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Research Article

Anthropogenic and Natural Disturbance Differentially Affect Sagebrush Bird Habitat Use

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ABSTRACT North American sagebrush (*Artemisia* spp.)-obligate birds are experiencing steep population declines due in part to increased disturbance, mainly human-caused, across their range. At the eastern edge of the sagebrush steppe, this issue may potentially be exacerbated because of natural disturbance by black-tailed prairie dogs (*Cynomys ludovicianus*). Our goal was to compare local and landscape models of habitat use by greater sage-grouse (*Centrocercus urophasianus*), Brewer's sparrow (*Spizella breweri*), and sage thrasher (*Oreoscoptes montanus*) with models including effects of natural (i.e., prairie dog) and anthropogenic disturbance. We used a combination of field data collection, and state and national datasets for the Thunder Basin National Grassland, eastern Wyoming, USA, to understand the factors that influence lek attendance by sage-grouse and habitat use by 2 passerines in this system. For all 3 species, models including big sagebrush (*Artemisia tridentata*) cover at local and landscape scales were the most competitive among univariate models, supporting the paradigm that sagebrush is key for these species. Models including anthropogenic disturbance (well density, road density) explained more variation than models of prairie dog disturbance alone for 2 of the 3 species, but long-term disturbance by prairie dogs did reduce abundance of Brewer's sparrows. Although long-term prairie dog disturbance has the potential to reduce sagebrush cover for sagebrush-obligate birds, such events are likely rare because outbreaks of plague (*Yersina pestis*) and lethal control on borders with private land reduce prairie dog disturbance. Conversely, anthropogenic disturbance is slated to increase in this system, suggesting potentially accelerated declines for sagebrush birds into the future.

KEY WORDS big sagebrush, Brewer's sparrow, energy development, prairie dog, sage-grouse, sage thrasher, Wyoming.

Avifauna in North American rangelands have suffered population declines in recent decades (Sauer et al. 2017, Rosenberg et al. 2019). Birds associated with sagebrush (*Artemisia* spp.) ecosystems are especially vulnerable because sagebrush was historically reduced to increase forage availability for livestock on grazing lands (Vale 1974, Beck and Mitchell 2000, Welch and Criddle 2003). This practice has become less common, but remaining sagebrush ecosystems face disturbance threats from energy development and other surface disturbances, altered fire cycles related to invasion of exotic annual grasses such as cheatgrass (*Bromus tectorum*), and encroachment of pinyon pine (*Pinus* spp.) and junipers (*Juniperus* spp.; Knick et al. 2003, Davies et al. 2011, Balch et al. 2013), all of which reduce resistance and resilience of these fragile systems (Chambers et al. 2016).

Reductions in habitat availability and quality have led to declines in populations of many sagebrush-obligate birds, most notably sage-grouse (*Centrocercus* spp.). The Gunnison sage-grouse (*C. minimus*) is currently limited in extent to southwestern Colorado and southeastern Utah, USA, and is federally threatened (U.S. Fish and Wildlife Service [USFWS] 2010). The widespread and more abundant greater sage-grouse (*C. urophasianus*), however, was considered warranted for federal listing in 2010 under the Endangered Species Act but was later determined to be not warranted because of extensive conservation efforts throughout its range (USFWS 2015). Although conservation efforts continue, greater sage-grouse populations are declining in many areas (Knick 2011). This is often directly in response to human activity because disturbance associated with energy development has been especially detrimental to sage-grouse (Walker et al. 2007, Doherty 2008, Gregory and Beck 2014, Heinrichs et al. 2019) and sagebrush-obligate songbirds (Gilbert and Chalfoun 2011,

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Hethcoat and Chalfoun 2015). Many populations of sage thrasher (*Oreoscoptes montanus*) and Brewer's sparrow (*Spizella breweri*) have also declined in recent decades (e.g., Badlands and Prairies Region 17; Sauer et al. 2017, Rosenberg et al. 2019), and are key targets for conservation throughout the sagebrush steppe. Management focusing on sage-grouse as umbrella species for other sagebrush songbirds has been addressed (Hanser and Knick 2011, Gamo et al. 2013, Barlow et al. 2020), yet some researchers indicate that this umbrella may not always be adequate, and sagebrush songbirds may have separate management requirements (Carlisle et al. 2018).

Conservation of sagebrush systems is further complicated on the eastern edge of the sagebrush steppe, along the ecotone with the Great Plains. This region has experienced unprecedented energy development in recent decades, which has reduced net primary productivity across rangelands, in turn affecting the availability of livestock forage, biodiversity, and wildlife habitat (Allred et al. 2015). Conversion of intact rangelands to tillage agriculture has also contributed to sagebrush loss within the northwestern Great Plains (Chambers et al. 2016, Smith et al. 2016).

Where avian conservation is concerned, management at the eastern edge of the sagebrush steppe is somewhat complex because managers must consider the needs of imperiled sagebrush-associated species and declining grassland birds (Duchardt et al. 2018). A pivotal character influencing habitat for grassland and sagebrush birds is the black-tailed prairie dog (*Cynomys ludovicianus*). This species is important for grassland birds including the mountain plover (*Charadrius montanus*) and burrowing owl (*Athene cunicularia*) because it alters vegetation and soil structure to provide breeding habitat for these species, but long-term prairie dog disturbance can reduce sagebrush cover, potentially reducing habitat availability for sagebrush birds in some areas (Duchardt et al. 2019). In addition, vegetation structure within sagebrush ecosystems along the eastern edge of sagebrush range differs from elsewhere in the sagebrush steppe (Chambers et al. 2016), exhibiting a denser grass understory, often a mixture of perennial and annual grasses (Porensky et al. 2018). More broadly, populations are generally lower and more variable in both space and time at the edge of a species' range (Andrewartha and Birch 1954, Kirkpatrick and Barton 1997). Despite these factors, sagebrush-obligate bird populations along this ecotone warrant additional research and may become more important for sustaining these species if predicted sagebrush loss due to climate change occurs in the hotter, southerly range or lower elevations within the sagebrush steppe (Bradley 2010, Chambers et al. 2016, Renwick et al. 2018).

