To the University of Wyoming:

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ABSTRACT

Duchardt. C.J. Effects of disturbance on avian diversity at a grassland-sagebrush ecotone. Ph. D., Department of Ecosystem Science and Management. 2019

Combating biodiversity loss caused by human land use is one of the greatest challenges facing conservation biologists and ecologists worldwide. As postulated by the habitat-heterogeneity hypothesis, biodiversity is often greatest in areas with high habitat heterogeneity, such as areas along transitional zones (i.e., ecotones) between biomes. As such, these ecotones are a natural focus of biodiversity conservation efforts, but the complexity of these landscapes may be especially challenging for management.

This issue is especially salient at the ecotone between the Great Plains and sagebrush (*Artemisia* spp.) steppe, where ecosystem services including livestock grazing and energy extraction are often at odds with the needs of extremely diverse wildlife, including imperiled guilds of grassland and sagebrush birds. These two guilds have very different habitat requirements and responses to disturbance, but both are major conservation targets both in Wyoming and across their ranges.

The intent of my dissertation was to provide a better understanding of the habitat requirements and disturbance tolerances of both grassland and sagebrush birds within the ecotonal landscape of the U. S. Forest Service–Thunder Basin National Grassland of northeastern Wyoming. The proximate application of this research is to inform both managers and citizens in the region of habitat requirements and tolerances of each avian species, with a goal of managing the landscape for long-term sustainability of all target populations.

My dissertation is presented in four journal-formatted chapters. The main objective of Chapter Two was to evaluate the responses of a suite of grassland and sagebrush birds to different aspects of two forms of natural disturbance common within this landscape: fire and black-tailed prairie

dog (*Cynomys ludovicianus*) burrowing and herbivory. We found that while sagebrush bird species were equally intolerant to both disturbance types due to loss of sagebrush, the mountain plover (*Charadrius montanus*) relied almost solely on prairie dog disturbance in this landscape. This chapter was published in *Ecosphere* in fall 2018 with coauthors L. Porensky, D. Augustine, and J. Beck (Duchardt, C. J., L. M. Porensky, D. J. Augustine, and J. L. Beck. 2018. Disturbance shapes avian communities on a grassland–sagebrush ecotone. *Ecosphere* 9(10):e02483).

Chapter 3 examined landscape-scale responses of shortgrass, midgrass and sagebrush birds to different aspects of black-tailed prairie dog disturbance. While sagebrush birds were most sensitive to the presence of long-term colony occupation, mid-grass species were more sensitive to distance to colony edge, reaching lowest abundances at colony cores. Most interesting, mountain plovers, which were found exclusively on prairie dog colonies, peaked in abundance within 500-800 m from a colony edge, declining nearer to colony cores. This is the first evidence that mountain plovers may not benefit from a "bigger is better" approach to prairie dog management. This chapter was published in *Landscape Ecology* in the spring of 2019 with coauthors D. Augustine and J Beck (Duchardt, C. J., D. J. Augustine, and J. L. Beck. Threshold responses of grassland and sagebrush birds to patterns of disturbance created by an ecosystem engineer. Landscape Ecology 34:895–909).

Chapter 4 provided a more in-depth analysis on the breeding ecology of one of the most imperiled species in the system, the mountain plover. We combined point count data with nest site-selection and survival data to better understand plover responses to different aspects of prairie dog disturbance and other features of this system. Supporting the findings of Chapter 3, plover abundance peaked in mid-sized (100–600 ha) prairie dog colonies, with lower abundances in small (<100) and very large (600–4000 ha) colonies, although abundance was also highest in areas occupied by prairie dogs >6 years with ample bare ground. Both adult density and nest-site

selection were influenced somewhat more by maximum vegetation height than visual obstruction. As with other precocial species, nest survival probability increased with nest age, but was also influenced by weather. This chapter was accepted by *The Condor: Ornithological Applications* in fall of 2019 with coauthors J. Beck and D. Augustine, with revisions submitted September 2019.

Chapter 5 provides an in-depth analysis on the effects of both natural and anthropogenic disturbance on sagebrush birds. We examined the effects of vegetation, prairie dog disturbance and anthropogenic disturbance (road density, oil wells, and mining) on two sagebrush passerines (Brewer's sparrow [*Spizella breweri*] and sage thrasher [*Oreoscoptes montanus*]) as well as greater sage-grouse (*Centrocercus urophasianus*) lek attendance. Although aspects of prairie dog disturbance did have negative impacts on sagebrush birds, these models were much less competitive than aspects of anthropogenic disturbance or sagebrush cover alone. Within this system, concerns about burgeoning energy development are likely more pressing than potential conflicts between sagebrush avifauna and black-tailed prairie dogs. This chapter has been formatted for submission in *The Journal of Wildlife Management* with coauthors J. Beck and D. Augustine.

EFFECTS OF DISTURBANCE ON AVIAN DIVERSITY AT A GRASSLAND-SAGEBRUSH ECOTONE

Courtney J. Duchardt

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The University of Wyoming

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DEDICATION

To Mr. Miller and Mr. Niles at KHS,
Who taught me how to bird,
and told me I was a fourth generation Leopold,
A role I am still trying to live up to

And to Dr. Goldman,
Who agreed that April was in fact the cruelest month,
At least for many birds

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I thank many individuals I've had the privilege to meet working in the Thunder Basin National Grasslands, including ARS crewmembers, Forest Service employees and graduate students, mainly for pretending to care when I talked about birds. I also thank Gwyn McKee for her focused efforts in prairie dog mapping, as well as Mike Huffman and Rochelle Renken for their friendship and mentorship, however brief. I especially thank Dr. Lauren Porensky and Dave Pellatz for extensive help coordinating research efforts and the dissemination of research results. I also thank Dave for risking his truck in the line of duty to rescue my crew multiple times.

Finally, I thank the many people I'm lucky to have in my support system. Friends near and far, my fellow PiE students, and especially the AM Coffee Shop Club. I also thank my family, especially my father, who has made a sincere effort to read all my manuscripts. Finally, I thank my husband Jake, who was always willing to help with fieldwork or help me battle my impostor syndrome, and is my cat's second favorite person.

TABLE OF CONTENTS

ACKNOWLEDGMENTS……..iv

TABLE OF CONTENTS……..…….……..v

LIST OF TABLES……...…….…….……..vii

LIST OF FIGURES……...……..……...…xi

CHAPTER 1. ……..……...….1

Introduction……..…….1

Literature Cited…….…....6

CHAPTER 2……...……...16

Disturbance shapes avian communities on a grassland–sagebrush ecotone……..…..…..16

Introduction……...…17

Methods……..21

Results……26

Discussion……..30

Literature Cited……..37

CHAPTER 3……...…….....62

Threshold responses of grassland and sagebrush birds to patterns of disturbance created by an ecosystem engineer…….62

Introduction……...….62

Methods……...67

Results…….73

Discussion……..…….75

Literature Cited……...…82

CHAPTER 4……...……..99

Mountain plover habitat selection and nest survival in relation to weather variability and spatial attributes of black-tailed prairie dog disturbance ……..….99

Introduction…….....101

Methods……..…..104

Results……..……112

Discussion…….114

Literature Cited…….120

CHAPTER 5……...……136

Sagebrush bird responses to natural and anthropogenic disturbance at the eastern edge of the sagebrush steppe…….……..140

Introduction…….....141

Methods…….....144

Results……..….151

Conclusions……..…….153

Literature Cited……157

CHAPTER 6 - CONCLUSIONS……..174

APPENDIX……..176

LIST OF TABLES

CHAPTER TWO

Table 1. Descriptive statistics and correlations between vegetation or topo-edaphic variables and bird community structure (coordinates in NMDS ordination space) in 2016–2017, Thunder Basin National Grassland, Wyoming, USA. Bolded variables were included as vectors in ordination space in Figure 4. …….52

Table 2. Top models for factors modulating bird community convergence on prairie dog colonies and burned areas in Thunder Basin National Grassland, Wyoming, USA, 2016–2017. All models include a random effect of Patch ID. Bold indicates the only additive or interactive model better than the best single-variable model…… 53

Table 3. Univariate models (A) predicting avian community dissimilarity, Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Base model consisted of random effect of patch ID. All additive combinations of variables >2AICc better than the null (bold) were explored. B) Additive models compared to disturbance type alone……54

CHAPTER THREE

Table 1. Parameter estimates (with standard errors) of covariates describing black-tailed prairie dog colony presence/absence, or distance to colony edge within the TBNG, eastern Wyoming, USA, 2015–2017 (Q1). Distance to edge models only included points that fell within a colony. Negative values indicate parameters were lower either inside a colony or moving towards colony core. Bolded parameter estimates indicate significance at alpha = 0.05. ……92

Table 2. Top models explaining avian abundance as a function of different aspects of prairie dog disturbance within the TBNG, eastern Wyoming, USA, 2015–2017. Only top models explaining >98% of total model weights are shown (bold), along with a base model. “LT” represents areas of long-term prairie dog disturbance. See Fig. 2 for avian 4-letter alpha codes……93

Table 3. Top models explaining avian abundance in response to composition and configuration of colonies in the TBNG, eastern Wyoming, USA, 2015–2017. Top models explaining >98% of total model weights are shown, along with a base model and the best model from Table 2. Bolded models indicate competitive landscape models. “LT” represents areas of long-term prairie dog disturbance. See Fig. 2 for avian 4-letter alpha codes……94

CHAPTER FOUR

Table 1. Variables used in models predicting Mountain Plover habitat use, nesting habitat use, and nest survival for data collected in the Thunder Basin National Grassland, USA, 2015–2017. ……130

Table 2. Results of model-building and model comparison predicting adult Mountain Plover habitat utilization in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. The conditional and zero-inflated portions of the model are specified by (c) and (zi), respectively. “Model” indicates whether the model represents univariate model exploration from step one of our modeling approach, the global model built from competitive variables, the reduced global model, or our an *a priori model* based on literature. ……132

Table 3. Summary results of model-building and model comparison predicting Mountain Plover nest-site selection in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017, including the global model, reduced model, an *a priori* literature model, top univariate model,

and null model. Full model set including all univariate models can be found in Appendix 4……..133

Table 4. Top univariate models predicting daily nest survival for Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. Model rankings using AIC_c as well as parameter estimates are included, as well as parameter estimates and AIC_c values for the final combined global model……..134

Table 5. Top univariate models differentiating between nest failure by abandonment and nest failure by predation for Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017, where positive parameter estimates indicate greater probability of predation. Model rankings using AIC_c as well as parameter estimates are included, as well as parameter estimates and AIC_c values for the final combined global model…….135

