Rangeland Ecology & Management 70 (2017) 95–105

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Extending Conifer Removal and Landscape Protection Strategies from Sage-grouse to Songbirds, a Range-Wide Assessment☆

J. Patrick Donnelly [a,*], Jason D. Tack [b], Kevin E. Doherty [c], David E. Naugle [d], Brady W. Allred [e], Victoria J. Dreitz [f]

[a] Landscape Ecologist, Intermountain West Joint Venture and US Fish and Wildlife Service, University of Montana, Missoula, MT 59812, USA
[b] Postdoctoral student, Avian Science Center, University of Montana, Missoula, MT 59812, USA
[c] Spatial Ecologist, US Fish and Wildlife Service, Lakewood, CO 80228, USA
[d] Professor, Large-Scale Wildlife Ecology, University of Montana and National Science Advisor–Sage Grouse Initiative, University of Montana, Missoula, MT 59812, USA
[e] Professor of Rangeland Ecology, University of Montana, University of Montana, Missoula, MT 59812, USA
[f] Director of Avian Science Center and Professor of Conservation Biology, University of Montana, University of Montana, Missoula, MT 59812, USA

ARTICLE INFO

Article history:
Received 5 February 2016
Received in revised form 14 October 2016
Accepted 17 October 2016

Key Words:
Brewer's sparrow
conifer removal
sagebrush landscape protection
sagebrush sparrow
sage-grouse
sage thrasher

ABSTRACT

Recent and unprecedented scale of greater sage-grouse (*Centrocercus urophasianus*) conservation in the American West enables assessment of community-level benefits afforded to other sagebrush-obligate species. We use North American Breeding Bird Survey (BBS) count data and machine-learning to assess predictors influencing spatial distribution and abundance of three sagebrush-obligate songbirds (Brewer's sparrow [*Spizella breweri*], sagebrush sparrow [*Artemisiospiza nevadensis*], and sage thrasher [*Oreoscoptes montanus*]). We quantified co-occurrence of songbird abundance with sage-grouse lek distributions using point pattern analyses and evaluated the concurrence of songbird abundance within sage-grouse habitat restoration and landscape protection. Sagebrush land-cover predictors were positively associated with the abundance of each songbird species in models that explained 16 − 37% of variation in BBS route level counts. Individual songbird models identified an apparent 40% threshold in sagebrush land-cover, over which songbird abundances nearly doubled. Songbird abundances were positively associated with sage-grouse distributions ($P < 0.01$); range-wide, landscapes supporting > 50% of males on leks also harbored 13 − 19% higher densities of songbirds compared with range-wide mean densities. Eighty-five percent of the conifer removal conducted through the Sage Grouse Initiative coincided with high to moderate Brewer's sparrow abundance. Wyoming's landscape protection (i.e., "core area") strategy for sage-grouse encompasses half the high to moderate abundance sagebrush sparrow and sage thrasher populations. In the Great Basin half the high to moderate abundance sagebrush sparrow and sage thrasher populations coincide with sage-grouse Fire and Invasive Assessment Tool priorities, where conservation actions are being focused in an attempt to reduce the threat of wildfire and invasive plants. Our work illustrates spatially targeted actions being implemented ostensibly for sage-grouse largely overlap high abundance centers for three sagebrush obligate passerines and are likely providing significant conservation benefits for less well-known sagebrush songbirds and other sagebrush-associated wildlife.

Introduction

Widespread degradation of sagebrush (*Artemisia* spp.) ecosystems in western North America poses an immense conservation challenge (Knick et al., 2003; Mac et al., 1998; Noss et al., 1995). Few of these landscapes remain intact post Euro-American settlement (Miller and Eddleman, 2001; West, 1996). Fragmentation has accelerated in past decades, driven by invading annual grasses, encroaching conifer, cultivation of native rangelands, and expanding rural urban and industrial development (Miller et al., 2011). It is unlikely sagebrush systems are to return to presettlement condition as scale and magnitude of these changes greatly exceeds available financial and logistical resources (Miller et al., 2011). To curb future loss, conservation strategies should focus on remaining intact sagebrush landscapes to maximize return on limited conservation investments (Bottrill et al., 2008; Hobbs and Kristjanson, 2003; Joseph et al., 2009).

Efforts to conserve sagebrush landscapes are driven largely by investments that benefit greater sage-grouse (*Centrocercus urophasianus;* hereafter, "sage-grouse") populations and their habitats, with the aim of precluding the need for an Endangered Species Act (ESA; Meinke et al., 2009) listing. Sage-grouse is a gallinaceous species endemic to sagebrush communities of western North America (Schroeder et al., 1999). Degradation and loss of sagebrush shrublands have contributed to extirpation of

☆ The US Fish and Wildlife Service Mountain Prairie Region 6 funded this research.
* Correspondence: Patrick Donnelly, 32 Campus Drive, FOR302, University of Montana, Missoula, MT 59812, USA.
E-mail address: patrick_donnelly@fws.gov (J.P. Donnelly).

http://dx.doi.org/10.1016/j.rama.2016.10.009
1550-7424/Published by Elsevier Inc. on behalf of The Society for Range Management.

the species from half its historic range and declines in many remaining populations (Schroeder et al., 2004). In 2010, heightened concern over the species population status resulted in a designation of warranted but precluded by the US Fish and Wildlife Service (USFWS) under the ESA (USFWS, 2010). Reevaluation of this designation in 2015 helped to stimulate more than 1.2 million ha of additional conservation to reduce primary threats impacting sage-grouse (USFWS, 2015). These actions were a contributing factor in the 2015 decision not to list sage-grouse as threatened or endangered (USFWS, 2015).

Conservation of sagebrush ecosystems continues to accelerate on private (NRCS, 2015a) and public lands (USFWS, 2015) in anticipation of the USFWS revisiting their sage-grouse listing decision in 2020. The Bureau of Land Management (BLM) and US Forest Service (USFS) have committed additional resources to conservation on federal lands encompassing more than half the current occupied range of sage-grouse (BLM and USFS, 2015). Conservation investments are being steered toward landscapes that support high-abundance sage-grouse populations (USFWS, 2015). Federal, state, and private land managers anticipate that broad-scale reduction in primary threats will benefit a suite of sagebrush-associated taxa (Copeland et al., 2014; NRCS, 2015a; Stiver et al., 2006; USFWS, 2013).

Extending benefits of single-species conservation to multiple taxa assumes spatial correlation across species (Andelman and Fagan, 2000; Caro and O'Doherty, 1999; Prendergast et al., 1993; Simberloff, 1998). Sage-grouse distributions are well known and exhibit highly clustered patterns (Knick and Hanser, 2011) that concentrate 75% of breeding populations within a quarter of the species range (Doherty et al., 2010b). Their broad distribution and obligate status have implicated sage-grouse as an indicator species of sagebrush ecosystem health (Rich et al., 2005). However, limited understanding of their spatial coincidence with other species (e.g., common sagebrush lizard *[Sceloporus graciosus]*, pigmy rabbit *[Brachylagus idahoensis]*) has restricted implementation of multispecies conservation efforts within sagebrush ecosystems (Rowland et al., 2006).

Passerine species endemic to sagebrush ecosystems—Brewer's sparrow (BRSP; *Spizella breweri*), sagebrush sparrow (SAGS; *Artemisiospiza nevadensis*), and sage thrasher (SATH; *Oreoscoptes montanus*)—are among the fastest declining bird groups in North America (NABCI, 2014). Like sage-grouse, these sagebrush-obligate songbirds (hereafter "songbirds") are considered important predictors of ecosystem condition because of their sensitivity to local and landscape-scale habitat change (Knick et al., 2003; Rotenberry and Wiens, 2009). The same threats facing sage-grouse are also linked to declines in songbirds; that is, conifer expansion (Knick et al., 2014), wildland fire (Knick et al., 2005), cultivation of grazing lands (Vander Haegen, 2007), invasion of exotic annual grasses (Earnst and Holmes, 2012), and energy development (Gilbert and Chalfoun, 2011; Mutter et al., 2015). Range overlap among breeding songbirds and sage-grouse is extensive but has proven to be a poor correlate of co-occurrence (Rich et al., 2005).

The unprecedented scale of sage-grouse conservation provides the opportunity for community-level benefits in other sagebrush-obligate species (Boyd et al., 2014; Davies et al., 2011). Sage-grouse planning efforts have assumed broader ecosystem and multiple species benefits (NRCS, 2015b; USFWS, 2015) but lack much of the empirical evidence needed to test assumptions of the range-wide strategies proposed (Rowland et al., 2006). We addressed this information gap by 1) identifying spatial patterns of sagebrush-obligate songbird abundance in relation to sage-grouse distribution across their range and 2) evaluating the potential for community-level benefits derived from targeted sage-grouse conservation. We first modeled spatial variability in relative abundance for the songbirds BRSP, SAGS, and SATH using count data from the North American Breeding Bird Survey (BBS; Pardieck et al., 2015). We then evaluated the dependence of songbird abundance on known sage-grouse distributions using point pattern analysis and summarized results within Western Association of Fish and Wildlife Agencies Sage-Grouse Management Zones I – VII (hereafter "management zones"; Stiver et al., 2006, Fig. 1). Lastly, we evaluated patterns of relative songbird abundance to coincidence of sage-grouse habitat restoration (invasive conifer removal) and landscape protection actions (i.e., Wyoming's Sage-Grouse Core Area Strategy [see Copeland et al., 2013] and Sage-Grouse Fire and Invasive Assessment Tool priority areas [FIAT; BLM, 2014]).