Within certain areas of this transitional zone, the size and distribution of black-tailed prairie dog colonies in this landscape have been monitored since the early 2000s (Cully et al. 2010), creating a unique opportunity to examine how such variation influences bird abundance. Previous research indicates that sagebrush-obligate passerines are more sensitive to local long-term disturbance than to the landscape context of disturbance (Duchardt et al. 2019), but little information exists concerning sage-grouse response to black-tailed prairie dog disturbance, in part because of the limited overlap between these 2 species. Understanding the interplay between natural disturbance and anthropogenic disturbance is important in this system, especially because much of this information is lacking in the eastern range edge for sagebrush birds, and most research has occurred in the Wyoming and Great Basins (Herman-Brunson et al. 2009, Swanson et al. 2013). Further, because this region provides habitat for sagebrush and prairie dog-associated species, and is likely to experience a rapid increase in energy development in the coming years (Allred et al. 2015), understanding potential effects of disturbance is especially important.

To better understand habitat use of target bird species along a sagebrush-grassland ecotone, we examined sagebrush bird responses to vegetation, and to anthropogenic and natural disturbance, in the United States Forest Service (USFS) Thunder Basin National Grassland (TBNG) of eastern Wyoming, USA. We asked the following questions related to the role of natural and anthropogenic disturbance in affecting habitat for sagebrush birds: 1) how do local habitat variables and disturbance affect greater sage-grouse lek attendance, and 2) how do local habitat variables and disturbance affect Brewer's sparrow and sage thrasher habitat use? We relied on *a priori* expectations based on previous research in our study system and on these specific sagebrush bird species to address our research questions and predicted responses. Based on previous findings reported in the literature, we predicted that anthropogenic disturbance associated with energy extraction would reduce habitat use for Brewer's sparrows and greater sage-grouse. We were also interested in whether disturbance influenced sage thrasher habitat use but did not expect a similar response because it has not been supported in the literature (Ingelfinger and Anderson 2004, Gilbert and Chalfoun 2011). We also anticipated that although prairie dogs may reduce habitat quality for these species, we did not expect prairie dog disturbance in our system to affect sagebrush bird habitat use at broader spatial scales (Duchardt et al. 2019).

STUDY AREA

We conducted our study within the TBNG in Campbell, Converse, Weston, and Niobrara counties, Wyoming (Fig. 1). This region is composed of a mosaic of grassland and sagebrush vegetation communities managed by the USFS and represents a considerable opportunity for the management and conservation of declining grassland and sagebrush birds. The TBNG covers >220,000 ha of public lands, interspersed with private holdings. Mean annual precipitation ranged from 25–35 cm (Porensky et al. 2018), mainly falling as rain in the spring and summer (Mar–Sep). Summer maximum temperatures ranged from 26°C to 32°C, and winter minimums ranged from −11°C to −4°C (https://www.ncdc.noaa.gov/cdo-web/search, accessed 17 May 2020). Elevation ranged 1,100–1,600 m, with land cover including relatively flat grasslands and shrublands, riparian areas,

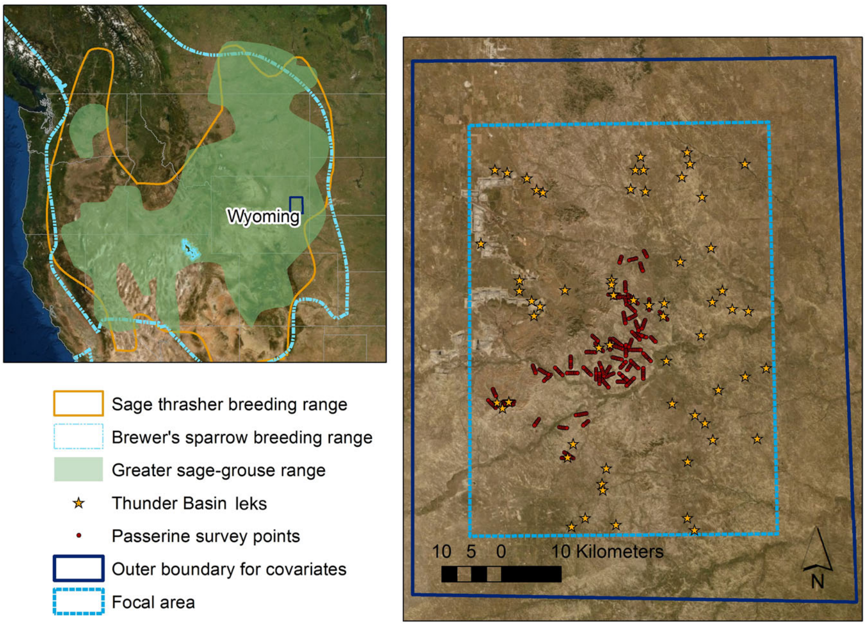

Figure 1. Study area and design focusing on sagebrush birds within the Thunder Basin National Grassland (TBNG), Wyoming, USA, 1999–2018. We present the range of 3 focal sagebrush species, including location of the TBNG (left) and the location of passerine survey points and sage-grouse leks within the TBNG (right).

badlands topography, and the Red and Rochelle hills. Common graminoids included blue grama (*Bouteloua gracilis*), western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Heterostipa comata*), and threadleaf sedge (*Carex filifolia*). Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) occurred in smaller, more dispersed patches in this region than elsewhere in the sagebrush steppe (Knight et al. 2014, Chambers et al. 2016), but it accounted for >30% canopy cover in some areas (Porensky et al. 2018). Dominant fauna in the region included black-tailed prairie dogs and pronghorn (*Antilocapra americana*), and a broad diversity of grassland and sagebrush mammals, birds, amphibians, and reptiles. Dominant land use in the region was livestock grazing but also included energy extraction and recreation.

A large complex of black-tailed prairie dog colonies existed within the south-central portion of the TBNG, providing habitat for many colony-associated wildlife species. These colonies have been mapped on-the-ground by the USFS staff and collaborators since 2001. As in many other portions of their range, prairie dogs in the TBNG experience outbreaks of sylvatic plague (*Yersinia pestis*), but boom-and-bust cycles of colony growth and die-off in this region are particularly severe (Cully et al. 2010), providing a unique opportunity to examine how colony distribution and size potentially influence sagebrush birds.