CHAPTER FIVE

Table 1. Covariates used in analyses of songbird and sage-grouse habitat use in the Thunder Basin National Grassland. ……166

Table 2. Results of model selection process for models predicting greater sage-grouse lek attendance within the Thunder Basin National Grassland 1999-2018. We present the top three models among all combinations of landscape variables, anthropogenic disturbance variables, and natural disturbance variables (Step 1), as well as the best model generated from examining all possible combinations of Step 1 top models (Step 2). …….168

Table 3. Results of model selection process for models predicting Brewer's sparrow abundance and sage thrasher presence within the Thunder Basin National Grassland 2015-2017. We present the top three models among all combinations of local variables, landscape variables,

anthropogenic disturbance variables, and natural disturbance variables (Step 1), as well as the best model(s) generated from examining all possible combinations of Step 1 top models (Step 2). ……..169

LIST OF FIGURES

CHAPTER TWO

Figure 1. Location of historically burned areas and active prairie dog colonies in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Surveyed patches shown in bold colors. [Inset: Location of the TBNG at the ecotone between the Great Plains and the sagebrush steppe]……55

Figure 2. Distance-adjusted densities (per ha) of 11 abundant avian species on and off fires (red) and off prairie dog colonies (blue) averaged across years, Thunder Basin, Wyoming, USA, 2016–2017. * indicates Partners In Flight (PIF) species in decline (rank 4 or 5), ** indicates species that are both PIF in decline and SGCN in Wyoming……..56

Figure 3. Non-metric multidimensional scaling ordination representing bird communities in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Points represent bird communities on prairie dog colonies (dark blue triangles), off prairie dog colonies (light blue squares), on burned areas (dark red circles), and off burned areas (light red squares). Ellipses represent standard deviations of each strata in each year……..57

Figure 4. Bird species locations in ordination space, as well as vector overlay of important site-level variables, Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Centroids for inside-outside pairs of communities are presented for prairie dog colonies (on = dark blue, off = light blue) and historically burned areas (on = red , off = pink)…….58

Figure 5. Variation in disturbance-independent (left figure panels) and disturbance-dependent (right figure panels) variables shaping bird communities, Thunder Basin National Grassland, Wyoming, USA, 2016–2017……..59

Figure 6. Alpha diversity (A), calculated as the Shannon index, Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Community dissimilarity or beta diversity (B), calculated as Bray-Curtis dissimilarity. Beta diversity was calculated as the difference between paired disturbed and undisturbed points for fires and prairie dog colonies……..60

Figure 7. Interactive effects of clay content (%) within disturbed patch and disturbance type on community dissimilarity in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017.……61

CHAPTER THREE

Figure 1. Location of the TBNG within eastern Wyoming, USA, where the range of the black-tailed prairie dog overlaps the sagebrush steppe. Inset: Avian point count locations (n = 439) within sagebrush and across long-term and new prairie dog colony habitat in the Thunder Basin, surveyed between 2015–2017……95

Figure 2. Species names and four-letter alpha codes for shortgrass, midgrass, and sagebrush bird species in the TBNG, eastern Wyoming, USA, 2015–2017. “Generalists” in this sense display wider niche breadth and tolerances of other habitat types (e.g., lark bunting utilized both midgrass and sagebrush), whereas specialists were found only within that habitat. Superscripts indicate Wyoming species of Conservation Need (A, WGFD 2010) and U.S. Forest Service Sensitive Species (B, U.S. Forest Service 2017)……96

Figure 3. Avian densities (log scale) inside and outside current prairie dog colonies across three years in the TBNG, eastern Wyoming, USA, 2015–2017. Bars represent 95% confidence intervals…….97

Figure 4. Top models of avian abundance (transformed to density per km2) in response to distance to current colony edge or historic colony edge of seven species in TBNG, eastern Wyoming, USA, 2015–2017. Envelopes in single-species figures represent 95% confidence envelopes. Grey shading indicates prairie dog colony. Bottom right figure combines models of abundance in response to current edge for all seven species (even where this was the second-best model). See Table 1 for alpha codes…….98

CHAPTER FOUR

Figure 1. Location of the Thunder Basin National Grassland in eastern Wyoming in relation to breeding range of Mountain Plover and annual range of Black-Tailed Prairie Dog, with inset representing study area (**A**). Black-Tailed Prairie Dog colony (**B**) and Mountain Plover (**C**) in Thunder Basin National Grassland……..136

Figure 2. Mountain Plover density as a function of prairie dog colony size (**A**) and age (**B**) in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. The first two size categories (5–99 ha and 100–500 ha) represent small and large colonies in previous studies, respectively. Colony sizes above 500 ha are unique relative to previous studies of breeding Mountain Plovers. Colony ages represent old (6–14), intermediate (3–5) and young (0–2) colonies. Error bars represent 85% confidence intervals. Values above bar plots are number of colonies in each size category……137

Figure 3. Probability of nest site use by Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. as a function of bare ground (**A**), maximum vegetation height (**B**), annual forbs (**C**), and cactus (**D**) in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. Dashed lines represent 85% confidence intervals……..138

Figure 4. Daily nest survival for Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017, in response to 0% (solid) and 10% (dashed) cactus cover, and the interaction between nest age and time of season. Dashed lines represent 85% confidence intervals……..139

CHAPTER FIVE

Figure 1. Study area and design focusing on sagebrush birds within the Thunder Basin National Grassland (TBNG). (A) Range of three focal sagebrush , including location of the TBNG. (B). Location of passerine survey points and sage grouse leks within the TBNG. (C) Overlaying spatial layers used in assessing sagebrush bird habitat use……. 170

Figure 2. Raw data trends max lek attendance as a function of well density and sagebrush …171

Figure 3. Top variables predicting Brewer's sparrow density within the Thunder Basin National Grassland (2015-2017)……172

Figure 4. Top variables predicting sage thrasher presence/absence within the Thunder Basin National Grassland (2015-2017)…….173

Chapter 1. Introduction

The loss and alteration of ecosystems worldwide is of critical import (Vitousek et al. 1997, Diaz et al. 2019), and is linked to losses of species diversity (Vitousek et al. 1997, Butchart et al. 2010), as well as changing climate (USGCRP 2018, Diaz et al. 2019). While much of the research focuses on protection and restoration of forested systems (Mori et al. 2013, Bastin et al. 2019), worldwide semi-arid and arid systems are equally if not more imperiled, contain sizeable (Sala et al. 2006) and in some cases more imperiled (Sala et al. 2000) resources in terms of biodiversity, provide critical ecosystem services (Bengtsson et al. 2019), and may be an equally important resource in terms of combating climate change (Dass et al. 2018). Within North America, less than 1% of tallgrass Prairie habitat remains, with mixed-grass and shortgrass systems not far behind (Samson and Knopf 1994). While comparably more acreage of sagebrush habitat remains in the western third of the country (reported reductions range up to 50% [Schroeder et al. 2004, Davies et al. 2011]) , over 90% of the sagebrush steppe is considered degraded (West 1998), and this ecosystem is considered to be critically imperiled and is declining rapidly (Noss et al. 1995).

Both grasslands and sagebrush systems have been reduced in part due to conversion to agricultural uses. Grassland systems have mainly suffered by transition to row-crop agriculture (Brennan and Kuvlesky 2005,Wright and Wimberly 2013), while sagebrush systems have declined, indirectly, due to livestock grazing. Although moderate grazing has been shown to have little effect on sagebrush cover (e.g., Courtois et al. 2004 Davies et al. 2011), heavy grazing may reduce sagebrush. More importantly, the practice of excavating sagebrush to increase forage for cattle was common throughout much of the sagebrush steppe historically (Vale 1974). To date, much of semi-arid habitat decline has been linked to human agriculture,

through recent research has focused on applying agricultural practices in ways that maintain these habitats (e.g., Fuhlendorf and Engle 2001, Evans et al. 2014, Audubon 2017).

In addition to agriculture, exurban development (Riebsame et al. 1996; Sala et al. 2017), invasive species (DiTomaso et al. 2017), and energy development (Allred et al. 2015) all contribute to semi-arid habitat decline, and these disturbances are critical drivers of declines among arid and semi-aridland associated wildlife. Ungulates have shown to alter behavior in response to energy development (Sawyer et al. 2009, Buchanan et al. 2014), and exurban expansion has been linked to bottlenecks in ungulate migration corridors (Sawyer et al. 2005, Polfus and Krausman 2012). Energy development has been negatively correlated with abundance of songbirds (Gilbert and Chalfoun 2011, Thompson et al. 2015, Daniel and Koper 2019), sage-grouse (*Centrocercus* spp.; Gregory and Beck 2014) , lizards (Leavitt and Fitzgerald 2013) and foxes (Warrick and Cypher 1998) as well as increased brood-parasitism by brown-headed cowbirds (*Molothrus ater*; Bernath-Plaisted et al. 2017), nest predation by small mammals (Sanders and Chalfoun 2019) and increased corvid abundance (a common predator of greater sage-grouse nests; Bui et al. 2010). More broadly, reduced patch sizes due to altered land use is linked to decreased habitat use in grassland (Helzer and Jelinski 1999, Fletcher 2005) and shrubland (Knick and Rotenberry 1995) birds.

Although the potential negative impacts of disturbance are commonly discussed, cessation of natural disturbance regimes can cause problems as well. Historically, most North American aridland systems were grazed by a number of native ungulates (e.g., Elk [*Cervus canadensis*], bison [*Bison bison*], Knapp et al. 1999) and burrowing mammals (e.g., Black-tailed prairie dog [*Cynomys ludovicianus*], Gunnison prairie dog [*Cynomys gunnisoni*], Miller et al. 1994), while much of the Great Plains also experienced episodic fire (Sayre 2017, Fuhlendorf et

al. 2017). As such, many species inhabiting these systems are considered “disturbance-dependent” (Brawn et al. 2001). Especially within grassland ecosystems, suppression of natural disturbance has been linked with reduced native species diversity (Fuhlendorf et al. 2006, Hovick et al. 2015, Duchardt et al. 2016), and the suppression of these disturbances identified as one of the major drivers of biodiversity loss in these systems (Fuhlendorf and Engle 2001).