Methods

Modeling Spatial Variability in Sagebrush-Obligate Songbird Abundance

We defined our modeling extent (1.7 million km^2; see Fig. 1) using a moving 50-km^2 sample frame to identify areas containing ≥ 1% sagebrush land cover (i.e., sagebrush shrubland) in the western United States, similar to methods used by Knick et al. (2003). Sagebrush extent was derived from LANDFIRE 90 m existing vegetation type dataset (LANDFIRE, 2012). Six sagebrush communities were used to define sagebrush extent: Great Basin xeric mixed sagebrush shrubland, Intermountain basins big sagebrush shrubland, Columbia Plateau low sagebrush steppe, intermountain basins big sagebrush steppe, intermountain basins montane sagebrush steppe, and Columbia Plateau silver sagebrush seasonally flooded shrub-steppe (NatureServe Explorer, 2012). Sagebrush shrublands in northern Arizona and New Mexico were omitted, as there was no potential for overlap within the range of sage-grouse.

We characterized patterns of relative abundance for BRSP, SAGS, and SATH during the breeding season. These species are ideal to test the ability of sage-grouse conservation to provide community-level benefits as they are 1) sufficiently ubiquitous to develop range-wide models of abundance, 2) broadly encompassed within the sage-grouse range such that conservation actions have the potential for overlap, and 3) identified as species of conservation concern (USFWS, 2008).

Count data from BBS (Pardieck et al., 2015) were used as an index to variation in abundance for each species. Counts occur in the spring on routes typically 40 km in length along secondary roadways. Volunteers conduct 3-min point counts annually at 50 sites spaced ~800 m apart along the route. Routes that did not meet the standards of BBS trend analyses (e.g., surveys conducted in inclement weather, occurring outside allotted time period) were omitted from analyses.

A total of 523 BBS routes were encompassed in our sampling frame. To reduce the effects of annual variation in bird abundance measured, we averaged total counts for each route by species across a 10-yr period (2004 – 2014). These 10-yr means were then used as a response variable for model-based analyses to provide an index to relative abundance (hereafter, "abundance"). Routes not surveyed within this period were omitted. A 10% subset of routes used in the analysis ($n = 52$) were randomly selected and withheld for model evaluation.

Songbird abundance is structured along multiscale ecological gradients that converge along patterns of land cover, landform, climate, and human disturbance (Knick et al., 2008). Using available spatial data, we applied a suite of landscape predictor variables to model distributions of BRSP, SAGS, and SATH. While each songbird species relies on intact sagebrush ecosystems during the breeding season, their habitat needs differ in structural and vegetative conditions at more local scales (Wiens et al., 1987). We accounted for this by including large-scale climate and productivity predictors that may give rise to habitat variation and observed differences in breeding songbird abundance within sagebrush ecosystems (Table 1).

We aimed to summarize covariate values that characterized the hierarchical process of habitat selection inherent in birds (Wiens et al., 1987), so we summarized each variable at a local (120 m^2) and landscape (6.4 km^2) spatial scale. Focal mean and standard deviation of covariate values were calculated by summarizing representative raster data at each scale to capture the central tendency and heterogeneity of habitat variables; however, for climate variables we simply used the raw value, as the spatial resolution was typically large (> 1 km^2; see Table 1). To append covariates to sample units, we buffered each route

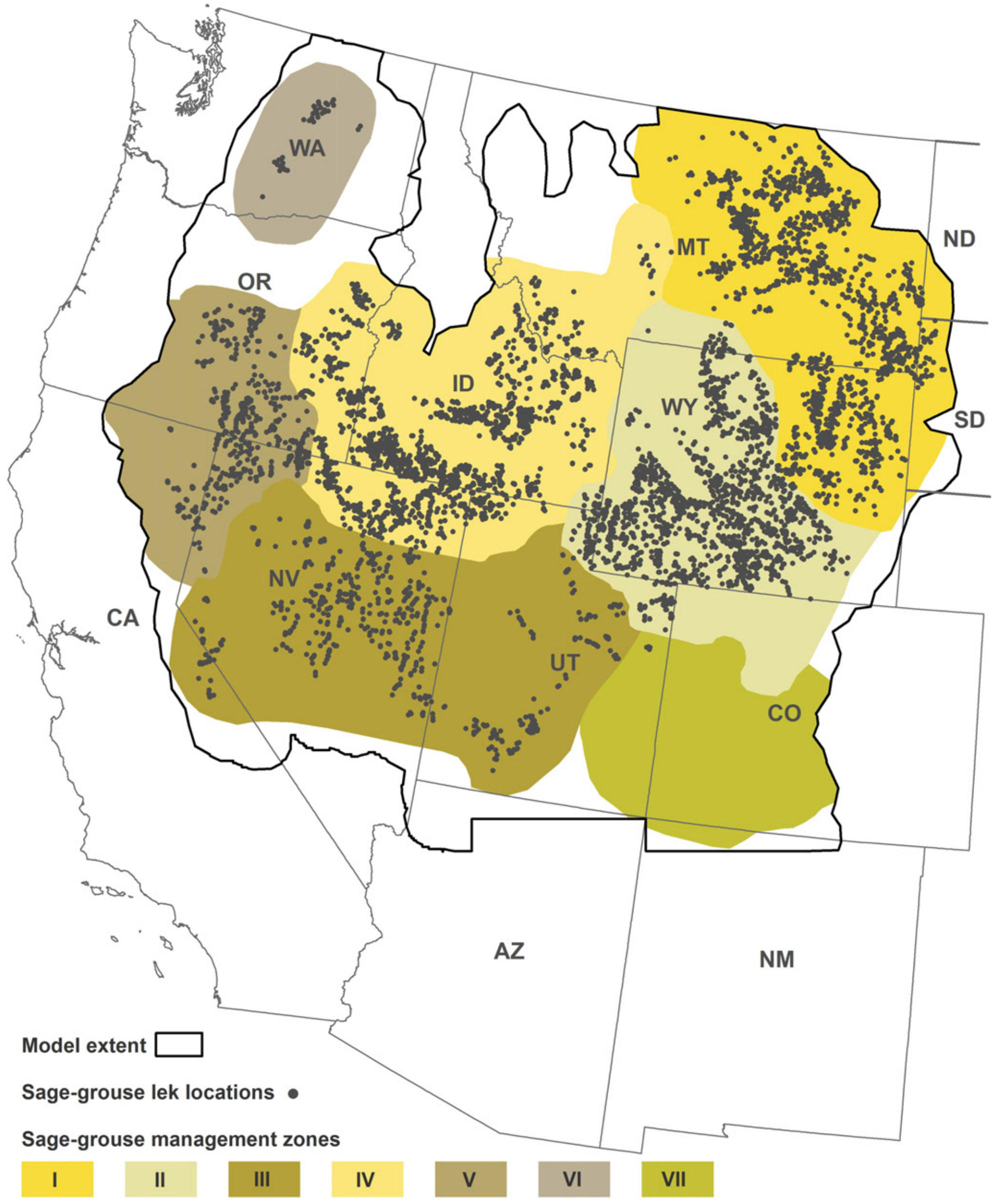

Figure 1. Study area encompassing >96% of sagebrush land-cover in western North America (>1.7million km2). Lek locations are representative of greater sage-grouse distributions in 10 of 11 western states containing populations (California, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah, Washington, and Wyoming; USA). Western Association of Fish and Wildlife Agencies Sage-Grouse Management Zones (I-VII) are representative of geographical population segments containing common ecological setting and stressors (Stiver et al., 2006). Small portions of sagebrush lands in northern Arizona and New Mexico were omitted, as there was no potential for overlap within the range of sage-grouse.

by 200 m, a distance for which each species had a nonzero probability of being detected using point counts (J. Tack unpublished data), and used the mean value of cells implicated within a buffered route.

We modeled the relationship between counts and environmental predictors for songbirds using Random Forest regression algorithms (Breiman, 2001). Random Forest uses a machine-learning approach and has demonstrated the ability to produce more accurate predictive models than generalized linear model (GLM) parameterizations, largely due to the ability to fit highly complex nonparametric interactions between predictors (Breiman, 2001). This modeling approach is less sensitive to many issues that confound inference from GLMs for use in species distributional models including collinearity among predictors while remaining robust to overfitting (Culter et al., 2007). We fit models using 5 000 trees following Random Forest model selection with the rfUtilities (parsimony value = 0.3) and Random Forest packages in program R (R Core Team, 2015). Spatial predictions were projected to 16.6-km^2 grid cells to generate continuous abundance surfaces for each songbird species. Grid cell size was roughly equivalent to sample unit area (200-m buffered BBS route). We evaluated the predictive capability of models by comparing the predicted to observed abundance classes using both model predictions and withheld data.

To aid data summary and data visualization, we grouped predicted songbird abundance surfaces into four classes. Class membership was determined by ranking songbird predictions (grid cells) from high to low and summarizing results into four bins, each containing 25% of the total predicted abundance. We classified these bins as "high," "moderate," "low," and "sparse." We used these classes for mapping products and as a metric to quantify co-occurrence estimates for sage-grouse and songbirds.