METHODS

Greater Sage-Grouse Lek Data

We obtained greater sage-grouse lek survey count data between 1999 and 2018 from the Wyoming statewide lek count database (T. Christiansen, Wyoming Game and Fish Department [WGFD], unpublished data), which contains data from lek surveys conducted using protocols approved by the WGFD (Christiansen 2012). We selected this date range to correspond with the temporal availability of prairie dog spatial data. To focus specifically on dynamics in the area of the TBNG, we selected all leks within a 5×7 township grid centered on the TBNG (Fig. 1), bounded roughly by Bill, Wyoming to the south and Wright, Wyoming to the north. Within this area there were 58 leks that were occupied (i.e., active for ≥1 season within the past 10 years; Hess and Beck 2012) during at least some portion of the study period. Although 6 of these leks did not have observed males within the study period (1999–2018), they did have observations of males in the mid-1990s, which represented <10 years prior to the beginning of the study.

For the analyses below, we evaluated dynamic models examining the effects of multiple habitat and disturbance variables on leks over time. Because not all leks were surveyed in all years and because many covariates were available at 2–3-year intervals (e.g., LANDFIRE, National Agriculture Imagery Program [NAIP] imagery), we binned lek data by the smallest interval that ensured all leks were visited at least once, and used the maximum count of male grouse within the binned interval (Doherty 2008). Intervals ranged 2–4 years, and final intervals were 1999–2001, 2002–2004, 2005–2008, 2009–2011, 2012–2014, 2015–2016, and 2017–2018. This yielded 287 lek-time interval data points (Table S1, available online in Supporting Information). Within this dataset we also included leks discovered after 1999, which was the initial year of our study (32 leks).

Songbird Data

We surveyed sagebrush and grasslands for songbirds from 2015–2017, using a point-transect sampling design

(Duchardt et al. 2019). Because TBNG is a patchwork of cover types, we established transects using 3 different criteria. First, we randomly placed colony core transects ($n = 10$, 8 points/transect) with the constraint that transects fell entirely within prairie dog colonies. Second, we randomly located colony edge transects ($n = 41$, 5–8 points/transect, $\bar{x} = 6.8$) with the requirement that transects crossed the edge of a prairie dog colony with 4 points located outside the colony and 1–4 within the colony, depending on colony size. Third, we selected sagebrush transects ($n = 10$, 8 points/transect) non-randomly in 10 known areas of extensive sagebrush to ensure our surveys included portions of the landscape supporting spatially extensive stands of sagebrush. Previous observers identified these locations during past surveys of greater sage-grouse, and transects represented a range of sagebrush cover and spatial location (i.e., easting and northing). All transects contained 5–8 points spaced 250 m apart ($n = 61$ transects containing 439 survey points).

We conducted surveys twice on each point, with the first round of surveys occurring between mid-May and early June, and the second round between early and late June each year from 2015–2017, surveying between sunrise and 1000 on days with low wind and no rain (Pavlacky et al. 2017). Surveys were 6 minutes in duration, and we recorded all birds seen or heard at the point. To adjust for detectability, we modeled Brewer's sparrow abundance using Program DISTANCE (version 6.0), comparing models including time of survey, wind, temperature, observer, travel method (all-terrain vehicle vs. on foot), and visual obstruction; Duchardt et al. (2019) provides detail on DISTANCE methods used. We used presence-absence of sage-thrashers because of low abundance; thus, we did not use distance-adjusted densities for this species (Table S1). All field data collection (point counts, vegetation surveys) was approved by the USFS.

Following point counts, we collected vegetation data at each survey point. We measured visual obstruction, a metric incorporating vegetation height and density, using a Robel pole (Robel et al. 1970) placed at 5-m increments along 30-m transects radiating from each point, perpendicular to the axis of the point count transect. We also recorded line-point intercept data at every meter along transects, recording basal and canopy cover for grasses, forbs, cacti, and shrubs. Ground cover categories included bare ground, litter, biological soil crust (BSC), lichen, and basal cover of vegetation classes (Herrick et al. 2009). We combined forb and grass data into an herbaceous canopy variable. In 2015, we collected shrub and cactus canopy cover data along these transects using the line-intercept method (Canfield 1941, Herrick et al. 2009). Because shrub canopy cover varies minimally over 1–3 years, we used these data to calculate percent cover of sagebrush and cactus at each point and used this value for all years.

Land Cover Data

We calculated sagebrush cover using LANDFIRE (2014) existing vegetation type data across the study period, which included data from 2001, 2008, 2010, 2012, and 2014. Sagebrush included any class type including the term sagebrush (e.g., big sagebrush steppe, big sagebrush shrubland) and montane riparian shrubland, which in this system generally corresponded to areas of silver sagebrush (*A. cana*). We calculated sagebrush cover at multiple spatial scales for point count locations and leks using the spatialEco package in R (Evans 2015). We interpolated years not included in the dataset by averaging between available datasets. We used these data to calculate percent sagebrush cover at multiple radii from songbird point count locations (250 m, 500 m, 1 km) and sage-grouse leks (500 m, 1 km, 5 km). Radii for point counts were focused on capturing territory and landscape scales. We applied a larger radius (5 km) around leks because previous studies indicate this radius captures the majority of habitat for nesting females (Holloran and Anderson 2005, Doherty et al. 2011, Coates et al. 2013). Because topographic features may also influence habitat use, we used a digital elevation model to generate topographic roughness (Gesch 2007, Porensky et al. 2018) within 100 m of point count and lek locations.