While disturbance was long-vilified among wildlife managers and stakeholders (Pynen1982, Brussard et al. 1994, Brunson and Huntsinger 2008, Harr et al. 2014), fire and ungulate grazing are becoming more common tools in semi-arid and aridland wildlife management. Where reintroduction of native large ungulates like bison is unfeasible, similar results can be obtained with domestic livestock (Fuhlendorf et al. 2006, Kohl et al. 2013). However, one agent of disturbance remains squarely in the crosshairs: the black-tailed prairie dog (Lamb and Cline 2003, Miller et al. 2007). Prairie dogs are colonial, burrowing mammals native to western North America (Hoogland 1995). Black-tailed prairie dogs are often especially identified as critical ecosystem engineers within the Great Plains, because this species lives at higher densities than other prairie dogs and also actively clips vegetation to maintain visibility on colonies (Hoogland 1995). Widely recognized as both an ecosystem engineer and keystone species (Kotliar et al. 1999, Van Nimwegen et al. 2008) because of these activities, black-tailed prairie dogs can also compete with cattle for forage (Derner et al. 2006; Augustine and Springer 2013) and as such are often subject to lethal control via poisoning and shooting on lands managed for livestock (Miller et al. 2007). In addition to lethal control, outbreaks of sylvatic plague (*Yersina pestis*) regularly lead to drastic local population reductions (>95% mortality in black-tailed prairie dogs; Cully and Williams 2001). These factors have severely reduced black-tailed prairie dog populations (occupying <3% of their historic range; Mulhern and Knowles

1997), pushing colony associates like the black-footed ferret (*Mustela nigripes*) to the brink of extinction (Dobson and Lyles 2000).

Given the numerous threats to North American aridland systems discussed above, it is no surprise that aridland avifauna are experiencing some of the steepest declines of North American birds (Sauer et al. 2017). The majority of breeding grassland and shrubland birds in North America are considered species of conservation need both at the state and federal level (e.g., Wyoming Game and Fish Department 2010, Rohweder 2015, U.S. Forest Service 2017), and many are considered near-threatened, vulnerable, or endangered by the International Union for the Conservation of Nature's Red List (e.g., Greater [*Tympanuchus cupido*] and lesser [*Tympanuchus pallidicinctus*] prairie chicken, greater [*Centrocercus urophasianus*] and Gunnison's [*C. minimus*] sage grouse, loggerhead shrike [*Lanius ludovicianus*], mountain plover [*Charadrius montanus*], chestnut-collared longspur [*Calcarius ornatus*], eastern meadowlark [*Sturnella magna*]). Management for so many species can be daunting – use of surrogate species (Caro and O'Doherty) has been advocated in many cases to simplify this challenge (e.g., Gamo et al. 2013). However, these approaches have been shown to have limited success in managing for multiple species (Simberloff 1999, Roberge and Angelstam 2004, Carlisle et al. 2018). As such, although umbrella species may be useful tools in some cases, management of aridland bird guilds will necessitate individual consideration of all species.

Indeed, it would be extremely unwise to consider all the aridland birds within a given area as equivalent, especially when it pertains to the role of disturbance. For example, while species like mountain plover have been shown to benefit from fire, grazing, and prairie dog burrowing (Dinsmore and Knopf 2005, Goguen 2012 Augustine and Skagen 2014), greater-sage grouse numbers often decrease following fire and heavy grazing due to loss of sagebrush

(Peterson et al. 2003, Knick et al. 2005, Beck et al. 2008). While this issue is likely theoretical in most places, it becomes empirical at the ecotone between the Great Plains and the sagebrush steppe, where a patchy mosaic of mixed grass and shortgrass rangelands overlaps with sagebrush-dominated systems. The heterogeneity of this zone of overlap is certainly a boon in terms of biodiversity (Odum 1971, Wiens 1992, Tews et al. 2004), but has the potential to be challenging in terms of management because of contrasting and potentially conflicting habitat requirements among species.

The Thunder Basin National Grassland (TBNG) of northeastern Wyoming is located squarely within this ecotone. Portions of TBNG have been designated as core area for greater sage-grouse (State of Wyoming 2011), and these areas also provide habitat for other sagebrush obligate birds including the Brewer's sparrow (*Spizella breweri*) and sage thrasher (*Oreoscoptes montanus*). Simultaneously, the TBNG has long-supported one of the largest complexes of black-tailed prairie dogs *(Cynomys ludovicianus*) in North America, and these colonies have been prioritized as a reintroduction zone for the endangered black-footed ferret (*Mustela nigripes*). These shortgrass prairie dog colonies also provide critical breeding habitat for the mountain plover (*Charadrius montanus*), a Wyoming Species of Greatest Conservation Need and USFS Species of Conservation Concern, as well as other imperiled shortgrass bird species including burrowing owls (*Athene cunicularia*). Furthermore, colony edges provide mixed-grass habitat important for grasshopper sparrows (*Ammodramus savannarum*) and lark buntings (*Calamospiza melanocorys*).

The aim of my research was to examine the avian communities within the ecotone between the Great Plains and the sagebrush steppe to identify the differing roles of disturbance among these guilds. The objective of Chapter Two was to evaluate the responses of a suite of grassland and sagebrush birds to different aspects of two forms of natural disturbance common

within this landscape: fire and black-tailed prairie dog burrowing and herbivory. Chapter 3 examined landscape-scale responses of shortgrass, midgrass and sagebrush birds to different aspects of black-tailed prairie dog disturbance. Chapter 4 was meant to provide a more in-depth analysis on the breeding ecology of one of the most imperiled species in the system, the mountain plover. Chapter 5 provides a more in-depth analysis on the effects of both natural and anthropogenic disturbance on sagebrush birds, examining point count data for Brewer's sparrow and sage thrasher from 2015-2017, and lek data for greater sage-grouse between 1999-2018.

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Chapter 2. DISTURBANCE SHAPES AVIAN COMMUNITIES ON A GRASSLAND-SAGEBRUSH ECOTONE

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ABSTRACT

Ecotones, or transitional zones between ecosystems, are often hotspots for biodiversity and targets for conservation. Where the Great Plains meet the sagebrush (*Artemisia* spp.) steppe, an opportunity exists to conserve habitat for the two most imperiled avian guilds in North America, grassland and shrub-steppe birds. This ecotone creates a unique challenge with respect to the management of disturbance processes, such as fire and grazing, because grassland and sagebrush-shrubland birds respond quite dissimilarly to disturbance. To address this management challenge and maximize conservation opportunities, we examined the responses of grassland and sagebrush bird communities to disturbance at a grassland-sagebrush ecotone in northeast Wyoming, USA. Specifically, we surveyed bird communities on active black-tailed prairie dog (*Cynomys ludovicianus*) colonies and burned areas, as well as on paired undisturbed points in 2016 and 2017. Bird community structure varied in response to both the presence and type of disturbance. Although alpha diversity of avian species was highest on undisturbed sites and burned areas, only prairie dog colonies provided breeding habitat for the imperiled shortgrass-obligate mountain plover (*Charadrius montanus*), and species turnover ("beta diversity") was greatest between on-colony and off-colony points. Furthermore, bird communities were shaped by both disturbance-dependent (e.g., disturbance age) and disturbance-independent (e.g.,

topography and soils) landscape features. Managers must balance the benefits of high species diversity in undisturbed sagebrush with habitat requirements of other imperiled species like the mountain plover. This may entail prioritizing the amount and distribution of disturbances in relation to population goals for species of conservation concern while simultaneously maintaining a mosaic of all three patch types in this landscape.

KEYWORDS: *biodiversity; Brewer's sparrow; fire; ecosystem engineer; grasshopper sparrow; mountain plover; prairie dog; topo-edaphic*

INTRODUCTION

Disturbance processes interact with underlying topo-edaphic heterogeneity to create unique vegetative patterns on the landscape, which in turn influence future patterns of disturbance (Risser et al.1984, Turner and Gardner 2001). This pattern-process link is at the center of landscape ecology (Turner 1989), but a pattern-process perspective has only recently been applied to the study and management of wildlife communities, especially in rangeland systems (Fuhlendorf et al. 2017). To conserve the diverse wildlife communities native to rangeland systems, it is critical to understand how disturbance regimes interactively shape and are shaped by wildlife habitat resources (Fuhlendorf et al. 2012).

In North American rangelands, grassland and shrubland bird guilds evolved under different historic disturbance regimes. Disturbances were common in the Great Plains, which evolved with drought, fire, ungulate grazing, and burrowing mammals (Sampson and Knopf 1994, Anderson 2006). In some parts of this region, disturbances were frequent, intense, and interactive, creating shifting vegetation mosaics that supported diverse habitats and led to increased biodiversity at broad scales (Fuhlendorf and Engle 2001, Skagen et al. 2018). North

American grassland birds evolved in the context of these frequent disturbances (Brawn et al. 2001), and some species benefit specifically from fire as well as biotic "ecosystem engineering" via grazing by large ungulates or burrowing and clipping action by prairie dogs (Johnson 1997, Grant et al. 2010, Augustine and Derner 2012, Ahlering and Merkford 2016). Further, vegetation heterogeneity engendered by patchy disturbance has been linked to higher bird diversity in tallgrass, mixed grass, and shortgrass prairies (Coppedge et al. 2009, Augustine and Baker 2013, Augustine and Derner 2015).

In contrast, shrubland birds, especially those dependent on sagebrush (*Artemisia* spp.), are less tolerant of disturbance (Knick et al. 2005, Hess and Beck 2012, Carlisle et al. 2018). Sagebrush systems evolved with less frequent and intense disturbance, generally lacking the vegetation clipping of black-tailed prairie dogs (*C. ludovicianus;* Hoogland 2013), and with reduced frequency of fire (Baker 2006). Most sagebrush species cannot resprout following fire (Shultz 2009), so recovery post-burn is on the scale of decades to centuries, instead of years to decades as in grasslands (Baker 2006, Baker 2011, Porensky et al 2018). Thus, whereas small disturbances may benefit some sagebrush obligate birds, these species tend to decline with high rates of disturbance (Knick et al. 2005, Beck et al. 2012, Carlisle et al. 2018).

In both ecosystems, habitat loss and shifting disturbance regimes have led to major declines in bird abundance. Following European settlement of the Great Plains mainly during the 1800s, many natural disturbances, including native ungulate herbivory, wildfires, and burrowing mammals, were suppressed to enhance agricultural outputs (Fuhlendorf and Engle 2001; Sampson and Knopf 1994; Davidson et al. 2012, Hoogland 2013, Sayre 2017). These changes may have served to homogenize rangeland landscapes in terms of vegetation structure and species composition (Fuhlendorf and Engle 2001), with negative consequences for many wildlife

species, in particular aridland birds (e.g., Brennan and Kuvlesky 2005, Fuhlendorf et al. 2006, Sauer et al. 2017). In contrast, in the sagebrush steppe, frequencies of disturbances such as wildfire have increased dramatically (Condon et al. 2011, Balch et al. 2013), destroying the sagebrush on which many bird species rely (Knick et al. 2005, Chambers et al. 2017).