Dependence of Songbird Abundance on Sage-Grouse Distributions

Sage-grouse distributions were modeled as a first step in evaluating songbird dependence. Results applied as a predictor variable to evaluate spatial co-occurrence with BRSP, SAGS, and SATH abundance. Models

Table 1
List of predictor variables considered for predictive models of sagebrush obligate songbird counts. To characterize hierarchical selection of sagebrush-obligate birds, we summarized variables within a local (120-m) and landscape (6.4-km) scale. Variables were then measured using the focal mean (mean) or standard deviation (SD) of values within the sample unit of 200-m buffered Breeding Bird Survey routes

Variable (abbreviation)	Scales	Measures	Source
Vegetation			
All sagebrush (AllSB)	120 m, 6.4 km	Mean, SD	LANDFIRE EVT (2010)[1]
Low sagebrush (LowSB)	120 m, 6.4 km	Mean, SD	LANDFIRE EVT (2010)[1]
Tall sagebrush (TallSB)	120 m, 6.4 km	Mean, SD	LANDFIRE EVT (2010)[1]
Grassland/Herbaceous (GH)	120 m, 6.4 km	Mean, SD	LANDFIRE EVT (2010)[1]
Canopy cover (CC)	120 m, 6.4 km	Mean, SD	LANDFIRE EVT (2010)[1]
Pinyon-juniper (PJ)	120 m, 6.4 km	Mean, SD	LANDFIRE EVT (2010)[1]
Climate			
Annual drought index (ADI)	120 m	Value	USFS (1961-1990)[2]
Gross primary productivity (GPP)	120 m	Value	MODIS (2009-2013)[3]
Degree days > −5°C (DD)	120 m	Value	USFS (1961-1990)[2]
Mean annual precipitation (MAP)	120 m	Value	USFS (1961-1990)[2]
Landform			
Elevation	6.4 km	Mean	NED (2013)[4]
Flat	6.4 km	Mean, SD	NED (2013)[4,5]
Rough	6.4 km	SD	NED (2013)[4,5]
Slope	6.4 km	Mean, SD	NED (2013)[4,5]
Steep	6.4 km	Mean, SD	NED (2013)[4,5]
Topographic Wetness Index (TWI)	6.4 km	Mean, SD	NED (2013)[4,6]
Anthropogenic disturbance			
Human disturbance index (HDI)	120 m, 6.4 km	Mean, SD	NLCD (2011)[7]
Oil and gas wells (OG)	6.4 km		IHS Database (- 2014)[8]

[1] US Forest Service LANDFIRE Existing Vegetation Type (EVT) data reclassified following Johnson et al. (2011).
[2] Normalized climate data derived from weather station data from 1961 to 1990 (Rehfeldt, 2006).
[3] Moderate resolution imaging spectroradiometer (MODIS; MOD17A2).
[4] USGS national elevation dataset.
[5] Landforms classified using Landscape Connectivity and Pattern Tools ArcGIS package (Theobald 2007).
[6] TWI derived as the natural log of contributing upslope area (m^2) divided by the tangent of slope.
[7] Landcover types indicative of human presence from National Land Cover Dataset (Homer et al. 2015).
[8] Density of oil and gas wells.

were derived from the sage-grouse lek survey and location data. Lek surveys have been widely used by resource agencies to monitor trends in sage-grouse populations and are considered an index of relative distribution and abundance (Reese and Bowyer, 2007). Leks are sites where male and female sage-grouse congregate in the spring to breed and are typically the focal point for conservation actions targeting the species (Connelly et al., 2000). High fidelity to leks and surrounding nesting sites are typical in sage-grouse with birds congregating at the same location each year (Connelly et al., 2011). We presumed all lek locations to be fixed within the context of broad species patterns examined in this study but acknowledge that shifts in lek locations may occur due to persistent disturbance or alteration of vegetative cover (Hovick et al., 2015; Walker et al., 2007).

To account for high variability in survey intervals and sampling intensity, we used the average of annual maximum male counts for known lek locations over a 10-yr period (2004−2014) as the basis for estimating distributions and population abundance. Lek counts were collected and provided by 10 of 11 state wildlife agencies where sage-grouse are found (California, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah, Washington, and Wyoming). Only leks averaging one or more males counted within the 10-yr period examined were included in the analysis ($n = 6\,272$). Lek counts that averaged less than one male ($n = 3101$) were omitted from analyses. All leks included in the study were assumed to be active through the period examined (2004−2014).

Because sage-grouse abundance is used to prioritize conservation areas (USFWS, 2015), leks were segmented into high and low abundance classes and applied as categorical factors to examine coincidence of songbird and sage-grouse distributions. We considered leks clustered within the known dispersal radius of nesting females (6.4 km; Colorado Division of Wildlife, 2008) to be a single breeding group, similar to Doherty et al. (2010b). Leks occurring within common 6.4-km radii were assigned a weighted value equal to the sum of their male counts using a kernel function applied in program R (R Core Team, 2015). Weighted values for leks not occurring within 6.4 km of another were generated by assigning a value equal to their nonweighted survey count. Starting with the highest weighted lek values, we then summed the number of counted males (nonweighted) until 50% of the total count was reached. This resulted in a spatial segmentation of high and low abundance populations (i.e., leks; Doherty et al., 2011; Fig. 2).

We evaluated the association of BRSP, SAGS, and SATH abundance to sage-grouse distributions using the Berman test implemented in program Programita (Wiegand and Maloney, 2004; Wiegand and Maloney, 2014). By first developing a null (e.g., random) model, the Berman test provides a goodness-of-fit measure between a univariate point pattern (i.e., leks) and a continuous spatial covariate (i.e., predicted abundance of songbirds; Berman, 1986). The resulting test statistic (Z_1), allows for a statistical comparison between observed and null models. For our practice, the Berman test provides a framework to test the hypothesis that sage-grouse lek locations can be better described by the predicted abundance of sagebrush-obligate songbirds than random.

The original Berman test assumes a homogeneous point process model that does not consider spatially clustered patterns, such as those found in sage-grouse lek distributions (Knick and Hanser, 2011), and tends to overpredict the significance of spatial associations (Wiegand and Maloney, 2004). We accounted for this by using stochastic null models ($n = 999$), which retained the spatial clustering evident in sage-grouse lek locations (Wiegand and Maloney, 2014). Model simulations maintained the observed clustering structure in lek locations by approximating model fit ($\alpha < 0.05$) to multiple-point pattern summary statistics, as outlined in Wiegand et al. (2013). Models were developed and simulated separately for high-abundance leks. Procedures were replicated independently for population segments defined by sage-

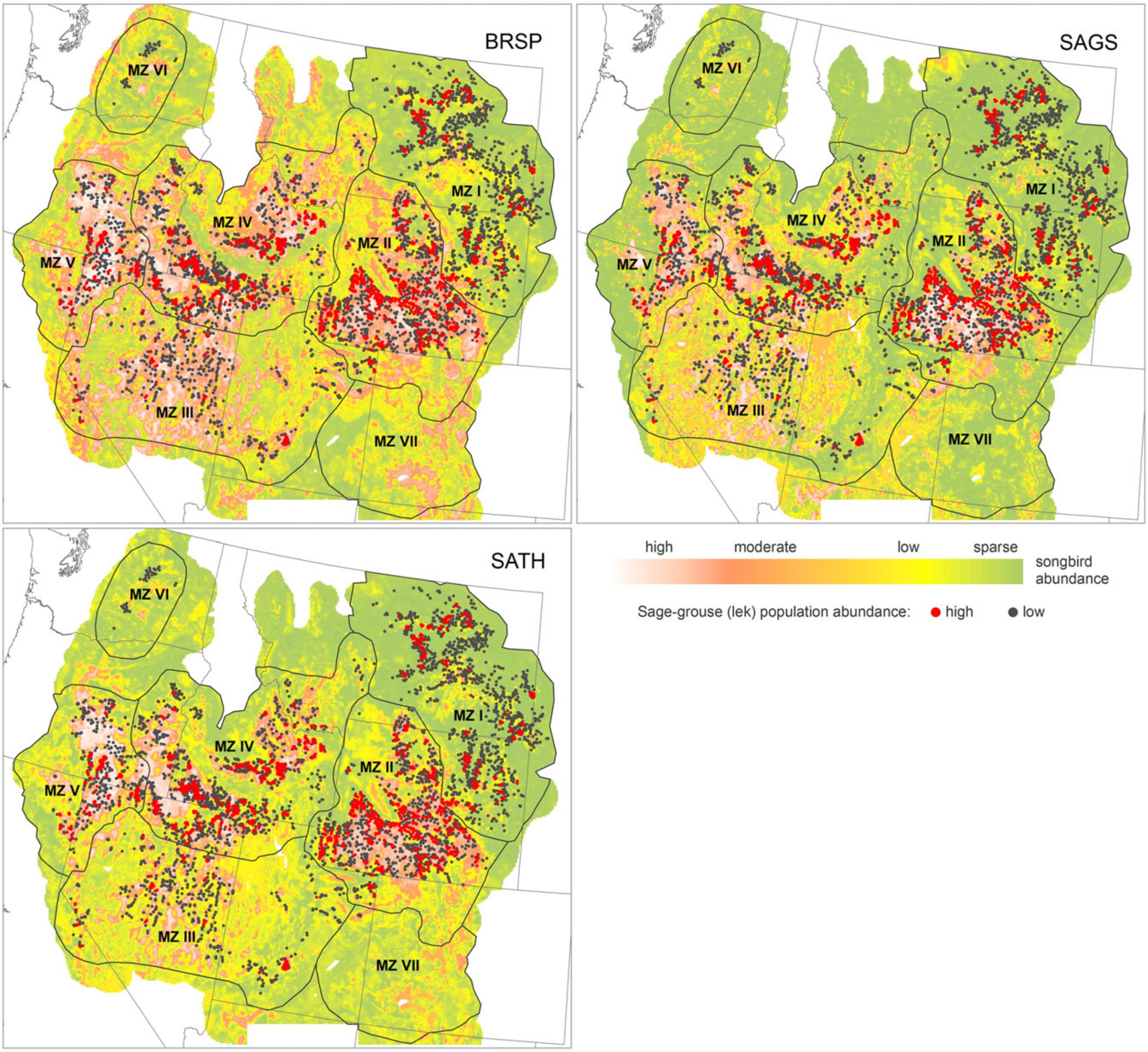

Figure 2. Predicted (BRSP) Brewer's sparrow, (SAGS) sagebrush sparrow, and (SATH) sage thrasher abundance shown within Western Association of Fish and Wildlife Agency Sage-Grouse Management Zones (MZ). Songbird abundance is displayed by high, moderate, low, and sparse. Class membership was determined by ranking predicted songbird abundance from high to low and summarizing results into four bins each containing 25% of the total. High abundance sage-grouse leks are representative high bird densities containing 50% of the known breeding population.

grouse management zones (Stiver et al., 2006; see Fig. 1) to account for variation in songbird abundance and sage-grouse distribution patterns throughout their range.