Natural and Anthropogenic Disturbance Data

The USFS and the Thunder Basin Grassland Prairie Ecosystem Association, a non-profit stakeholder group, mapped perimeters of black-tailed prairie dog colonies in the study area each year between 2001 and 2018 using a handheld global positioning system device following methods of Cully et al. (2010). Colony spatial data are currently curated by the Thunder Basin Grassland Prairie Ecosystem Association. They focused mapping efforts on public lands, and although they occasionally mapped colonies on private lands, colony area in a given year likely represents minimum coverage throughout the grassland. To maintain consistency, we included only areas that they mapped on public lands in all years. Colonies experienced large fluctuations across the study period due to outbreaks of sylvatic plague in 2001, 2005, and 2017, and cycles of re-colonization and population growth post-plague. Minimum colony area in 2007–2008 amounted to approximately 1,400 ha, and maximum area exceeded 20,000 ha in 2017. We used these data to determine presence-absence of prairie dog colonies at the 0.5-km and 1-km scales, generate values of colony cover at the 5-km scale, and calculate distance to prairie dog colony for sage-grouse (Table 1). We examined only presence-absence of prairie dog disturbance at the point count location, either current or long-term (>4 yr) for songbirds because researchers indicate other aspects of prairie dog disturbance are relatively unimportant to songbirds (Duchardt et al. 2019).

We obtained publicly available spatial data associated with anthropogenic disturbance in the TBNG. We obtained road spatial data from the Wyoming Geospatial Hub (https://geospatialhub.org/, accessed 5 May 2019), and calculated density of all roads at 2 sets of spatial scales corresponding to sage-grouse and sagebrush passerines, as discussed above. We obtained well pad location and production data from the Wyoming Oil and Gas Conservation Commission (2019).

Table 1. Covariates used in analyses of songbird and sage-grouse habitat use in the Thunder Basin National Grassland, Wyoming, USA, 1999–2018.

Sagebrush songbirds	Greater sage-grouse	Data source
Landscape cover		
Year	Year	
Topographic roughness	Topographic roughness	Digital elevation model U.S. Geological Survey
Sagebrush cover	Sagebrush cover	LANDFIRE (2014)
1 km	5 km	
500 m	1 km	
250 m	500 m	
Anthropogenic disturbance		
Wells	Wells	
Presence-absence (1 km)	Density class (5 km)	The Wyoming Oil and Gas Conservation Commission (2019)
Presence-absence (500 m)	Presence-absence (1 km)	
Presence-absence (250 m)	Presence-absence (500 m)	
Road density	Road density	
Road density (1 km)^2	Road density (5 km)^2	Wyoming Geospatial Hub (https://geospatialhub.org/)
Road density (500 m)^2	Road density (1 km)^2	
Road density (250 m)^2	Road density (500 m)^2	
	Distance to mine^2[a]	2008 National Agriculture Imagery Program imagery
Natural disturbance		
Long-term prairie dog disturbance (0, 1)	Prairie dog disturbance (0, 1)[b]	U.S. Forest Service digitized boundaries 1999–2018
Prairie dog disturbance (0, 1)	Distance to nearest prairie dog colony	
Local vegetation cover[c]		
Big sagebrush cover		Field measurements Duchardt et al. (2019)
Shrub cover		
Visual obstruction		
Litter		
Bare ground		
Brome cover		
Herbaceous canopy		
Cactus cover		

[a] The North Rochelle Mine was a similar distance from most of the songbird study area, so we did not include this variable in the analyses for songbirds.
[b] We examined prairie dog presence-absence within 0.5 km and 1 km; at the 5-km scale we used a categorical variable of prairie dog cover with 3 categories (none = 0, low = 0.01–10%, high = >10%).
[c] We collected local vegetation data as part of another study, and the data were only available for songbirds.

We included only wells marked as active within the study area during the study period, and visually checked well locations and dates using NAIP imagery across multiple years. Because multiple well points were often associated with 1 pad, we then merged all data points within 60 m of another point, similar to Harju et al. (2010) and Gamo and Beck (2017). We then calculated year-specific well density at 2 sets of spatial scales corresponding to sage-grouse and sagebrush passerines (Table 1). Well density was extremely low and zero inflated in the songbird study area and within smaller sage-grouse lek buffers; therefore, we used a binary presence or absence variable for these analyses. At the 5-km scale for greater sage-grouse, we assigned density classes as class 3 = >0.4 wells/km^2, class 2 = <0.4 and >0.1, class 1 = <0.1 and >0, and class 0 = 0. Finally, we assessed the potential effect of mining disturbance on both species. The North Antelope Rochelle Mine (Peabody Energy, Saint Louis, MO, USA) is one of the largest active coal strip mines in the country, located in Campbell County, Wyoming. Because we anticipated mine disturbance might also influence lek attendance, we calculated distance to the mine using a digitized layer from 2008 NAIP imagery for each point count and lek location. Although the mine increased during the study period, we used distance to mine center, which has not changed substantially. Although mine expansion directly reduces habitat, at least temporarily, non-destructive effects (e.g., noise, traffic) are less well understood for sagebrush birds and especially sagebrush songbirds, and should be captured by this metric.

Analyses

We assessed the response of maximum lek attendance over time using generalized additive models (GAM) in the mgcv package in R (Wood 2011) with an autoregressive correlation structure (lek within yr) to address non-independence among data points within leks across years. In addition to being well-suited to longitudinal data, GAMs extend off generalized models using a non-parametric smoothing term to fit the data (Hastie and Tibshirani 1986), which can be used in place of traditional quadratic variables (where effects are indicated as quadratic, we indicate non-linearity within a GAM with 3 knots). We applied a 2-step information-theoretic approach to modeling, using Akaike's Information Criterion for small samples (AIC_c; Burnham and Anderson 2002) to examine all potential combinations of variables within 3 different modeling categories (landscape, anthropogenic disturbance, natural disturbance; Table 1). Because of the potential for quadratic effects of roads and topography (Doherty 2008, Aldridge et al. 2012), we included these effects but specified them using non-parametric smoothing limited to 3 knots (Wood 2011), which mimics the quadratic effect. Because well density was relatively low in this area, we created a categorical variable of well density class (Table 1) and therefore did not consider a quadratic response of this effect. We then took the top model based on lowest AIC_c value (Burnham and Anderson 2002) from each category and examined all possible combinations of these top models and compared them to a null model. In all models, we reduced problems associated with multicollinearity by not including variables with Pearson correlation coefficients >0.5.