Thus, despite their differing habitat and disturbance requirements, grassland and shrubland bird species are both in critical need of conservation. There exists an opportunity to manage and conserve both of these imperiled bird guilds within the Thunder Basin National Grassland, located in northeastern Wyoming at the ecotone between the Great Plains and sagebrush steppe. While ecotones may be complex from an ecological standpoint, they are crucial foci for managers, as they are often hotspots for biodiversity (Risser et al. 1995). The Thunder Basin landscape currently supports at least 20 bird species listed by the state of Wyoming as Species of Greatest Conservation Need (SGCN; Wyoming Game and Fish Department 2016), in addition to black-tailed prairie dogs, which have experienced approximately a 98% range-reduction following European settlement (Mulhern and Knowles 1997) and are also a SGCN in the state. Some species of concern, including the mountain plover (*Charadrius montanus*), often rely on disturbed habitat for nesting (Augustine and Derner 2012, Goguen 2012), and benefit from prairie dogs or fire. Conversely, imperiled sagebrush-obligates including the sage thrasher (*Oreoscoptes montanus*), Brewer's sparrow (*Spizella breweri*), and the greater sage-grouse (*Centrocercus urophasianus*), which was recently removed from the list of species warranted for federal listing under the Endangered Species Act in 2015 (USFWS 2015), may respond poorly to disturbances that destroy sagebrush plants.

Within the Thunder Basin ecotone, juxtaposed disturbance regimes and substantial heterogeneity in topography and soils (Gosz 1993, Risser et al. 1995) create highly

heterogeneous vegetation structure, ranging from mature shrublands to barren prairie dog colonies, at a relatively fine scale (<10 km). However, it is unclear how grassland and shrubland bird communities that co-occur and interact in this landscape may respond to disturbances and habitat variability at this scale. Identifying how different types of disturbance impact multiple bird species of conservation concern is critical for effective management and conservation in this avian biodiversity hotspot.

To evaluate the consequences of multiple forms of disturbance for a diverse, co-occurring suite of birds in Thunder Basin, we examined avian community response to historic wildfires and active prairie dog colonies within the grassland-sagebrush ecotone. We specifically asked: 1) how do bird communities and alpha diversity (site level) differ between two types of disturbance (burned areas, prairie dog colonies) and undisturbed habitat, 2) what disturbance-dependent and disturbance-independent factors shape the bird community, 3) how do the size and timing of disturbance (time since disturbance; disturbance duration) influence bird communities, and 4) how does beta diversity (species turnover) vary in relation to fire and prairie dog colony disturbances?

We hypothesized that presence versus absence of disturbances (fire or prairie dogs) would be the strongest driver of divergence in bird community composition, and that disturbance type (fire vs. prairie dogs) would additionally predict significant but less dramatic differences in community composition. Furthermore, we anticipated that both disturbance types would reduce species richness relative to communities in undisturbed habitats (due to reduced vertical structure; MacArthur and MacArthur 1961), but that disturbed habitats would support unique species, leading to increased beta diversity across the landscape. Alternatively, we examined whether disturbance-independent factors, particularly underlying topoedaphic heterogeneity,

could mitigate or mask the effects of disturbances, or whether variation among patches with the same disturbance type could be similar to or greater than variation among patches with different disturbance history. Finally, we tested two hypotheses regarding the size and duration of disturbances. First, we hypothesized that larger disturbances would have more distinctive bird communities because they provided a greater area of habitat distinct from the matrix. Second, we hypothesized that disturbance duration would affect community structure on prairie dog colonies but not burned areas, because vegetation communities remain relatively stable, dominated by native perennial grasses, for decades after fire (Porensky and Blumenthal 2016; Porensky et al. 2018).

METHODS

Study area

Our study was conducted within the U. S. Forest Service (USFS)–Thunder Basin National Grassland in Converse, Weston, and Campbell counties, Wyoming (Fig. 1). Mean annual precipitation ranged from 25–35 cm, and generally fell during spring and summer (Porensky et al. 2018). Dominant shrub species included Wyoming big sagebrush (*A. tridentata wyomingensis*), greasewood (*Sarcobatus vermiculatus*), broom snakeweed (*Gutierrezia sarothrae*), and other sagebrush species. Common graminoids included blue grama (*Bouteloua gracilis*), western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Heterostipa comata*), and threadleaf sedge (*Carex filifolia)*. Prairie dog colonies had a high proportion of bare ground and were dominated by western wheatgrass, plains prickly pear (*Opuntia polyacantha*), and short-lived forb species.

Study Design

In 2016 and 2017 we conducted point counts for birds on prairie dog colonies and paired off-colony sites, as well as on burned areas and paired off-burn sites. We sampled 33 colonies (40 point-pairs total) and 14 burned areas (37 point-pairs total). Spatial perimeters for fires were obtained from the USFS, and prairie dog colony perimeters were mapped by the USFS and researchers in 2015 and 2016. Historic wildfires ranged in size from approximately 5–3500 ha and colonies ranged from 6–4000 ha. Fires occurred between 5–43 ($\bar{x}$ = 14.6) years prior to the project, and colonies, which were all active during the study, were established between 0–15 ($\bar{x}$ = 5) years before our research. For prairie dog colonies, we utilized data from 33 larger transects randomly placed perpendicular to colony edges, composed of 5–8 points (depending on colony size) spaced apart by 250 m. On and off colony paired points for our study were randomly selected from each of these transects, such that only two points of each transect were included, and inter-point distances ranged between 0.25–1.25 km. Survey locations on burned areas also represented a subset of locations surveyed for a separate study (Porensky et al. 2018), which describes methodologies for sampling point selection. For both colony and burned area points, the minimum distance between paired points was 150 m to minimize spatial overlap in surveys. We surveyed the avian community at each point once in each year between late May and late June. During each 6-minute count, we recorded all species detected from the survey point. We recorded the distance and direction of each detection to facilitate distance sampling. Surveys occurred between 30 minutes before sunrise and 10:00 AM on days without high wind or rain (Pavlacky et al. 2017). By traveling to many points via off-road vehicle we ensured more effective detection of mountain plovers, which display more cryptic behavior in response to observers on-foot (Dinsmore 2003). Although our methods allowed us to detect plovers and passerines, they were not well-designed to detect greater sage-grouse, which are better assessed

through counts at leks, brood counts, winter flight surveys, or other techniques (Connelly et al. 2003).

We modeled detection probability for focal species using Program DISTANCE (version 6.0). We used the complete point-count dataset described in the methods for analysis of focal species abundance, meeting the minimum requirement of 40 detections per species (Buckland et al. 2001). We examined covariates with the potential to affect detectability of each species including weather (temperature, wind, cloud cover), observer, and vegetation structure in a multiple covariate distance sampling (MCDS) framework. We used Akaike's Information Criterion adjusted for small sample sizes (AICc) and goodness-of-fit (Chi-squared) to compare models (Burnham and Anderson 2002). Distance-adjusted densities were generated for each species using the top-ranked models. We then used densities to calculate Shannon's diversity (H'), which is a diversity metric that incorporates both species richness and evenness (Shannon 1948, Spellerberg and Fedor 2003).

Vegetation and landscape composition

In June and July each year, we measured visual obstruction (Robel 1970) in two directions every 5 m along a 30-m transect centered on the point count location (n = 14 readings per point per year). We recorded whether the obstructing vegetation was a shrub or herbaceous plant, allowing calculation of both total visual obstruction and herbaceous-only obstruction. We also collected shrub canopy cover data on transects in 2014–2015 using the line-intercept method (Canfield 1941, Herrick et al. 2009). Because shrub canopy cover likely varies minimally across years, we used these data to calculate percent sagebrush cover at each point for the entirety of our two-year study.

Avian habitat quality can be influenced by soils and topography both directly and indirectly via vegetation responses to underlying topo-edaphic patterns (Renfrew and Ribic 2002, Lipsey and Naugle 2017). Further, disturbance may be mitigated or enhanced by these same features (Reading and Matchett 1997, Augustine and Derner 2014, Harris and Taylor 2017). As such, we examined both soils and topography within 100 m of each point. We chose this 100-m scale as it was large enough to capture variation in these variables within a "territory scale" for most focal bird species, but also small enough to minimize overlap between adjacent point-count locations. We used a digital elevation model to generate average values of elevation, slope, and aspect, and we generated a topographic roughness index (TRI) and topographic wetness index (TWI; Gesch 2007, Porensky et al. 2018). We used the SSURGO database (NRCS 2017) to characterize average soil texture (% clay, silt, or sand) from 0–30 cm at each point, and we estimated average 30-yr maximum and minimum temperature at each point (PRISM 2004).

Data analyses

To assess the magnitude of bird community differences among burned areas, prairie dog colonies, and undisturbed habitat, we calculated permutational multivariate analysis of variance (PerMANOVA; Anderson 2001) using the 'adonis' function of the vegan package in R (Oksanen et al. 2017). As a non-parametric analogue to MANOVA, PerMANOVA partitions variance to generate a test statistic and used permuational methods to generate *P* values. We examined the effects of strata type (prairie dog colony, burned area, undisturbed) and year on community structure.

We used non-metric multidimensional scaling (NMDS; Kruskal 1964) to examine patterns of community structure among disturbance types, disturbance traits, and site-level

characteristics to test hypotheses related to Questions 1 and 2 above. NMDS is an unconstrained ordination technique that plots points based on the rank-order dissimilarity of multivariate data (here, avian community), such that points with similar communities occur in close proximity in ordination space. Goodness-of-fit of the ordination is determined by ordination stress (Kruskal 1964). We used Bray-Curtis distance as the measure of ecological dissimilarity (Field et al. 1982). We then used the 'envfit' function to examine correlations between variables associated with vegetation structure, topography, and soils with NMDS ordination axes. Vectors represent the direction of most rapid change in a given variable, with length corresponding to the level of correlation between the variable and ordination. Thus, vectors of the greatest length explain more variation in community structure. We present vectors with correlation coefficients (Oksanen et al. 2017) of $r^2 > 0.05$.