Songbird Coincidence with Sage-Grouse Habitat Restoration

Sage-grouse conifer removal treatments were used as a habitat restoration variable to summarize songbird coincidence. Conifer treatments, primarily in the Great Basin Region (management zones III — V), have increased exponentially since 2010 (NRCS, 2015c) to offset impacts of invasive woodlands that have been detrimental to sagebrush-obligate wildlife (Miller et al. 2000; Miller et al., 2011). Songbird coincidence was summarized by spatially linking conifer removal locations to BRSP, SAGS, and SATH abundance surfaces. We completed analyses using the zonal statistical function in program ArcGIS (Environmental Systems Research Institute, Redlands, California). Results were summarized within songbird abundance classes to determine the proportion of conifer treatments occurring within each. Conifer treatment data used for analysis were provided by the Natural Resources Conservation Service (NRCS)–Sage Grouse Initiative. All treatments identified sage-grouse habitat restoration as their primary objective and were completed from 2010 to 2015 or are slated for completion by 2021. Sites encompassed > 180 000 ha and were largely confined to private lands (NRCS, 2015c; Fig. 3).

Songbird Coincidence with Sage-grouse Landscape Protection

Coincidence of sage-grouse landscape protection with songbird abundance was assessed using Wyoming's sage-grouse core area strategy (State of Wyoming Executive Department, 2011) and sage-grouse FIAT priority areas (BLM, 2014; see Fig. 3). These actions are stratified geographically between the more productive eastern Rocky Mountain sagebrush environments (i.e., Wyoming) and dryer sage-steppe ecosystems of the Great Basin (i.e., FIAT). The efforts are mutually exclusive and provide an opportunity to examine potential songbird benefits under scenarios addressing landscape stressors

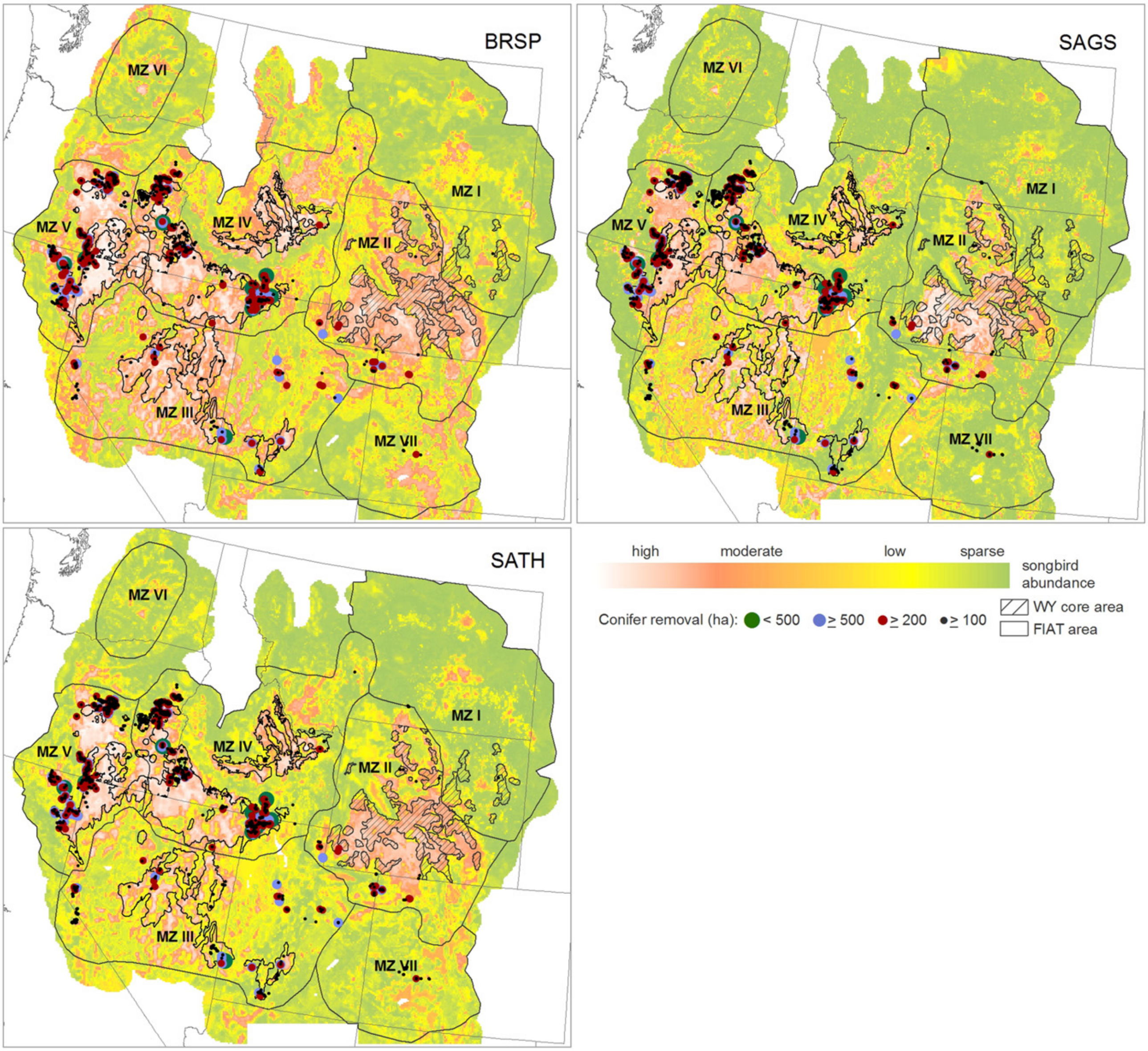

Figure 3. Predicted (BRSP) Brewer's sparrow, (SAGS) sagebrush sparrow, and (SATH) sage thrasher shown within Western Association of Fish and Wildlife Agency Sage-Grouse Management Zones (MZ). Songbird abundance is displayed by class; high, moderate, low, and sparse. Class membership was determined by ranking predicted songbird abundance from high to low and summarizing results into four bins each containing 25% of the total within the study area. Points representative of sage-grouse conifer removal treatments on private lands that were completed between 2010-2015 or are slated for completion by 2021. Wyoming's sage-grouse core areas and FIAT (Fire and Invasive Assessment Tool) priority areas (polygons) include private, state, and federally owned lands within Wyoming and the Great Basin region.

unique to each region. Wyoming's approach primarily focuses on human-induced fragmentation (e.g., rural subdivision and energy development) that has resulted in sharp reductions in sagebrush-obligate populations (Bayne et al., 2008; Braun et al., 2002; Doherty et al., 2011; Gilbert and Chalfoun, 2011; Ingelfinger and Anderson, 2004; Mutter et al., 2015; Stiver et al., 2006; USFWS, 2013; Walker et al., 2007). FIAT in the Great Basin attempts to address habitat loss and fragmentation due to wildfire and invasive plants that are widely recognized as a significant threat to sage-grouse (Miller et al., 2011; Stiver et al., 2006; USFWS, 2013) and songbirds (Knick et al., 2005).

We assessed songbird coincidence with Wyoming's core areas strategy by summarizing BRSP, SAGS, and SATH abundance surfaces within its boundaries (6.2 million ha; see Fig. 3). Summaries were stratified by songbird abundance classes to evaluate proportion of high to moderate populations occurring within. We then evaluated summaries to determine the area of high to moderate songbird abundance encompassed by core area boundaries relative to the total high to moderate population areas estimated within the state of Wyoming. Analyses were completed using the zonal statistical function in program ArcGIS.

Songbird coincidence with sage-grouse FIAT priorities was assessed following procedures outlined previously for Wyoming's core area strategy. Proportion of high to moderate songbird abundance was evaluated within FIAT priority polygons (16.4 million ha), and summaries were compared with high to moderate totals within the entire Great Basin (i.e., management zones III − V; see Fig. 3).