We applied generalized additive mixed models (GAMMs) to investigate factors influencing songbird habitat use using the GAMM4 package in R (Wood 2011, Wood and Scheipl 2020). We did not specify correlation structure for these models but included a random effect of transect to address spatial autocorrelation, which reduced the autocorrelation structure in the data as ascertained using Moran's I (Moran 1950). Because sage thrashers and Brewer's sparrows are considered obligate sagebrush nesters (Reynolds et al. 1999, Rotenberry et al. 1999), we removed any points that occurred in areas without sagebrush cover at a 250-m radius in LANDFIRE, to help avoid zero-inflation. This process removed 45 of 439 points in each year. We applied AIC_c to compare models of the effects of local and landscape-scale vegetation, natural disturbance, and anthropogenic disturbance (Table 1) on sage thrashers and Brewer's sparrows, examining the same models for both species. In some cases, we used binary or categorical variables instead of continuous variables, especially where data were unevenly distributed, as was the case with well data surrounding point count locations (Table 1). Similar to the approach described above, we applied a 2-step approach to modeling, examining all potential combinations of variables within 4 different modeling categories (landscape, anthropogenic disturbance, natural disturbance, local habitat variables; Table 1), and then examined all possible combinations of these top models compared with a null model.

We modeled Brewer's sparrow abundance using a Poisson distribution. Because distance-adjusted densities generated by Program DISTANCE are not compatible with a Poisson distribution, we modeled instead the response of raw abundance with an offset variable in all models to include the effect of species detectability (Aldridge et al. 2011, Timmer 2017). For sage thrashers, we modeled presence-absence using logistic regression because when this species was present at a point, we typically only detected 1 individual. We built top models of local vegetation, landscape-scale vegetation, and disturbance by comparing univariate models within each category with models that included pairwise and 3-way combinations of predictors, based on minimization of AIC_c to determine which best described habitat use in each species.

RESULTS

Step 1 of our modeling process for sage-grouse generated top models of landscape cover, natural disturbance, and anthropogenic disturbance (Table 2). The most-supported scales (radii) based on a comparison of univariate models were 5 km for sagebrush cover and well density and 1 km for road density (Table S2, available online in Supporting Information). After examining all potential combinations of top models from step 1, step 2 yielded a top model that included aspects of disturbance types and landscape ($R^2 = 0.27$; Table 2). Variables in the top model included a

Table 2. Results of the model selection process for models predicting greater sage-grouse lek attendance within the Thunder Basin National Grassland, Wyoming, USA, 1999–2018. We present the top 3 models among all combinations of landscape variables, anthropogenic disturbance variables, and natural disturbance variables (step 1) and the best model generated from examining all possible combinations of step 1 top models (step 2). Columns represent Akaike's Information Criterion adjusted for small sample sizes (AIC_c), difference between a given model and the top model (ΔAIC_c), number of parameters (K), and model weight (w_i).

Model	AIC_c	ΔAIC_c	K	w_i
Step 2				
Well density category (5 km) + distance to mine^2 + road density (1 km)^2 + sagebrush cover (5 km) + topographic roughness[a] + prairie dog disturbance (0.5 km)	3,738.07	0.00	11	0.93
Well density category (5 km) + distance to mine^2 + road density (1 km)^2 + sagebrush cover (5 km) + topographic roughness[a]	3,743.31	5.24	10	0.07
Prairie dog disturbance (0.5 km) + well density category (5 km) + distance to mine^2 + road density (1 km)^2	4,089.18	351.11	9	0.00
Step 1				
Anthropogenic disturbance				
Well density category (5 km) + distance to mine^2 + road density (1 km)^2	4,125.15	0.00	8	1.00
Well density category (5 km) + distance to mine^2 + road density (5 km)^2	4,159.03	33.88	8	0.00
Well density category (5 km) + distance to mine + road density (1 km)^2	4,196.80	71.65	7	0.00
Natural disturbance				
Prairie dog disturbance (0.5 km)	4,779.54	0.00	2	1.00
Prairie dog colony category (5 km)	4,794.24	14.70	3	0.00
Null	4,809.67	30.12	1	0.00
Landscape cover				
Sagebrush cover (5 km) + topographic roughness^2	4,583.64	0.00	4	1.00
Sagebrush cover (5 km) + topographic roughness	4,625.56	41.92	3	0.00
Sagebrush cover (5 km)	4,644.70	61.06	2	0.00

[a] Although a non-linear effect of topographic roughness was in the top landscape model in step 1, the non-linear effect was dropped in step 2 of modeling process.

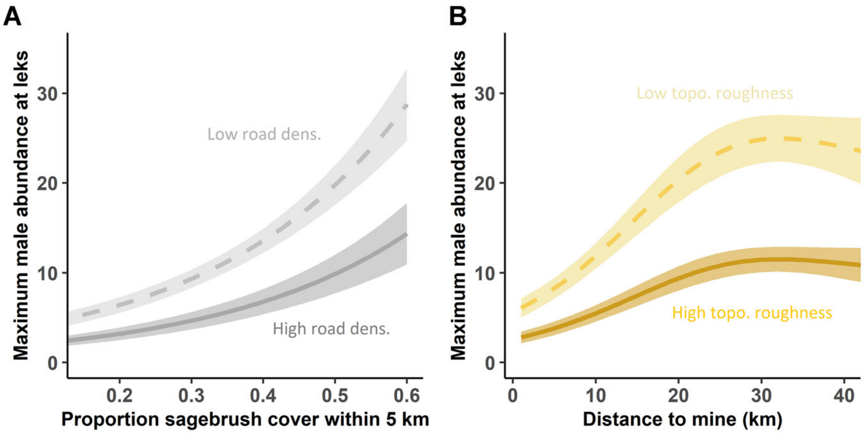

Figure 2. Trends in maximum lek attendance for male greater sage-grouse as a function of A) sagebrush cover within 5 km of a lek at low (2 km/km^2) and high (8 km/km^2) road density (dens.), and as a function of B) distance to mine at low (0.2) and high (0.8) topographic (topo.) roughness within 100 m in the Thunder Basin National Grassland, Wyoming, USA, 1999–2018.

positive effect of sagebrush cover within 5 km ($\beta = 3.75 \pm 0.24$ [SE]), with average lek attendance doubling with approximately every 20% increase in sagebrush cover (up to 38 birds at 60% cover at this scale). We also observed a non-linear effect of road density at 1 km and distance to mine (Fig. 2), with lek attendance being 2 times greater at locations >30 km from the mine as compared to locations 10 km away. Although a non-linear effect of topographic roughness was in the top landscape model in step 1, the non-linear effect was dropped by the GAM in step 2, yielding a linear negative effect of topographic roughness ($\beta = -1.55 \pm 0.18$). Other variables included a positive effect of prairie dog presence within 500 m of a lek ($\beta = 0.23 \pm 0.08$), and non-significant negative effects of the 2 highest well density classes within 5 km ($\beta_{category2} = -0.08 \pm 0.07$; $\beta_{category3} = 0.15 \pm 0.14$; Table S2).