To understand whether abiotic factors and disturbance age or size modulated the community-level avian response to disturbance, we measured the distance in ordination space between points for communities located on prairie dog colonies and the centroid of the prairie dog cluster, and similarly measured the distance between points on burned areas and the centroid of the burned area cluster in each year. We reasoned that points closer to centroids represented communities more “typical” of a given disturbance type, whereas those farther from centroids showed more variation, and thus more divergence from those semi-discrete communities. We then used a mixed-model framework to examine distance to centroid as a function of age of disturbance, size of disturbance, as well as a suite of abiotic variables including soils and topography, along with a random effect of patch identification (ID; unique identifier for each wildfire or prairie dog colony), to determine whether any of these variables affected community divergence. We modeled burned areas and prairie dog colonies separately, as “age” of colony

has a very different meaning in terms of disturbance intensity compared with age of fire (i.e., colony “age” is more a metric of disturbance duration, whereas fire age indicates time since disturbance). Single variable models of distance to centroid were compared using AICc (Burnham and Anderson 2002). Where multiple variables were >2 AICc better than the null, we also explored interactions.

Finally, we calculated community dissimilarity (beta diversity; Anderson et al. 2011) between paired points on versus off disturbance types using the 'betapart' package in R (Baselga et al. 2017). The level of community dissimilarity between points on and off disturbed patches may be a function of disturbance type, underlying abiotic differences between points, or some combination of these drivers. Therefore we first explored single-variable models predicting community dissimilarity between inside-outside point pairs, examining the effects of disturbance type and size, as well as the between-point difference in abiotic qualities (e.g., difference between maximum temperature) and biotic structure (e.g., difference in VOR). This variable set included all abiotic and biotic factors considered above (also see Table 1), as well as a univariate model of inter-point distance between pairs, because proximity may correlate with community similarity irrespective of other habitat traits (Legendre and Legendre 1998). We then examined all combinations of variables that occurred in the best univariate models.

Because we were interested in how disturbance may directly interact with topo-edaphic features within a patch, we also compared two-way interactions between disturbance type and abiotic variables at inside-patch points, to see if these interactions explained beta diversity better than disturbance type alone. All community dissimilarity models included a random effect of Patch ID. We did not explore models including more terms or interactions because of limitations in sample size.

RESULTS

We observed 50 species during the two years of study, which in addition to our focal species also included raptors, migrants, non-rangeland species (e.g., riparian birds), and 8 species that were only detected once (Appendix S1: Table S1). We modeled distance-adjusted densities for the 11 most abundant grassland or shrubland species (Vickery et al. 1999, Paige and Ritter 1999), all of which were either ground or shrub nesters within the study area (Fig. 2). This community included ten birds recognized as species in steep decline by Partner's in Flight (PIF 2017; Appendix S1: Table S2), five of which were also species of conservation concern within Wyoming (mountain plover, loggerhead shrike [*Lanius ludovicianus*], Brewer's sparrow, grasshopper sparrow [*Ammodramus savannarum*], and sage thrasher; see Fig. 2). Horned larks (*Eremophila alpestris*) and western meadowlarks (*Sturnella neglecta*) made up the majority (>50%) of counts in all strata. We documented distinct differences among bird communities related to the presence and type of disturbance (Fig. 2). Mountain plovers were exclusively observed on prairie dog colonies, and horned larks reached their greatest abundance on prairie dog colonies (Fig. 2). Conversely, western meadowlarks and grasshopper sparrows reached their highest abundances on burned sites, and the latter was entirely absent on prairie dog colonies. Sagebrush obligates, including the Brewer's sparrow and sage thrasher, were rare on both prairie dog colonies and burned areas and were most abundant on undisturbed sites.

We used distance-adjusted densities of these 11 avian species for multivariate community analyses. PerMANOVA analyses indicated stark ($P < 0.001$, $F_{2,304} = 24.04$) differences among communities on burned areas, prairie dog colonies, and undisturbed points, while differences

between years were only significant at an alpha of 0.05 (P = 0.02, $F_{1, 304}$= 2.69). We found no evidence of an interaction between stratum type and year.

The NMDS ordination converged on a two-dimensional solution with stress of 0.15 and non-metric fit R^2 = 0.977. Disturbed sites scored lower on the second (vertical) axis, and bird communities on prairie dog colonies were the most distinct of the four types, both in terms of standard deviation hull overlap (Fig. 3) and species locations in ordination space (Fig. 4). Species locations in ordination space indicate groupings including shortgrass species (mountain plover and horned lark), mixed-grass species (western meadowlark and grasshopper sparrow), and species requiring some component of shrub cover (Brewer's sparrow, sage thrasher; Fig. 4). Nine of fourteen abiotic and vegetation predictors had an r^2 >0.05 (Table 1), and were therefore mapped onto the ordination (Fig. 4). Disturbance-dependent and disturbance-independent site features varied among burned areas, prairie dog colonies, and undisturbed sites (Fig. 5). Prairie dog colonies showed the most distinctive vegetation structure in terms of extremely low visual obstruction and sagebrush cover, followed by burned areas (Fig. 5), but there were also some differences among undisturbed sites, mainly due to their location within the grassland (Fig. 4, Fig. 5).

Sage thrashers and Brewer's sparrows, most common on unburned sites, were associated with greater sagebrush cover and visual obstruction, and both lark buntings (*Calamospiza melanocorys*) and vesper sparrows (*Pooecetes gramineus*) also trended in this direction (Fig. 4). Loggerhead shrikes and mourning doves *(Zenaida macroura*) were associated with greater topographic roughness, slope and greater minimum temperatures. Grasshopper sparrows, and to some extent western meadowlarks, were associated with burned sites. Finally, prairie dog colonies, which were associated with more clayey soils, higher maximum temperatures, lower

vegetation structure and sagebrush cover, and gentle topography, supported peak abundances of mountain plovers and horned larks.

On average, bird communities varied slightly more among sites with prairie dogs than among burned sites ($\bar{x}$ = 1.29 and $\bar{x}$ = 1.0, respectively), as measured by our community convergence metric (i.e., distance from community points to centroids in ordination space). However, an examination of the different drivers of community convergence is more interesting; disturbance size and age predicted community convergence on prairie dog colonies, such that older and larger colonies tended to have more typical bird communities, while areas with greater average annual precipitation showed more community variation (Table 2). No models including the interactions of colony age or area with abiotic features improved upon an additive model including the main effects of age (β = -0.035, SE 0.021) and area (β = 0.318, SE 0.133). Conversely, neither disturbance age nor area affected bird community response to historic wildfires (Table 2). Instead, yearly variation was the best predictor and distance to centroid was highest in 2017, whereas minimum temperature performed only marginally (<2 AIC_c) better than the null model.

Alpha diversity (site diversity) was lowest on prairie dog colonies and highest on burned areas and undisturbed sites (Fig. 6). However, beta diversity (community dissimilarity between disturbed sites and paired undisturbed points) was higher for prairie dog disturbance than wildfire disturbance (Fig 6). This difference was likely a product both of lower diversity on prairie dog colonies and the presence of unique species on those colonies. To better understand why community dissimilarity differed between disturbance types, we compared a model including disturbance type (fire or prairie dog) with univariate models of a suite of disturbance-dependent (e.g., VOR) and disturbance-independent (e.g., topography) variables (Table 3a).

Disturbance type was the best predictor with >98% of the model weight, but inter-point distance (km), difference in clay content, and difference in maximum temperature (C) were also >2AIC_c better than the base model (Table 3a). Examination of additive effects of these four variables indicated a top model including disturbance type ($\beta_{prairie\ dog}$ = 0.21, SE 0.055) and interpoint distance (β = 0.14, SE 0.067; Table 3b), but there was substantial model uncertainty (i.e., no one model carried most of the model weight). Only one model examining the interaction between abiotic traits within patch and disturbance type improved on disturbance type alone (Appendix S1: Table S3). The interaction of % clay within a patch with disturbance type was marginally (0.8 AIC_c) better than disturbance type alone, indicating increasing dissimilarity on prairie dog colonies with increasing clay content (Fig. 7).

DISCUSSION

Disturbance is a key driver maintaining heterogeneity in rangeland vegetation structure (Pickett and White 1985, Ceballos et al. 1999, Fuhlendorf et al. 2017), yielding a mosaic of patches at the landscape scale that provides habitat for diverse wildlife species (Warui et al. 2005, Fuhlendorf et al. 2006, Davidson et al. 2012, Ricketts and Sandercock 2016). Our results show that in a sagebrush-grassland ecotone, disturbances such as wildfire and small burrowing mammals create habitat mosaics that strongly influence avian distribution and diversity. Contrary to our expectation, disturbance type played a larger role than simple presence/absence of disturbance relative to undisturbed habitat. Indeed, prairie dog colonies harbored the most distinct communities in NMDS ordinations relative to burned areas or undisturbed sites (Fig. 4). Although prairie dog colonies had relatively low alpha diversity, they contributed most to beta diversity relative to undisturbed habitat, largely because they were the only sites to contain mountain plovers. Neither historically burned areas, prairie dog colonies, nor undisturbed habitat

were alone capable of supporting the full suite of avian species—instead, all three patch types were necessary to maintain avian biodiversity in this landscape.

Several important species of conservation concern (sage thrasher, Brewer's sparrow, and loggerhead shrike) were most abundant in the sagebrush-dominated habitats that form a large portion of the undisturbed matrix across this landscape. Although our surveys were not well-suited to detecting them, greater sage-grouse also occur in the study region and depend on relatively large, dense stands of sagebrush (Connelly et al. 2011, Knick and Hanser 2011). Sagebrush-associated birds rely on sagebrush for both nesting and foraging substrate (Connelly et al. 2011, Rotenberry and Wiens 1998), and in the case of sage-grouse, for food (Peterson 1970, Wallestad et al. 1975). These species have been shown to decline in response to a wide range of factors that reduce the extent and connectivity of sagebrush shrublands, especially anthropogenic disturbances associated with energy extraction (e.g., Gilbert and Chalfoun 2011, Hess and Beck 2012, LeBeau et al. 2014) and cultivation (Smith et al. 2016), as well as wildfire (e.g., Knick et al. 2005, Hess and Beck 2012, Holmes et al. 2013).

Fire and prairie dog grazing reduce sagebrush cover in the northern Great Plains (Johnson-Nistler et al. 2004, Baker 2006, Porensky et al., 2018, Connell et al. 2018). As we hypothesized, these disturbances reduce available habitat for sagebrush birds (Fig. 2), but simultaneously provide opportunities for distinct grassland bird communities which vary by disturbance type. Continuous herbivory and clipping by prairie dogs provided the short, sparse plant structure preferred by the mountain plover and horned lark, as well as burrowing owls (*Athene cunicularia*). Although only two observations of burrowing owls occurred in our dataset, this Wyoming SGCN was also confined to prairie dog colonies (see Appendix S1: Table S1). Consistent with our hypothesis, larger and older prairie dog colonies tended to have more distinct

communities, with higher abundances of these shortgrass species. Our results highlight the critical importance of prairie dogs for mountain plover conservation in this region. Although mountain plovers often benefit from disturbance by prairie dogs within rangelands across the western Great Plains, it appears that in Thunder Basin, as in much of the northern Great Plains, they are almost completely reliant on habitat created by prairie dogs (Dinsmore et al. 2005, Augustine and Baker 2013).