Results

Sagebrush land-cover variables were consistently the most important predictors in explaining variation for songbird counts, as two of the top three variables for each species contained some measure of sagebrush (Table 2). A partial dependence plot of all sagebrush land-cover types within 120 m, the second most important variable across

Table 2
Variable importance. Ranked variable importance from random forest models of songbird abundance for Brewer's sparrow (BRSP), sagebrush sparrow (SAGS), and sage thrasher (SATH). Importance was determined by percent increase in mean squared error (MSE) when variable was included in bootstrap samples. Dashed entries indicate that a variable was not included in a random forest model following model selection

	Variable rank (% increase in MSE)		
Variable	BRSP	SAGS	SATH
AllSB120 m	2 (29.06)	2 (31.56)	2 (27.06)
DD 120 m	1 (29.44)	–	3 (26.58)
AllSB 6.4 km mean	3 (25.18)	4 (29.23)	1 (31.77)
ADI 120 m mean	6 (23.24)	–	4 (24.93)
TallSB 120 m	7 (21.77)	1 (32.34)	8 (23.13)
ADI 120 m SQRT	5 (23.47)	–	6 (24.49)
TallSB 6.4 km mean	10 (18.58)	6 (26.33)	7 (23.67)
Steep 6.4 km SD	–	8 (17.99)	–
CC 6.4 km mean	–	3 (31.14)	15 (16.63)
Elev	9 (19.01)	–	9 (20.45)
AllSB 6.4 km SD	4 (24.17)	9 (16.56)	17 (15.47)
GPP mean	–	7 (25.12)	13 (17.79)
LowSB 6.4 km SD	8 (19.43)	–	12 (18.72)
MAP 120 m	20 (10.75)	5 (28.23)	5 (24.58)
Steep 6.4 km mean	–	10 (16.01)	–
GH 6.4 km SD	–	–	11 (19.65)
PJ 6.4 km SD	12 (18.07)	–	–
PJ 6.4 km mean	13 (17.97)	–	–
Flat 6.4 km mean	14 (17.56)	–	–
GH 46.4 km mean	–	–	14 (17.65)
LowSB 120 m	18 (14.43)	–	10 (19.76)
TallSB 6.4 km SD	11 (18.22)	–	19 (12.04)
LowSB 6.4 km mean	15 (16.6)	–	16 (16.56)
Slope 6.4 km SD	16 (15.12)	–	–
Flat 6.4 km SD	17 (15.08)	–	–
CC 46.4 km SD	–	–	18 (12.52)
Slope 46.4 km mean	19 (13.61)	–	–
GPP SD	–	–	20 (11.52)

DD indicates Degree days; ADI, Annual drought index; SQRT, square root; SD, standard deviation; CC, Canopy cover ; GPP, Gross primary productivity; MAP, Mean annual precipitation; GH, Grassland/Herbaceous; PJ, Pinyon-juniper.

species, shows that the relationship between songbird counts and sagebrush is positive and nonlinear. Furthermore, there is an apparent threshold across species at a mean of 40% sagebrush lands-cover

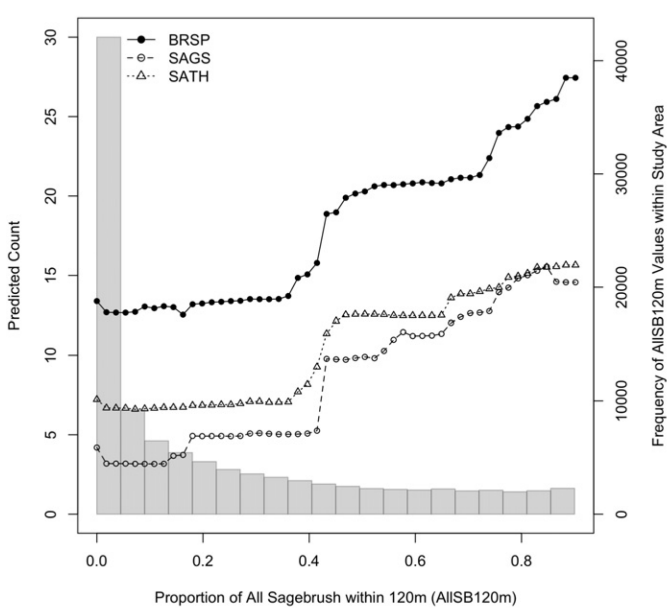

Figure 4. Partial dependence plot displays the predicted relationships between the proportion of all sagebrush classes within 120m (AllSB120m) and predicted counts of Brewer's sparrow (BRSP), sagebrush sparrow (SAGS), and sage thrasher (SATH). The background histogram represents the frequency of values for all sagebrush landscape cover (see Table 1; AllSB120m) contained within the study area.

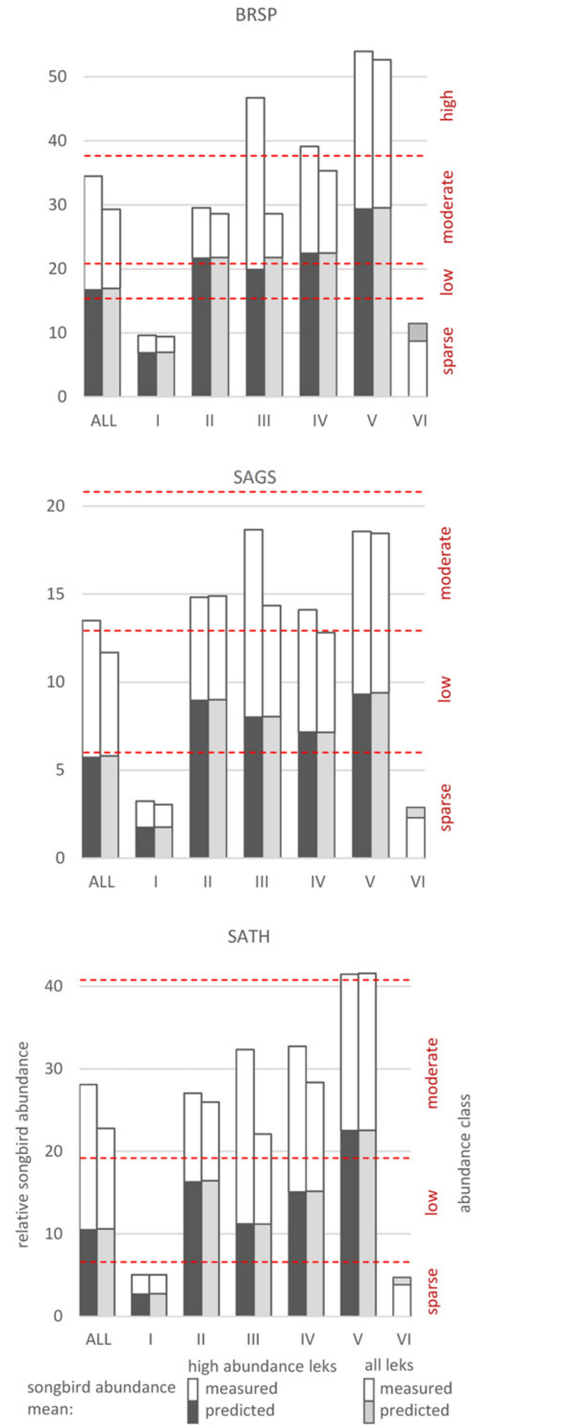

Figure 5. Stacked bar graph compares measured Brewer's sparrow (BRSP), sagebrush sparrow (SAGS), and sage thrasher (SATH) abundance means at lek sites (white) to predicted mean abundance (black/gray) generated using null model lek distributions. Comparisons were made among high density leks (black) and all leks (gray) by management zone (I-VI) and for all management zones combined (ALL). Management zone VI did not contain any high abundance sage-grouse leks. Right axis representative of songbird abundance classes. Class membership was determined by ranking predicted songbird abundance from high to low and summarizing results into four bins each containing 25% of the total within the study area.

(Fig. 4). The distribution of this particular covariate across the landscape is highly skewed, with > 76% of sampled sites containing values of "all sagebrush" lower than the apparent threshold. While sagebrush was an important predictor in models, climate (drought indices and

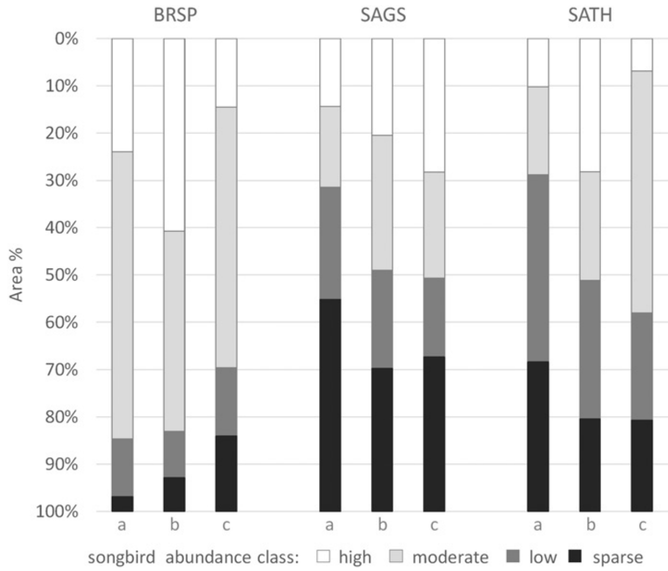

Figure 6. Stacked bar graph depicting relative coincidence of Brewer's sparrow (BRSP), sagebrush sparrow (SAGS), and sage thrasher (SATH) contained within (a) conifer removal treatments (>180,000 ha) (b) Wyoming's sage grouse core areas (6.2 million ha), and (c) FIAT (Fire and Invasive Assessment Tool) priority areas (16.8 million ha). Coincidence was estimated as a percent area encompassed by abundance classes; high, moderate, low, and sparse.

temperature) and landscape topography and elevation were influential in predicting counts across species (see Table 2).

