may require actions at smaller scales of selection, and we caution against implementing smaller-scale actions based on the results presented here. Our results suggest that multiscale (first- to third-order) and cumulative effects should be investigated simultaneously in future research.

The complexities of ecological context fundamentally influence how species respond to other components in the system. In other words, where you draw your study boundaries fundamentally determines what you learn about the ecology of the species. We show this is true, even for a species as specialized as sage-grouse. Often, models do not encompass the entire range of a focal species, and therefore, biological relationships or thresholds of disturbance are extrapolated to novel areas not included in the development of the models. Extrapolation of results into novel landscapes is often required as managers are mandated by law to make decisions based upon the best available scientific information. Unfortunately, setting conservation targets based upon thresholds defined in other regions is precarious (Rhodes et al. 2008) because thresholds can vary tremendously across species and landscapes (van der Hoek et al. 2015). For example, our results indicate that at the first-order level, disturbance thresholds defined in the Great Basin management zones would likely exceed sage-grouse occupancy requirements if extrapolated to the Great Plains and Columbia Basin management zones. When potential for conflict is high and thresholds are extrapolated into novel landscapes, clearly defined adaptive management goals and monitoring systems would be prudent. Within this adaptive management framework, it is also critical that assumptions are stated explicitly and tested with data whenever possible.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1462/supinfo