In contrast, mixed-grass species like the grasshopper sparrow were entirely absent on prairie dog colonies, but were abundant on burned areas. Grasshopper sparrows are associated with disturbance in the eastern and midwestern portion of their range (e.g., Rahmig et al. 2009, Duchardt et al. 2016), but in semi-arid portions of the Great Plains this and other mixed-grass associates (e.g., western meadowlark) are often intolerant of grazing regimes or fire that suppress vegetation height and cover (Bock and Webb 1984, Saab et al. 1995, Augustine and Derner 2015). Both grasshopper sparrows and western meadowlarks rely on grass clumps and a moderate litter layer for construction and concealment of ground nests (Vickery 1996), and these habitat features are available within burned areas in the northern Great Plains (Porensky et al. 2018, Vermeire et al. 2011), but entirely absent on prairie dog colonies in the Thunder Basin ecotone. We did not expect fire age to affect bird communities but were surprised that communities did not differ substantially by any aspect of fire disturbance, including size. Given the substantial variation of grasshopper sparrow abundance among burned areas (Fig. 2), it may be that other unmeasured site-level variables or social cues (e.g. Andrews et al. 2015) play a greater role in habitat selection than patch size.

Importance of topo-edaphic drivers

Although disturbance was the most important factor structuring bird communities, other disturbance-independent landscape features mediated avian species composition. For example, loggerhead shrike abundance was greater in areas of rough topography. It is likely that shrikes do not show a preference for rugged topography itself, but instead utilize the isolated clusters of trees present along drainages. These sparse areas of tree cover, relatively rare in the landscape, provide shrikes with nesting and perching substrates (Becker et al. 2009).

Soils and topography also have the potential to interact with disturbance processes, leading to increased variation in vegetation structure. For example, our results are consistent with previous studies showing that prairie dogs tend to utilize relatively flat areas (e.g., Reading and Matchett 1997). Flat topography combined with constant prairie dog-driven soil disturbance leads to more bare ground exposure and birds associated with bare ground, such as mountain plovers. We also observed a marginal interactive effect of prairie dog disturbance with soil clay content, such that sites on prairie dog colonies where clay content was highest were most dissimilar to paired undisturbed points, while clay content had little effect on dissimilarity of bird communities on burned sites. Clayey soils have been identified as playing a role in prairie dog burrow construction (Reading and Matchett 1997, Augustine et al. 2012), and may be preferred by prairie dogs; although clay content was higher on prairie dog colonies relative to burned areas or undisturbed habitat (Fig 5), we still observed variation in clay content on these sites (23.3–45.0%). Compared to coarser-textured soils, clayey soils support shorter, less dense herbaceous vegetation in this ecosystem (Porensky et al. 2018) and have relatively slow infiltration rates, which can lead to more overland flow and/or evaporative loss of soil moisture following heavy spring and summer rains (Martinez-Mena et al. 1998). Thus, soil texture may act synergistically

with prairie dog activity to increase bare ground exposure on colony sites, increasing their suitability for shortgrass bird species.

Implications for management

Rangeland landscapes that have not been extensively fragmented by anthropogenic land conversions (e.g., to croplands, exurban development, and/or energy extraction) are becoming increasingly rare worldwide. Remaining minimally fragmented landscapes are increasingly expected to sustain viable local populations of a diverse suite of species of conservation concern, often with conflicting habitat needs. Our findings clearly support the idea that maintaining all components of historic disturbance regimes is necessary to sustain the full suite of native birds, and potentially other guilds of vertebrates, as has also been shown for other iconic and extensive rangelands of North America (Fuhlendorf et al. 2006; Hovick et al. 2014), Africa (du Toit et al. 2003; Gregory et al. 2010), and Australia (Doherty et al. 2017).

Our findings also highlight that sustaining the full suite of native species will require improved knowledge of how to manage a shifting mosaic of multiple disturbances in amounts and configurations that match conservation priorities and species needs. Unlike some grasslands where transitions among habitats for different species can occur within several years (e.g., Hovick et al. 2014), the multi-decadal transition time from disturbed patches back to a shrubland state in ecosystems like Thunder Basin, combined with our finding that burns and prairie dog colonies support unique and distinct bird communities, create substantial complexity for the management of disturbance regimes. Large, contiguous areas of sagebrush-dominated rangeland are needed to support greater sage-grouse conservation (Holloran and Anderson 2005, Connelly et al. 2011, Knick and Hanser 2011, Smith et al. 2016) and sagebrush stands additionally support

the greatest number of species of conservation concern (Fig. 2). A major challenge in such landscapes will be to maintain adequate amounts of multiple disturbances to support their associated conservation targets, while still minimizing their negative impact on the amount and fragmentation of matrix, undisturbed habitats.

In the case of Thunder Basin, a key consideration in determining the balance between burned versus colony patches is likely to be the colony-associated mountain plover, which has a far lower global population than the other bird species we detected (Appendix S1: Table S2), and occurs at a much lower population density than other bird species. As a result, a key future research need is to understand the amount and configuration of prairie dog colonies that will sustain mountain plover populations, while still minimizing impacts of prairie dogs on sagebrush extent and connectivity. This conflict may point toward management to promote a greater proportion of colony areas relative to burns, because small burned patches can support much higher densities of conservation targets such as grasshopper sparrows, as compared to plovers on colonies.

Additional complexity arises from the fact that uncontrolled wildfires periodically occur despite the best efforts of land managers. Similarly, prairie dog colonies experience dramatic spatial and temporal variability in their location and extent in response to die-offs induced by plague (*Yersinia pestis*; Augustine et al. 2008; Cully et al. 2010; Hoogland 2013). Thus, managers of extensive rangeland landscapes will need to increasingly consider existing patterns of disturbance of the landscape, desired amounts to meet conservation objectives, and tradeoffs associated with potential, uncontrollable future patterns of disturbance, as they attempt to adaptively manage disturbance regimes. These realities emphasize the need to manage

disturbance processes in rangelands in relation to their inherent variability rather than for a theorized optimal landscape.

Just as wildfires and prairie dog colonies are not static in time or space, climatic variability also shapes both avian communities and disturbance processes. We found that year, a proxy of weather variability, interacted with avian community responses to disturbance drivers. Thunder Basin experienced both drought and extremely high temperatures during the survey period in 2016 (NOAA 2016), and abundance of species relying on taller grasses (e.g., grasshopper sparrow) was reduced throughout the study area. Heat and summer droughts are predicted to increase with climate change (USGCRP 2014), and these shifts have the potential to negatively influence bird species that rely on dense vegetation. Over the longer-term, increased climate variability may also impact shortgrass obligate birds, albeit indirectly, via changes in prairie dog population dynamics (Eads and Hoogland 2017). Across broad spatial and temporal scales, climate change has the potential to shift range limits of wildlife species (Walther et al. 2002, Root et al. 2003). The Thunder Basin ecotone currently represents the western or eastern range limit of many grassland and sagebrush bird species, respectively. In this and other ecotones, climate change may shift species composition more rapidly, and potentially in unexpected ways (e.g., Allen and Breshears 1988).

CONCLUSIONS

In an ecotone between the sagebrush steppe and the Great Plains, bird communities responded strongly to fire and burrowing mammals, lending further support for the critical role of disturbance regimes in driving biodiversity in North American rangelands (Kotliar et al. 1999, Fuhlendorf et al. 2006, Engle et al. 2008, Augustine and Derner 2015). For example, without

black-tailed prairie dogs, the imperiled mountain plover would be rare in or entirely absent from our study area (see also Dinsmore et al. 2005). Prairie dog disturbance also interacted with soil texture such that bird communities on colonies with clayey soils were more distinct relative to those with less clay content. Although disturbance is crucial, the amount and configuration of undisturbed habitat is also important to consider in this ecotonal landscape. Undisturbed habitat is necessary to support sagebrush-obligate birds (e.g., greater sage grouse, sage thrasher), because sagebrush recovers slowly following disturbance (Baker 2011, Beck et al. 2012). However, we acknowledge the unpredictability of both disturbance regimes and climate (both current and future) in this system. To guide management in this heterogeneous and dynamic environment, we suggest that future research focus on identifying threshold responses of avian species to the amount and spatiotemporal configuration of multiple disturbances in the landscape.

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TABLES

Table 1. Descriptive statistics and correlations between vegetation or topo-edaphic variables and bird community structure (coordinates in NMDS ordination space) in 2016–2017, Thunder Basin National Grassland, Wyoming, USA. Bolded variables were included as vectors in ordination space in Figure 4.

Variable	Mean	Range	r^2	Pr (>r)
Visual obstruction (cm)	**5.5**	**0.1-45.4**	**0.207**	**<0.001**
Sagebrush (%)	**4.7**	**0.0-62.6**	**0.188**	**<0.001**
Mean roughness	**1.1**	**0.1-5.2**	**0.142**	**<0.001**
Herbaceous VOR (cm)	**4.8**	**0.5-35.5**	**0.091**	**<0.001**
Clay (%)	**32.9**	**8.5-45.0**	**0.068**	**<0.001**
Min Temperature (C°)	**0.2**	**-0.09-1.3**	**0.064**	**<0.001**
Max Temperature (C°)	**15.5**	**13.9-16.1**	**0.059**	**<0.001**
Sand (%)	38.3	17.0-66.6	0.043	0.002
Annual precipitation (mm)	322.1	288.6-335.4	0.035	0.006
Topographic Wetness Index	5.4	3.1-16.2	0.034	0.006
Aspect	168.7	2.2-359.5	0.021	0.041
Silt (%)	28.9	1.7-57.65	0.002	0.779

Table 2. Top models for factors modulating bird community convergence on prairie dog colonies and burned areas in Thunder Basin National Grassland, Wyoming, USA, 2016–2017. All models include a random effect of Patch ID. Bold indicates the only additive or interactive model better than the best single-variable model.

MODELS	k	AICc	ΔAICc	weight
Prairie dog				
Age of disturbance + Area of disturbance	**4**	**121.3**	**0**	**0.43**
Area of disturbance	3	122	0.6	0.31
Age of disturbance	3	124.6	3.2	0.085
Precipitation	3	126.5	5.2	0.032
Year of study	3	127	5.7	0.025
Aspect	3	127.2	5.8	0.023
Null	*2*	*127.6*	*6.3*	*0.019*
Historic Fire				
Year of study	3	82.2	0	0.964
Minimum temperature	3	91.1	8.9	0.011
Maximum temperature	3	91.9	9.7	0.01
Null	*1*	*89.7*	*9.8*	*0.01*

Table 3. Univariate models (A) predicting avian community dissimilarity, Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Base model consisted of random effect of patch ID. All additive combinations of variables >2AIC_c better than the null (bold) were explored. B) Additive models compared to disturbance type alone.