Models for BRSP, SAGS, and SATH explained 17%, 17%, and 37% of the variation in BBS count data, respectively, when comparing out-of-sample data with training data within the Random Forest algorithm. All species models were good classifiers of the lowest abundance threshold for predicted and withheld data (> 76%), while misclassification rates increased with a decreasing sample size of the largest abundance bins. However, routes were more likely misclassified as adjacent abundance bins (e.g., lowest abundance class misclassified as second lowest abundance class).

Berman's test suggested that range-wide measures of songbird abundance were higher at lek sites ($P < 0.0001$, $Z_1 = 9.6$ [BRSP], 9.4 [SAGS], 9.9 [SATH]) than null model predictions, indicating that BRSP, SAGS, and SATH abundances were positively associated with lek locations (Fig. 5). High-abundance sage-grouse leks (i.e., 50% of the population containing leks with the highest male counts) averaged 15% (BRSP), 13% (SAGS), and 19% (SATH) higher songbird abundance versus all sage-grouse leks. Across their range, sage-grouse distributions were associated with higher BRSP abundance compared with SAGS and SATH (see Fig. 5).

Spatial variability in songbird abundance patterns influenced population effect size and rates of co-occurrence among songbirds and sage-grouse populations by management zone. Lek locations were associated with higher songbird abundance ($P < 0.001$, $\overline{Z}_1 = 5.6$ [BRSP], 5.4 [SAGS], 5.5 [SATH]) in all but zone VI ($P \geq 0.29$, $Z_1 = -1$ [BRSP], 0.6 [SAGS], −0.7 [SATH]; see Figs. 2 and 5). Low songbird predictions in management zones I and VI resulted in measured abundance rates 80% (BRSP, SAGS) and 86% (SATH) below management zones II−V (see Figs. 2 and 5).

Table 3
Percentage of separate high to moderate songbird populations encompassed by sage-grouse landscape protection strategies, Wyoming's core area strategy, and Fire and Invasive Assessment Tool priorities within the entire state of Wyoming and the Great Basin (see Fig. 3)

	Wyoming	Great Basin
BRSP	39.5%	39.0%
SAGS	48.0%	50.6%
SATH	49.9%	54.5%

BRSP indicates Brewer's sparrow; SAGS, sagebrush sparrow; SATH, sage thrasher.

Sage-grouse populations were associated with highest BRSP and SAGS abundance in management zones III and V (see Figs. 2 and 5). Associated SATH abundance was highest in zone V (see Figs. 2 and 5).

Coincidence of songbird abundance with conifer treatments, Wyoming's core area strategy, and FIAT priority areas were similar to co-occurrence trends observed with sage-grouse distributions. Greater than 85% of conifer cuts targeting sage-grouse habitat restoration occurred within high to moderate BRSP abundance areas (see Figs. 3 and 6). Conversely, only ~30% of sage-grouse conifer treatments occurred within high to moderate abundance SAGS and SATH areas (see Figs. 3 and 6). Wyoming's core areas and FIAT priorities contained a greater proportion of high to moderate abundance areas for SAGS (49−51%) and SATH (52−58%) than observed in conifer treatments (see Figs. 3 and 6). Core area and FIAT boundaries encompassed 40% and 39% (BRSP), 48% and 51% (SAGS), and 50% and 55% (SATH), respectively, of high to moderate abundance songbird areas occurring separately within Wyoming and the Great Basin (see Fig. 3; Table 3).

Discussion

We provide the first landscape view of sagebrush-obligate songbird distribution and abundance linked to ecological gradients across the western United States. Relating bird abundance to ecological patterns explained 19−37% of variation in count data. Resulting spatially explicit surfaces offer a tremendous improvement to the resolution in predicted bird distributions over traditional BBS distribution maps. Our continuous estimates of songbird abundance are consistent with coarse distributions of breeding ranges of each species (Martin and Carlson, 1998; Reynolds et al., 1999; Rotenberry et al., 1999). Sagebrush land-cover predictors were primary determinants of songbird abundance (see Table 2). Each songbird model independently inferred a threshold of > 40% sagebrush landscape cover (i.e., percentage of sagebrush shrubland occurring within a 16.6-km^2 sample grid) as an ecological minimum above which songbird abundances nearly doubled (see Fig. 4); predictions were further enhanced by attributes explaining drought, temperature, topography, and elevation. Previous sage-grouse research shows 90% of active leks are set in landscapes with > 40% sagebrush land cover (Knick et al., 2013), and high probability of lek persistence is associated with > 50% land cover (Wisdom et al., 2011), further suggesting long-term viability of songbird and sage-grouse breeding habitats may be closely linked through this common landscape requisite. Not surprisingly, our findings are also consistent with past regional-scale evaluations that identify large patch size and continuous sagebrush land cover as factors predictive of sagebrush songbird distributions (Knick and Rotenberry, 1995; Wiens et al., 1987).

Our point-process analyses quantitatively support the long-held notion that sage-grouse distributions spatially predict songbird abundance in sagebrush ecosystems. Populations for each of three species aligned themselves with sage-grouse distributions ($P < 0.0001$, $Z_1 > 9.4$; see Figs. 2 and 5). Range-wide, landscapes containing > 50% of males on leks also supported 13−19% higher songbird abundance compared with all leks. Patterns in sage-grouse and songbird configurations converged within landscapes of high sagebrush land cover (see Fig. 4) with concentrations largely centered within sage-grouse management zones II−V (see Fig. 2). Previous studies demonstrate the importance of landscape features in shaping songbird (Knick et al., 2008) and sage-grouse distributions (Doherty et al., 2010a; Donnelly et al., 2016) and identify common threats influencing their distribution and abundance. In particular, sage-grouse and songbirds are sensitive to anthropogenic disturbance including energy development (Gilbert and Chalfoun, 2011; Walker et al., 2007), cultivation (Knight et al., 2014; Tack, 2009), conifer encroachment (Baruch-Mordo et al., 2013; Holmes et al., 2017-this issue), and exotic annual grass invasion (Earnst and Holmes, 2012).

In addition to quantifying range-wide alignment, our spatial analyses also identified regional variation in songbird abundance that is best explained by common threats facing grouse and passerines. Most apparent are differences between desert sage-steppe habitats of the Great Basin (management zones III − V) and the more eastern and productive Rocky Mountain sagebrush environments (management zones I, II; see Figs. 2 and 5). In the Great Basin, sage-grouse and songbirds are caught within the "big squeeze" of expanding conifer impacts at mid to upper elevations and catastrophic wildfire and cheatgrass invasion in dryer low-lying habitats (Chambers et al., 2014b; Davies et al., 2011). Targeted tree removal in the mid to upper elevations has expanded availability of sage-grouse nesting habitat (Severson et al., 2016) and increased BRSP abundance by + 55% (Holmes et al., 2017-this issue). Our co-occurrence analyses found 85% of restorative conifer cuts, all conducted in a manner similar to Holmes et al., 2016, coincide with areas of high to moderate BRSP abundance, suggesting comparable benefits may be accruing over roughly 180 000 ha of the Great Basin (see Figs. 3 and 6). Outcome-based evaluations following tree removal (Holmes et al., 2016) corroborate previous studies that suggested BRSP as a primary beneficiary of sagebrush restoration occurring through conifer removal (Rowland et al., 2006; Hanser and Knick, 2011).

Findings suggest that reducing wildfire and cheatgrass threats will benefit songbird composition and abundance different from that of conifer removal. Greater than 50% of FIAT priorities were made up of areas containing high to moderate SAGS and SATH abundance (see Fig. 6). These areas also represented 51% and 55% of the total estimated SAGS and SATH abundance within the Great Basin (see Table 3). This compares to conifer restorations that occurred within high to moderate abundance areas of these same species only ~30% of the time (see Fig. 6) largely because SAGS and SATH occupy dryer and lower elevation sites (Martin and Carlson, 1998; Reynolds et al., 1999) less affected by conifer encroachment (Miller et al., 2008; Davies et al., 2011). High rates of co-occurrence in FIAT landscapes are where sage-grouse conservation actions are most likely to translate into community-level benefits for SAGS and SATH (Hanser and Knick, 2011).

Threats facing sage-grouse and songbirds in the Rocky Mountain states (management zones I, II; see Fig. 2) are primarily anthropogenic including energy development (Harju et al., 2010; Gilbert and Chalfoun, 2011), subdivision, and cultivation of sagebrush rangelands. As 1 of 11 sage-grouse states, Wyoming contains 37% of the species-wide distribution. Wyoming's core area strategy focuses on minimizing landscape stressors within a quarter of the state's land base containing 80% of the state's grouse population (see Fig. 3). Since 2010, $147 million have been invested in conservation easements to reduce subdivision impacts in core areas (Copeland et al., 2013a; NRCS, 2015c). Co-occurrences show that restrictive energy policy and easements are also helping reduce fragmentation across ~40 − 50% of the areas containing high to moderate songbird abundance in the state (see Table 3). Habitat diversity captured within Wyoming's landscape protection strategies likely explain elevated coincidence of sage-grouse protections with both SAGS and SATH (Wiens et al., 1987). Low co-occurrence in other Rocky Mountain states (i.e., management zone I) is more an artifact of geography than of habitat quality or threats (Miller et al., 2011); states such as eastern Montana and the Dakotas lay within a transition zone from sagebrush to prairie ecoregions. Intact sagebrush landscapes in these geographies may support high abundance of songbird species beyond the scope of our evaluation (e.g., lark bunting [*Calamospiza* melanocorys] and western meadowlark [*Sturnella* neglecta]; Lipsey, 2015).