Local and broad-scale variables were important in explaining sagebrush-obligate songbird habitat use, but the role of disturbance varied by species. For Brewer's sparrow, after examining all potential combinations of top models from step 1 (Table S3, available online in Supporting Information), the full model had the lowest AIC$_c$ and an $R^2 = 0.26$ (Table 3). Within this model, local variables included positive effects of local sagebrush cover ($\beta = 2.25 \pm 0.29$), herbaceous canopy

Table 3. Results of model selection process for models predicting Brewer's sparrow abundance within the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. We present the top 3 models yamong all combinations of local, landscape, anthropogenic disturbance, and natural disturbance variables (step 1) and the best model(s) generated from examining all possible combinations of step 1 top models (step 2). Columns represent Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$), difference between a given model and the top model (ΔAIC$_c$), number of parameters (K), and model weight (w_i).

Model	AIC$_c$	ΔAIC$_c$	K	w_i
Step 2				
Long-term prairie dog disturbance (0, 1) + well category (500 m) + road density (1 km)^2 + sagebrush cover (250 m) + topographic roughness^2 + year + sagebrush + litter + herbaceous canopy	2,795.36	0.00	14	1.00
Long-term prairie dog disturbance (0, 1) + sagebrush cover (250 m) + topographic roughness^2 + year + sagebrush + litter + herbaceous canopy	2,817.76	22.40	11	0.00
Sagebrush cover (250 m) + topographic roughness^2 + sagebrush + litter + herbaceous canopy + well category (500 m) + road density (1 km)^2	2,866.35	70.99	13	0.00
Step 1				
Local vegetation cover				
Sagebrush + litter + herbaceous canopy	2,997.24	0.00	5	0.62
Sagebrush + litter + herbaceous canopy + cactus	2,998.32	1.08	6	0.36
Sagebrush + bare + herbaceous canopy	3,007.23	9.99	5	0.00
Landscape cover				
Year + sagebrush cover (250 m) + topographic roughness^2	3,020.83	0.00	7	0.47
Year + sagebrush cover (250 m)	3,021.36	0.53	5	0.36
Year + sagebrush cover (250 m) + topographic roughness	3,022.93	2.10	6	0.17
Natural disturbance				
Long-term prairie dog disturbance (0, 1)	3,079.10	0.00	3	1.00
Current prairie dog disturbance (0, 1)	3,176.04	96.94	3	0.00
Null	3,306.73	227.64	2	0.00
Anthropogenic disturbance				
Well category (500 m) + road density (1 km)^2	3,268.77	0.00	5	0.42
Well category (500 m) + road density (500 m)^2	3,268.98	0.21	5	0.38
Well category (500 m) + road density (1 km)	3,270.40	1.63	4	0.19

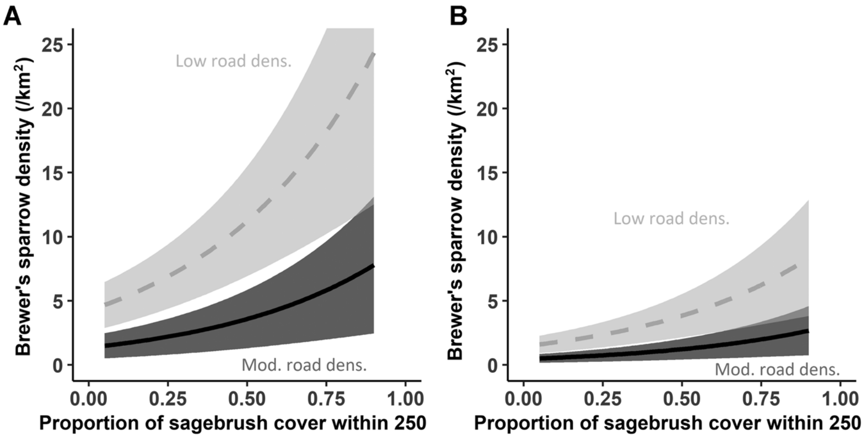

Figure 3. Effects of sagebrush cover within 250 m at 2 levels (1 km/km^2, 3 km/km^2) of road density on Brewer's sparrow density (dens.) in areas without A) and with B) long-term prairie dog disturbance within the Thunder Basin National Grassland, Wyoming, USA, 2015–2017.

cover ($\beta = 0.59 \pm 0.21$), and broad-scale effects of sagebrush cover at 250 m ($\beta = 1.94 \pm 0.26$). This corresponded to a predicted difference of approximately 6.5 birds/km^2 at 10% local sagebrush cover and 10% herbaceous cover with 31 birds/km^2 at 60% sagebrush cover (the maximum) and 90% herbaceous canopy cover. The top model also included a negative effect of litter cover ($\beta = -0.26 \pm 0.17$), a non-linear effect of topographic roughness, and a year effect. Aspects of anthropogenic (well presence within 500 m [$\beta = -0.64 \pm 0.20$], a non-linear effect of road density within 1 km) and natural (long-term prairie dog disturbance [$\beta = -1.07 \pm 0.13$]) disturbances also reduced Brewer's sparrow density (Fig. 3).