A) MODEL	AIC_c	ΔAIC_c	K	weight
Disturbance Type	**34.5**	**0**	**4**	**0.986**
Inter-point distance	**43.2**	**8.7**	**4**	**0.013**
Clay%[D]	**49.2**	**14.7**	**4**	**<0.001**
Maximum Temperature[D]	**53.5**	**19**	**4**	**<0.001**
Minimum Temperature [D]	55.1	20.6	4	<0.001
Study year	55.4	20.9	4	<0.001
Sand %[D]	55.6	21.1	4	<0.001
Silt %[D]	56.7	22.1	4	<0.001
Annual Precipitation[D]	57	22.5	4	<0.001
Base Model	57.1	22.6	3	<0.001

B) MODEL	AIC_c	ΔAIC_c	K	weight
Disturbance Type + Interpoint distance	***32.4***	***0***	***5***	***0.289***
Disturbance Type + Interpoint distance + %Clay D	***33.3***	***0.9***	***6***	***0.188***
Disturbance Type + Interpoint distance +Maximum Temperature	***34.4***	***2***	***6***	***0.106***
Disturbance Type	34.5	2.1	4	0.1

[D]Indicates the absolute value of the difference between values of inside-outside point pairs

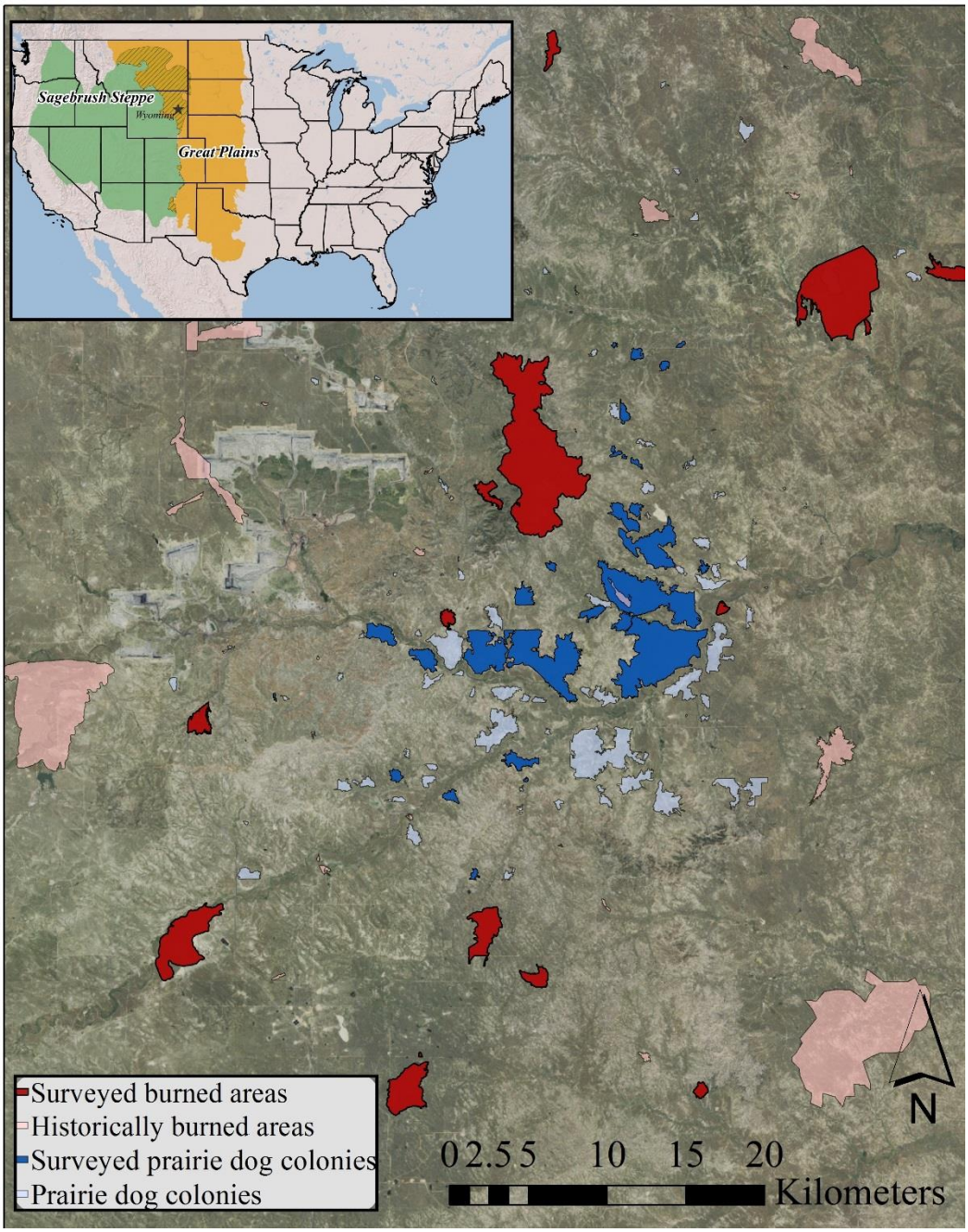

Figure 1. Location of historically burned areas and active prairie dog colonies in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Surveyed patches shown in bold colors. [Inset: Location of the TBNG at the ecotone between the Great Plains and the sagebrush steppe]

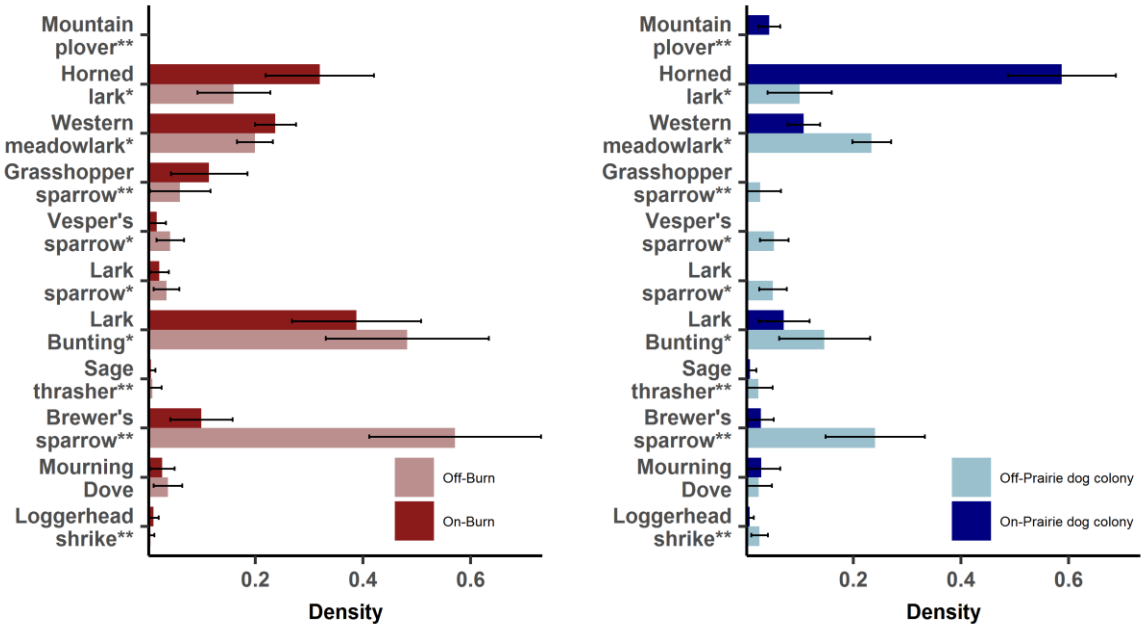

Figure 2. Distance-adjusted densities (per ha) of 11 abundant avian species on and off fires (red) and off prairie dog colonies (blue) averaged across years, Thunder Basin, Wyoming, USA, 2016–2017. * indicates Partners In Flight (PIF) species in decline (rank 4 or 5), ** indicates species that are both PIF in decline and SGCN in Wyoming.

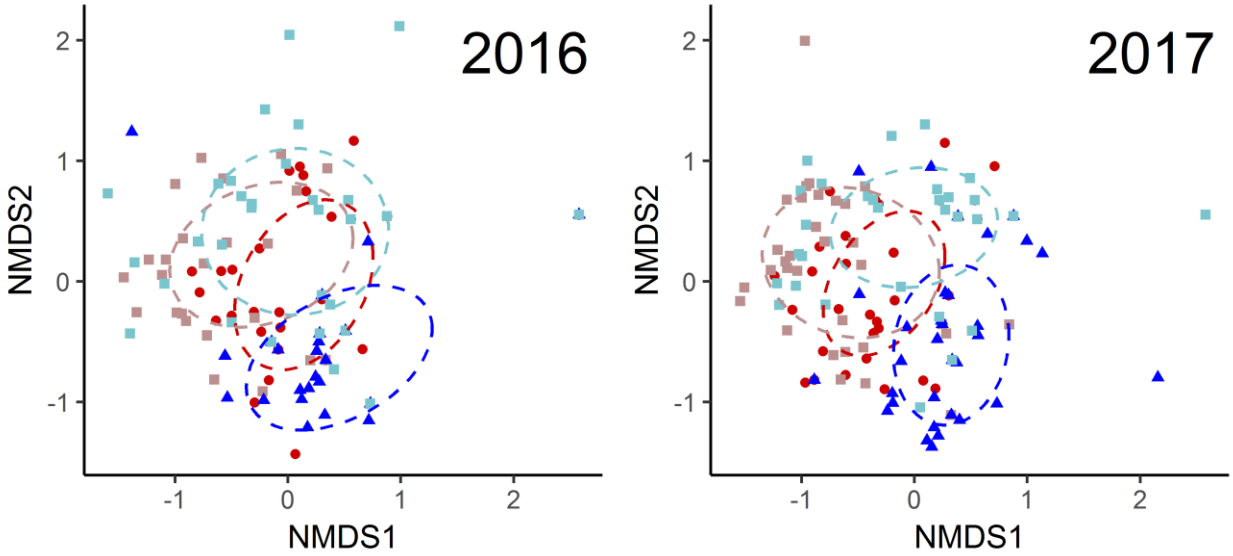

Figure 3. Non-metric multidimensional scaling ordination representing bird communities in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Points represent bird communities on prairie dog colonies (dark blue triangles), off prairie dog colonies (light blue squares), on burned areas (dark red circles), and off burned areas (light red squares). Ellipses represent standard deviations of each strata in each year.