Implications

To date, sagebrush songbird conservation has garnered comparatively less attention than sage-grouse. Conservation partners predict that by 2020 habitat restoration and protection actions targeting sage-grouse will increase by > 35 million ha (NRCS, 2015b; USFWS, 2015). The future of sagebrush songbirds may hinge in part on our ability to identify mutually beneficial outcomes generated through sage-grouse conservation, as suggested by the 55 − 85% increase in passerine abundance in conifer cuts (Holmes et al., 2016) designed to expand the availability of sage-grouse nesting habitat (Severson et al., 2016). We offer our mapping products as additional decision support tools to further accelerate the targeting and integration of community-level benefits resulting from sage-grouse conservation. Newly available spatial datasets mapping conifer extent and density (Falkowski et al., 2017-this issue) can be combined with our predictive songbird maps to further enhance practitioners' ability to regionally target ongoing sagebrush habitat restorations.

Acknowledgments

The authors thank the NRCS Sage Grouse Initiative for helping foster and coordinate this science. We also thank those who collected and provided sage-grouse lek data for analyses in 10 states: the California Department of Fish and Game; Idaho Fish and Game; Montana Fish Wildlife and Parks; Nevada Department of Wildlife; North Dakota Game and Fish Department; Oregon Department of Fish and Wildlife; South Dakota Game, Fish, and Parks; Utah Division of Wildlife Resources; Washington Department of Fish and Wildlife; and Wyoming Game and Fish Department.

References

Andelman, S.J., Fagan, W.F., 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Science 97, 5954–5959.
Baruch-Morodo, S., Evens, J.S., Severson, J.P., Naugle, D.E., Maestas, J., Kiesecker, J.M., 2013. Saving sage-grouse from the trees: a proactive solution to reducing a key threat to a candidate species. Biology Conservation 167, 233–241.
Bayne, E.M., Habib, L., Boutin, S., 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conservation Biology 22, 1186–1193.
Berman, M., 1986. Testing for spatial association between a point process and another stochastic process. Journal of the Royal Statistical Society: Series C (Applied Statistics) 35, 54–62.
[BLM] Bureau of Land Management, 2014. Greater sage-grouse wildfire, invasive annual grasses & conifer expansion assessment (Fire and Invasive Assessment Tool). Prepared by Fire and Invasive Assessment Team (Appendix 5) 43 pp.
[BLM] Bureau of Land Management, [USFS] US Forest Service, 2015,. Bureau of Land Management and Forest Service greater sage-grouse 98 land use plans and environmental impact statement record of decisions.
Bottrill, M.C., Joseph, L.N., Carwardine, J., Bode, M., Cook, C., Game, E.T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R.L., Walker, S., Wilson, K.A., Possingham, H.P., 2008. Is conservation triage just smart decision making? Trends in Ecology and Evolution 23, 649–654.
Boyd, C.S., Johnson, D.D., Kerby, J.D., Svejcar, T.J., Davies, K.W., 2014. Of grouse and golden eggs: can ecosystems be managed within a species-based regulatory framework? Rangeland Ecology & Management 67, 358–368.
Braun, C.E., Oedekoven, O.O., Aldridge, C.L., 2002. Oil and gas development in western North America: effects on sagebrush steppe avifauna with particular emphasis on sage grouse. Presented at the Trans North America Wildlife Natural Resource Conference. Wildlife Management Institute, Washington, DC, USA, pp. 337–349.
Breiman, L., 2001. Random forests. Machine Learning 45, 5–32.
Caro, T.M., O'Doherty, G., 1999. On the use of surrogate species in conservation biology. Conservation Biology 13, 805–814.
Chambers, J.C., Pyke, D.A., Maestas, J.D., Pellant, M., Boyd, C.S., Campbell, S.B., Espinosa, S., Havalina, D.W., Mayer, K.E., Wuenschel, A., 2014. Using resistance and resilience concepts to reduce impacts of invasive annual grasses and altered fire regimes on the sagebrush ecosystem and greater sage-grouse: a strategic multi-scale approach (General Technical Report No. RMRS-GTR-326). US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA p. 76.
Colorado Division of Wildlife, 2008. Colorado greater sage-grouse conservation plan. Colorado Parks and Wildlife, Fort Collins, CO, USA p. 297.
Connelly, J.W., Hagen, C.A., Schroeder, M.A., 2011. Characteristics and dynamics of greater sage-grouse populations. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats No. 38. University of California Press, Berkeley, CA, USA, pp. 53–67.
Connelly, J.W., Schroeder, M.A., Sands, A.R., Braun, C.E., 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28, 967–985.
Copeland, H.E., Pocewicz, A., Naugle, D.E., Griffiths, T., Keinath, D., Evans, J., Platt, J., 2013a. Measuring the effectiveness of conservation: a novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. PLoS ONE 8, e67261.
Copeland, H.E., Sawyer, H., Monteith, K.L., Naugle, D.E., Pocewicz, A., Graf, N., Kauffman, M.J., 2014. Conserving migratory mule deer through the umbrella of sage-grouse. Ecosphere 5, art117.