Sage thrasher presence or absence was also explained by variables at the local and landscape scale and by natural disturbance but not anthropogenic disturbance (the null was the top model for this category; Table S4, available online in Supporting Information). After examining all potential combinations of models from step 1, the model including local and landscape effects but no disturbance effects had the lowest AIC$_c$ (area under the curve [AUC] = 0.82; Table 4). The model included local effects of sagebrush cover ($\beta = 7.12 \pm 1.41$) and litter ($\beta = 1.35 \pm 0.70$), broad-scale effects of sagebrush cover at 1 km ($\beta = 4.14 \pm 1.46$), and a weakly significant effect of year (Fig. 4). The best natural disturbance model included a negative effect of long-term prairie dog disturbance, but this variable was not included in the final model (Table 4).

DISCUSSION

We identified a suite of factors influencing the habitat use of imperiled sagebrush avifauna at the eastern edge of their range. Overall, our findings indicated a much stronger role of habitat variables and anthropogenic disturbance than prairie dog disturbance alone based on top models for all 3 species. We observed a strong effect of covariates related to human disturbance (well density, road density) on greater sage-grouse (Fig. 2) and Brewer's sparrow (Fig. 3) in this system. A number of researchers have concluded there is a potential for energy development to have effects on greater sage-grouse (Gregory and Beck 2014), and sagebrush-obligate passerines (Gilbert and Chalfoun 2011) and a few have also looked specifically at effects within the eastern edge of the range of the greater sage-grouse within Western Association of Fish and Wildlife Agencies Sage-Grouse Management Zone I (Doherty 2008, Gamo and Beck 2017). In an analysis based on data collected 10 years before ours, Doherty (2008) also identified a threshold where male sage-grouse lek attendance declined in areas with greater than approximately 0.39 wells/km^2. This is consistent with our finding that lek attendance was lowest in landscapes with the 2 highest well

Table 4. Results of model selection process for models predicting sage thrasher presence within the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. We present the top 3 models among all combinations of local, landscape, anthropogenic disturbance, and natural disturbance variables (step 1) and the best model(s) generated from examining all possible combinations of step 1 top models (step 2). Columns represent Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$), difference between a given model and the top model (ΔAIC$_c$), number of parameters (K), and model weight (w_i).

Model	AIC$_c$	ΔAIC$_c$	K	w_i
Step 2				
Sagebrush cover (1 km) + year + sagebrush + litter	510.57	0.00	7	0.70
Long-term prairie dog disturbance (0, 1) + sagebrush cover (1 km) + year + sagebrush + litter	512.30	1.73	8	0.29
Sagebrush + litter	520.37	9.80	4	0.01
Step1				
Local vegetation cover				
Sagebrush + litter	520.37	0.00	4	0.22
Shrub + bare	521.85	1.48	4	0.10
Sagebrush + litter + herbaceous canopy	522.12	1.75	5	0.09
Landscape cover				
Year + sagebrush cover (1 km)	546.53	0.00	5	0.27
Year + sagebrush cover (500 m)	547.14	0.61	5	0.20
Year + sagebrush cover (250 m)	547.38	0.85	5	0.17
Natural disturbance				
Long-term prairie dog disturbance (0, 1)	550.34	0.00	3	0.95
Current prairie dog disturbance (0, 1)	557.41	7.07	3	0.03
Null	558.19	7.86	2	0.02
Anthropogenic disturbance				
Null	558.19	0.00	2	0.13
Road density (250 km)	558.71	0.51	3	0.10
Well category (500 m)	559.48	1.29	3	0.07

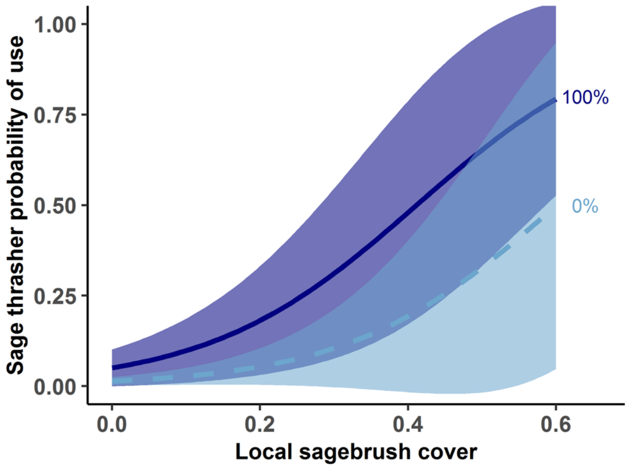

Figure 4. Effect of local sagebrush and 2 levels (0% and 100%) of litter cover on sage thrasher presence or absence within the Thunder Basin National Grassland, Wyoming, USA, 2015–2017.

density categories, which corresponds to 0.4 wells/km^2. Male lek attendance was actually highest at low well density (0.01–0.1 wells/km^2). Other researchers have also failed to show a decrease in lek attendance at extremely low well densities, and in some regions responses are not observed below 1 well/km^2, densities much higher than those found in the TBNG (Harju et al. 2010).

Other researchers have linked oil and gas disturbance to reduced sage-grouse chick survival (Aldridge and Boyce 2007), brood survival (Kirol et al. 2015), and yearling survival (Holloran et al. 2010). Furthermore, Sanders and Chalfoun (2019) reported that populations of a main nest predator of sagebrush passerines (deer mouse [*Peromyscus maniculatus*]) increased with oil and gas disturbance. Fewer researchers have noted effects of coal mining, but the increase in lek attendance with increasing distance to mine up to approximately 30 km that we observed could be largely due to direct loss of habitat via mine expansion. Other indirect effects including increased noise and traffic could also play a role (Blickley et al. 2012), but we did not examine these variables directly in this study.

Other researchers reported negative effects of roads directly (Ingelfinger and Anderson 2004), or indirectly (Blickley et al. 2012), an effect that we identified for grouse and Brewer's sparrows. The relationship we identified, however, was quadratic, with lowest abundances at low and higher road density. We do not know of any other research indicating this quadratic road effect; we present 2 potential explanations for this observed response. The first relates to distribution of our sampling locations. Few locations had low road density (<2 km of road/km^2); moderate (2–6 km/km^2) to high (>6 km/km^2) density was far more common, so the response at low road densities was influenced by very few points. In the case of greater sage-grouse, when we removed 1 lek with low road density from the dataset, the trend instead changed to a threshold response where lek attendance remained stable at lower to moderate road densities, and then declined at high road density. This *post hoc* analysis suggests our conclusion of reduced lek attendance with increasing road density is robust, but additional sampling to examine lek attendance in areas of low road density is needed.

The lack of response of sage thrashers to any metric of anthropogenic disturbance is consistent with prior studies of this species (Gilbert and Chalfoun 2011, Mutter et al. 2015) but highlights the potential downside of the umbrella concept, and of assuming all sagebrush birds respond similarly to changes to habitat (Carlisle et al. 2018). Gilbert and Chalfoun (2011) proposed either an insensitivity to disturbance or high site fidelity as potential mechanisms of response. Our finding of some level of sensitivity to prairie dog disturbance in this study, and to fire in a previous study (Duchardt et al. 2018), gives support to Gilbert and Chalfoun's (2011) site fidelity hypothesis being supported in this system. Especially considering low densities of sage thrashers at range edge, site fidelity may serve to increase the probability of encountering potential mates across a large area.

Overall, although prairie dog disturbance explained some variation in abundance for all 3 species, models with only prairie dog variables had less support than models including effects of habitat characteristics or anthropogenic disturbance (Tables 2 and 3). Despite extensive discussion by rangeland stakeholders in this region about the potential for prairie dogs to negatively affect sage-grouse, we did not find much support for this concept. At the 500-m scale the relationship between sage-grouse and prairie dog colony cover was actually positive (potentially an edge effect of prairie dog colonies at the 500-m scale), whereas at the 5-km scale only high (>10%) prairie dog cover was associated with reduced maximum lek attendance (Table S2). Very few leks were located within or near core prairie dog colonies since leks were first surveyed in the area (~1970s), which pre-dates the expansion of prairie dog colonies during the 2000s. The lack of sage-grouse habitat in the core of our study area may be due to long-term (multiple decades), heavy prairie dog disturbance. This seems unlikely because prairie dog control was an approved management option on public lands through the 1990s and early 2000s, and amount of colony expansion that occurred during our study (i.e., 2014–2017) did not occur in prior decades (U.S. Department of Agriculture Forest Service 2009, Cully et al. 2010). Alternatively, the paucity of sage-grouse near prairie dog colonies in our study area may be associated with increased tree cover near riparian areas and along higher elevation areas near the largest colony complexes because tree cover has been identified as an important influence of decreased habitat quality for sage-grouse, especially within Management Zone I (Doherty et al. 2016). Another possibility is that this portion of the study area has not supported high sagebrush cover for the past 4 decades for reasons other than prairie dog disturbance; such factors could include historical tillage agriculture or other rangeland practices focused on reducing sagebrush cover (Bureau of Land Management 2010) but could also be a function of naturally lower sagebrush cover throughout Management Zone I (Knick 2011).

Among sagebrush passerines, prairie dog disturbance in a given year had less support than other habitat or landscape features. Although long-term occupancy of prairie dogs may reduce sagebrush bird abundance, prairie dog occupancy within a given year has a much smaller effect (Duchardt et al. 2019). This is likely because the clipping and girdling actions of prairie dogs kill sagebrush only after multiple years of grazing pressure (Ponce-Guevara et al. 2016). Prairie dogs generally avoid expanding into shrub-dominated areas (Garrett et al. 1982, Reading and Matchett 1997, Milne-Laux and Sweitzer 2006), and if such expansions occur, they typically follow dry years where food is limiting (U.S. Department of Agriculture Forest Service 2009), and are often followed by plague outbreaks that decimate populations (Augustine et al. 2008, Cully et al. 2010). After these outbreaks, prairie dogs typically regroup in areas with naturally shorter vegetation (C. J. Duchardt, University of Wyoming, personal observation) and often do not reoccupy the same areas occupied during prior population lows (Augustine et al. 2008); as a result, multi-year clipping of sagebrush by prairie dogs may be relatively rare.

Least surprising among our results was the strong positive relationship between the 3 focal bird species and sagebrush cover. The most important spatial scales representing sagebrush cover scaled with the body size and territory size of each species; sagebrush cover was most important at 250 m, 1 km, and 5 km, for Brewer's sparrow, sage thrasher, and greater sage-grouse, respectively. Topographic roughness also played a role, with a quadratic effect for Brewer's sparrow and a negative effect for sage-grouse, which has been reported for sage-grouse previously (Chambers et al. 2016). At the local scale, modeling indicated relationships between sagebrush-obligate bird abundance or presence and aspects of the sagebrush understory, which has received much less attention than aspects of sagebrush cover. Habitat use of both passerine species was correlated with litter cover, but in opposing ways; this may be linked to the differing foraging strategies of the 2 species (Reynolds et al. 1999, Rotenberry et al. 1999). As ground foragers, sage thrashers may benefit from increased litter cover if this leads to increased insect abundance, whereas this likely does not affect the foliage-gleaning Brewer's sparrow. Two other studies have also identified this link to litter cover with the sage thrasher (Petersen and Best 1991, Timmer 2017).

MANAGEMENT IMPLICATIONS

Our results support the idea that sagebrush birds as a group are disturbance intolerant and anthropogenic disturbance plays a larger role in their abundance than disturbance by black-tailed prairie dogs. Male sage-grouse attendance at leks was 2–3 times higher when leks were in areas of low-to-moderate road density versus high road density, with a similar trend for Brewer's sparrows, although road densities were overall lower in point count areas. Although long-term disturbance from prairie dogs can reduce sagebrush (and thus habitat availability) for songbirds, in most years these areas make up a small proportion of the landscape, and they are minimally overlapping with current sage-grouse distribution in the Thunder Basin. These findings have implications for proposals to revise local land management plans including the most recent version of the Thunder Basin Management Plan (U.S. Department of Agriculture Forest Service 2019), and for future planned increases to oil and gas development in the area. Managers should consider that the potential for long-term prairie dog occupation to affect sagebrush bird habitat suitability may be limited relative to the current expansion of anthropogenic disturbance within the eastern edge of the sagebrush steppe.

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