Culter, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J.C., Lawler, J.J., 2007. Random forests for classification in ecology. Ecology 11, 2783–2792.
Davies, K.W., Boyd, C.S., Beck, J.L., Bates, J.D., Svejcar, T.J., Gregg, M.A., 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biology Conservation 144, 2573–2584.
Doherty, K.E., Naugle, D.E., Copeland, H.E., Pocewicz, A., Kiesecker, J.M., 2011. Energy development and conservation tradeoffs: systematic planning for sage-grouse in their eastern range. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats No. 38. University of California Press, Berkeley, CA, USA, pp. 505–516.
Doherty, K.E., Naugle, D.E., Walker, B.L., 2010a. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. Journal of Wildlife Management 74, 1544–1553.
Doherty, K.E., Tack, J.D., Evens, J.S., Naugle, D.E., 2010. Mapping breeding densities of greater sage-grouse: a tool for range-wide conservation planning. United States Bureau of Land Management completion report: Interagency Agreement #L10PG00911, p. 31.
Donnelly, J.P., Naugle, D.E., Hagen, C.A., Maestas, J.D., 2016. Public lands and private waters: scarce mesic resources structure land tenure and sage-grouse distributions Ecosphere 7, 1-15.
Earnst, S.L., Holmes, A.L., 2012. Bird-Habitat relationships in interior Columbia Basin shrubsteppe. The Condor 114, 15–29.
Falkowski, M.J., Evens, J.S., Naugle, D.E., Henaren Khalyani, A., Hagen, C.A., Ponzanovic, A., Maestas, J.D., 2017. Mapping invasive woody species in support of proactive prairie grouse conservation in Western North America. Rangeland Ecology & Management 70, 15–24 (this issue).
Gilbert, M.M., Chalfoun, A.D., 2011. Energy development affects populations of sagebrush songbirds in Wyoming. Journal of Wildlife Management 75, 816–824.
Hanser, S.E., Knick, S.T., 2011. Greater sage-grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats No. 38. University of California Press, Berkeley, CA, USA, pp. 475–488.
Harju, S.M., Dzialak, M.R., Taylor, R.C., Hayden-Wing, L.D., Winstead, J.B., 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74, 437–448.
Hobbs, R.J., Kristjanson, L.J., 2003. Triage: how do we prioritize health care for landscapes? Ecology Management Restoration 4, S39–S45.
Holmes, A.L., Maestas, J., Naugle, D.E., 2017. Songbird responses to mechanical removal of western juniper in sagebrush-steppe. Rangeland Ecology & Management 70, 87–94 this issue.
Homer, C.G., Dewitz, J.A., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N.D., Wickham, J.D., Megown, K., 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing 81, 345–354.
Hovick, T.J., Allred, B.W., Elmore, R.D., Fuhlendorf, S.D., Hamilton, R.G., Breland, A., 2015. Dynamic disturbance processes create dynamic lek site selection in a prairie grouse. PLoS ONE 10, e0137882.
Ingelfinger, F., Anderson, S., 2004. Passerine response to roads associated with natural gas extraction in a sagebrush steppe habitat. Western North American Naturalist 64, 385–395.
Johnson, D.H., Holloran, M.J., Connelly, J.W., Hanser, S.E., Amundson, C.L., Knick, S.T., 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats, studies in avian biology. University of California Press, Berkeley, CA, USA, pp. 407–450.
Joseph, L.N., Maloney, R.F., Possinghamp, H.P., 2009. Optimal allocation of resources among threatened species: a project prioritization protocol. Conservation Biology 23, 328–338.
Knick, S.T., Dobkin, D.S., Rotenberry, J.T., Schroeder, M.A., Vander Haegen, W.M., van Riper, C., 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. The Condor 105, 611–634.
Knick, S.T., Hanser, S.E., 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats No 38. University of California Press, Berkeley, CA, USA, pp. 383–406.
Knick, S.T., Hanser, S.E., Leu, M., 2014. Ecological scale of bird community response to piñon-juniper removal. Rangeland Ecology & Management 67, 553–562.
Knick, S.T., Hanser, S.E., Preston, K.L., 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: implications for population connectivity across their western range, U.S.A. Ecology and Evolution 3, 1539–1551.
Knick, S.T., Holmes, A.L., Miller, R.F., 2005. The role of fire in structuring sagebrush habitats and bird communities. Studies in Avian Biology 30, 1–13.
Knick, S.T., Rotenberry, J.T., 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. Conservation Biology 9, 1059–1071.
Knick, S.T., Rotenberry, J.T., Leu, M., 2008. Habitat, topographical, and geographical components structuring shrubsteppe bird communities. Ecography 31, 389–400.
Knight, E.C., Mahony, N.A., Green, D.J., 2014. Crop type influences edge effects on the reproduction of songbirds in sagebrush habitat near agriculture. Avian Conservation Ecology 9, 8.
LANDFIRE, 2012. LANDFIRE 1.0.0 existing vegetation type layer. US Geological Survey Available at: http://landfire.cr.usgs.gov/viewer/. Accessed 1 September 2015.
Lipsey, M.K., 2015. Cows and plows: science-based conservation for grassland songbirds in agricultural landscapes. University of Montana, Missoula, MT, USA.
Mac, M.J., Opler, P.A., Pucket, C.E., Doran, P.D., 1998. Status and trends of the nation's biological resources (No. Vol. 1 and 2). US Geological Survey, Reston, VA, USA.
Martin, J.W., Carlson, B.A., 1998. Sage sparrow (*Amphispiza belli*). In: Poole, A., Gill, F. (Eds.), The birds of North America online. Cornell Lab of Ornithology, Ithaca, NY, USA.
Meinke, C.W., Knick, S.T., Pyke, D.A., 2009. A spatial model to prioritize sagebrush landscapes in the Intermountain West (U.S.A.) for restoration. Restoration Ecology 17, 652–659.
Miller, R.F., Eddleman, L.E., 2001. Spatial and temporal changes of sage grouse habitat in the sagebrush biome (No. 151). Agricultural Experiment Station, Oregon State University, Corvallis, OR, USA.
Miller, R.F., Knick, S.T., Pyke, D.A., Meinke, C.W., Hanser, S.E., Wisdom, M.J., Hild, A.L., 2011. Greater sage-grouse: ecology and characteristics of sagebrush habitats and limitations to long-term conservation. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats, studies in avian biology. University of California Press, Berkeley, CA, USA, pp. 145–184.
Miller, R.F., Svejcar, T.J., Rose, J.A., 2000. Impacts of western juniper on plant community composition and structure. Journal of Range Management 53, 574–585.
Miller, R.F., Tausch, R.J., McArthur, E.D., Johnson, D.D., Sanderson, S.C., 2008. Development of post settlement piñon–juniper woodlands in the Intermountain West: a regional perspective. Research Paper Report No. RMRS-RP-69. USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, CO, USA.
Mutter, M., Pavlacky, D.C., Van Lanen, N.J., Grenyer, R., 2015. Evaluating the impact of gas extraction infrastructure on the occupancy of sagebrush-obligate songbirds. Ecology Application 25, 1175–1186.
[NABCI] North American Bird Conservation Initiative, US Committee, 2014m. The state of the birds 2014 report. US Department of Interior, Washington, DC, USA.
NatureServe Explorer, 2012. NatureServe Explorer ecological systems records [WWW Document]. Available at: http://explorer.natureserve.org/. Accessed 21 September 2015.
Noss III, R.F., LaRoe, E.T., Scott, J.M., 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. National Biological Service Biological Report 28.
[NRCS] Natural Resources Conservation Service, 2015a. Sage Grouse Initiative; Success on the range. US Department of Agriculture, Natural Resources Conservation Service, Washington, DC, USA.
[NRCS] Natural Resources Conservation Service, 2015b. Sage Grouse Initiative 2.0 investment strategy, FY 2015-2018. US Department of Agriculture, Natural Resources Conservation Service., Washington, DC, USA.
[NRCS] Natural Resources Conservation Service, 2015c. Outcomes in conservation: Sage Grouse Initiative. US Department of Agriculture, Natural Resources Conservation Service, Washington, DC, USA.
Pardieck, K.L., Ziolkowski, D.J., Hudson, M.-A.R., 2015. North American breeding bird survey dataset 1966 − 2014, version 2014.0. US Geological Survey, Patuxent Wildlife Research Center, Patuxent, MD, USA.
Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., Gibbons, D.W., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365, 335–337.
R Core Team, 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Reese, K.P., Bowyer, R.T., 2007. Monitoring populations of sage-grouse, station bulletin. University of Idaho, College of Natural Resources, Moscow, ID, USA.
Rehfeldt, G.L., 2006. A spline model of climate for the western United States. Gen. Tech. Rep. RMRS-GTR-165. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.
Reynolds, T.D., Rich, T., Stephens, D., 1999. Sage thrasher (*Oreoscoptes montanus*). In: Poole, A., Gill, F. (Eds.), Birds of North America online. Cornell Lab of Ornithology, Ithaca, NY, USA Available at: https://birdsna.org. Accessed 11 October 2015.
Rich, T., Wisdom, M.J., Saab, V.A., 2005. Conservation of sagebrush steppe birds in the interior Columbia Basin. In: Ralph, C.J., Rich, T., Long, L. (Eds.), Proceedings of the Third International Partners in Flight Conference. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, USA, pp. 589–606.
Rotenberry, J.T., Patten, M.A., Preston, K.L., 1999. Brewer's sparrow (*Spizella breweri*). In: Poole, A., Gill, F. (Eds.), The birds of North America. The Birds of North America, Inc., Ithaca, NY, USA.
Rotenberry, J.T., Wiens, J.A., 2009. Habitat relations of shrubsteppe birds: a 20-year retrospective. The Condor 111, 401–413.
Rowland, M.M., Wisdom, M.J., Suring, L.H., Meinke, C.W., 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biology Conservation 129, 323–335.
Schroeder, M.A., Aldridge, C.L., Apa, A.D., Bohne, J.R., Braun, C.E., Bunnell, S.D., Connelly, J.W., Deibert, P.A., Gardner, S.C., Hilliard, M.A., Kobriger, G.D., McAdam, S.M., McCarthy, C.W., McCarthy, J.J., Mitchell, D.L., Rickerson, E.V., Stiver, S.J., 2004. Distribution of sage-grouse in North America. The Condor 106, 363–376.
Schroeder, M.A., Young, J.R., Braun, C.E., 1999. Sage Grouse (*Centrocercus urophasianus*). In: Poole, A., Gill, F. (Eds.), Birds of North America online. Cornell Lab of Ornithology, Ithaca, NY, USA.
Severson, J.P., Hagen, C.A., Maestas, J.D., Naugle, D.E., Forbes, J.T., Reese, K.P., 2017. Short-term response of sage-grouse nesting to conifer removal in the northern Great Basin. Rangeland Ecology & Management 70, 50–58 (this issue).
Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Conservation Biology and Biodiversity Strategy 83, 247–257.
State of Wyoming Executive Department, 2011. Greater sage-grouse core area protection executive order 2011-5. Wyoming Office of the Governor, Cheyenne, WY, USA.
Stiver, S.J., Apa, A.D., Bunnell, S.D., Deibert, P.A., Gardner, S.C., Hilliard, M.A., McCarthy, C.W., Schroeder, M.A., 2006. Greater sage-grouse comprehensive conservation strategy. Western Association of Fish and Wildlife Agencies, Cheyenne, WY, USA.
Tack, J.D., 2009. Sage-grouse and the human footprint: Implications for conservation of small and declining populations. University of Montana, Missoula, MT, USA.
[USFWS] US Fish and Wildlife Service, 2015. Endangered and threatened wildlife and plants; 12-month finding on a petition to list greater sage-grouse *(Centrocercus urophasianus)* as an endangered or threatened species; proposed rule (No. Federal Register 80). US Fish and Wildlife Service, Denver, CO, USA.

[USFWS] US Fish and Wildlife Service, 2013. Greater sage-grouse *(Centrocercus urophasianus)* conservation objectives: final report. US Fish and Wildlife Service, Denver, CO, USA.
[USFWS] US Fish and Wildlife Service, 2010. Endangered and threatened wildlife and plants; 12 month findings for petitions to list the greater sage-grouse *(Centrocercus urophasianus)* as threated or endangered; proposed rule (No. Federal Register 75). US Fish and Wildlife Service, Denver, CO, USA.
[USFWS] US Fish and Wildlife Service, 2008. Birds of conservation concern 2008. Department of Interior, Fish and Wildlife Service, Division of Migratory Birds, Arlington, VA, USA.
Vander Haegen, W.M., 2007. Fragmentation by agriculture influences reproductive success of birds in a shrubsteppe landscape. Ecology Applications 17, 934–947.
Walker, B.L., Naugle, D.E., Doherty, K.E., 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71, 2644–2654.
West, N.E., 1999. Synecology and disturbance regimes of sagebrush steppe ecosystems. In: Entwistle, P.G., DeBolt, A.M., Kaltenecker, J.H., Steenhof, K. (Eds.), Sagebrush steppe ecosystems symposium. Bureau of Land Management Idaho State Office, Boise, ID, USA, pp. 15–26.
Wiegand, T., Maloney, K.A., 2004. Rings, circles, and null-models for point pattern analysis in ecology. Oikos 104, 209–229.
Wiegand, T., He, F., Hubbell, S.P., 2013. A systematic comparison of summary characteristics for quantifying point patterns in ecology. Ecography 36, 92–103.
Wiegand, T., Maloney, K.A., 2014. A handbook of spatial point pattern analysis in ecology. Chapman and Hall/CRC Press, Boca Raton, FL, USA.
Wiens, J.A., Rotenberry, J.T., Van Horne, B., 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48, 132–147.
Wisdom, M.J., Meinke, C.W., Knick, S.T., Schroeder, M.A., 2011. Factors associated with extirpation of sage-grouse. In: Knick, S.T., Connelly, J.W. (Eds.), Greater sage-grouse: ecology and conservation of a landscape species and its habitats, studies in avian biology. University of California Press, Berkeley, CA, USA, pp. 451–474.