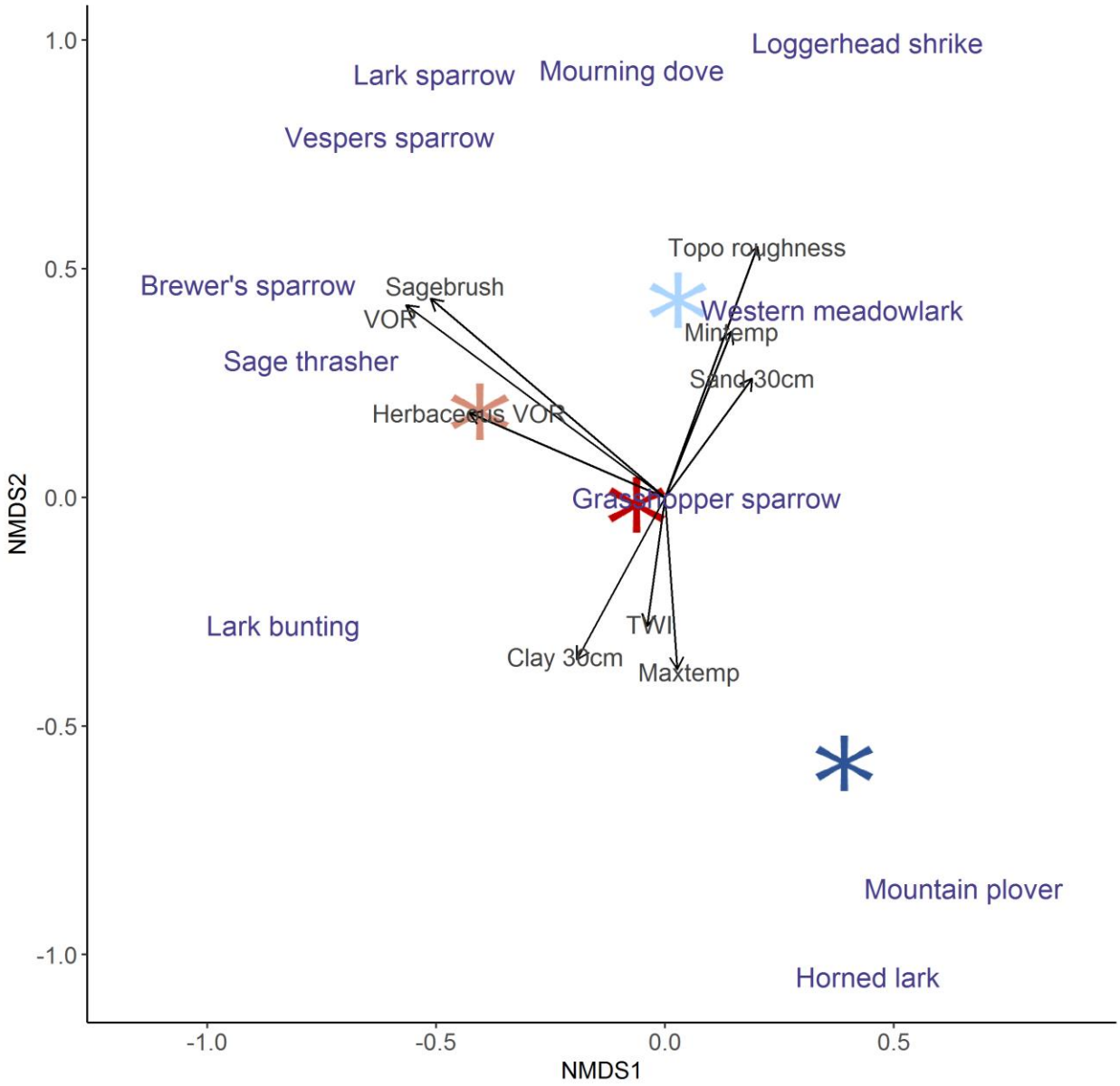

Figure 4. Bird species locations in ordination space, as well as vector overlay of important site-level variables, Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Centroids for inside-outside pairs of communities are presented for prairie dog colonies (on = dark blue, off = light blue) and historically burned areas (on = red , off = pink).

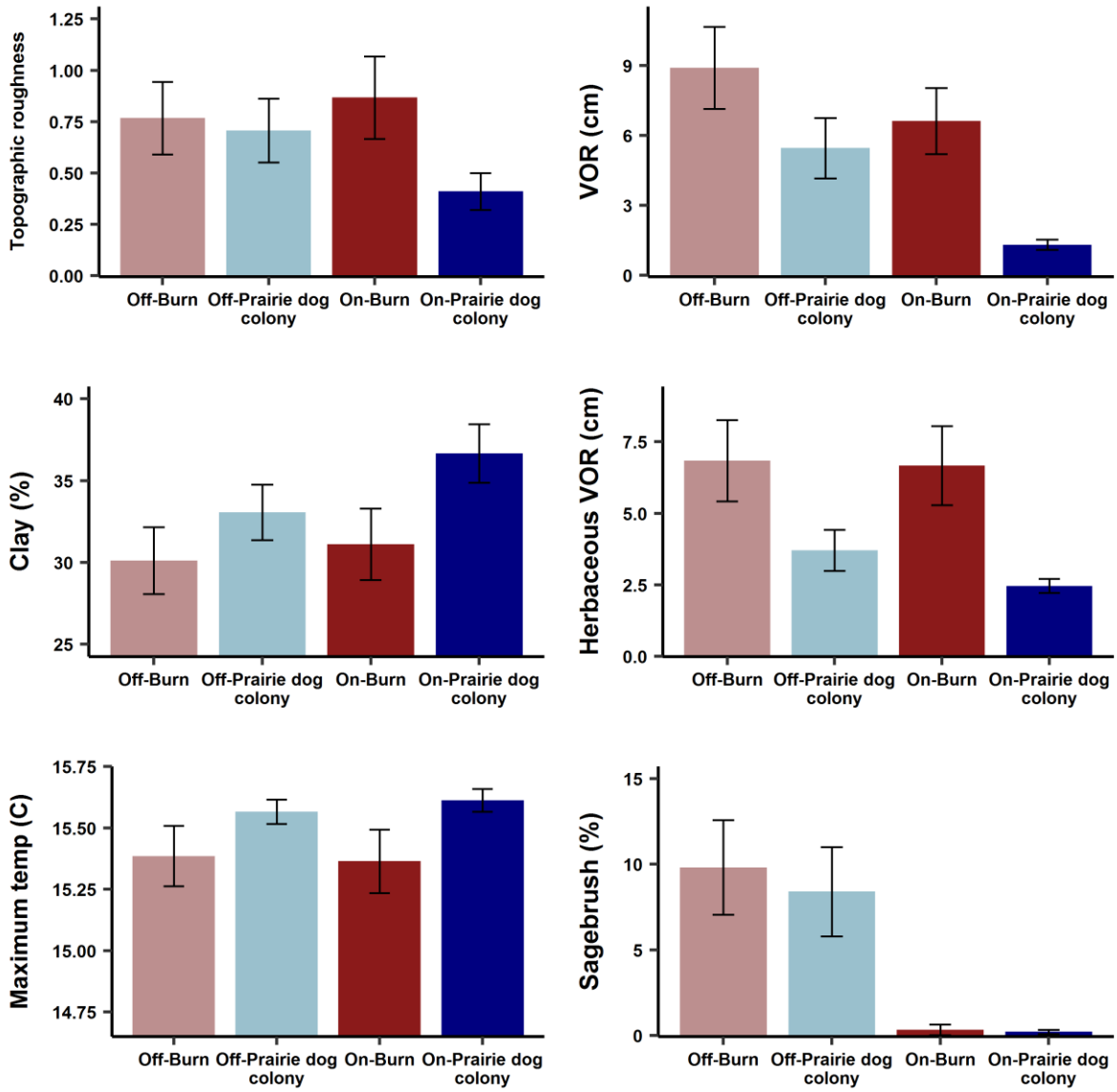

Figure 5. Variation in disturbance-independent (left figure panels) and disturbance-dependent (right figure panels) variables shaping bird communities, Thunder Basin National Grassland, Wyoming, USA, 2016–2017.

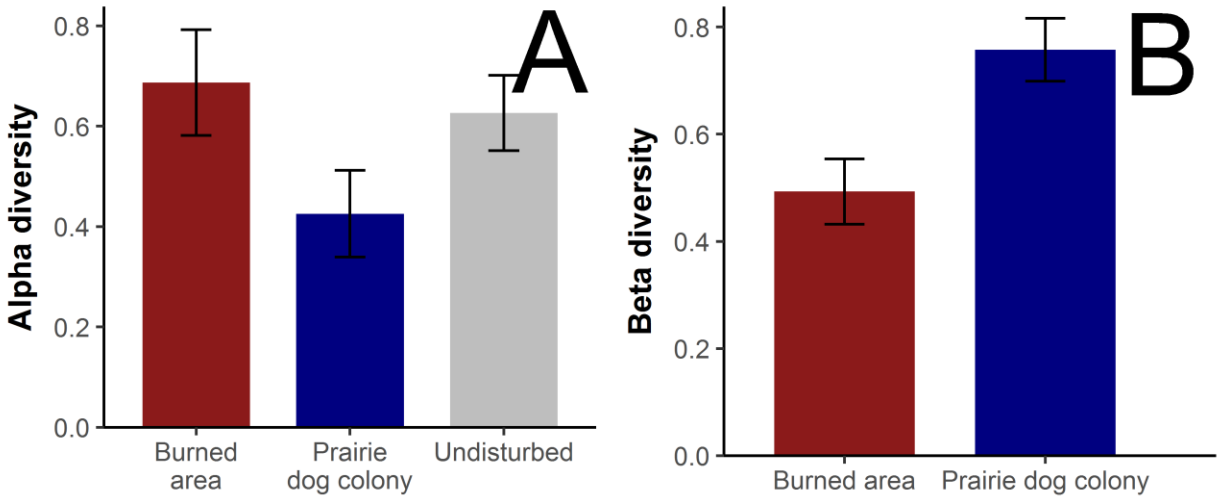

Figure 6. Alpha diversity (A), calculated as the Shannon index, Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Community dissimilarity or beta diversity (B), calculated as Bray-Curtis dissimilarity. Beta diversity was calculated as the difference between paired disturbed and undisturbed points for fires and prairie dog colonies.

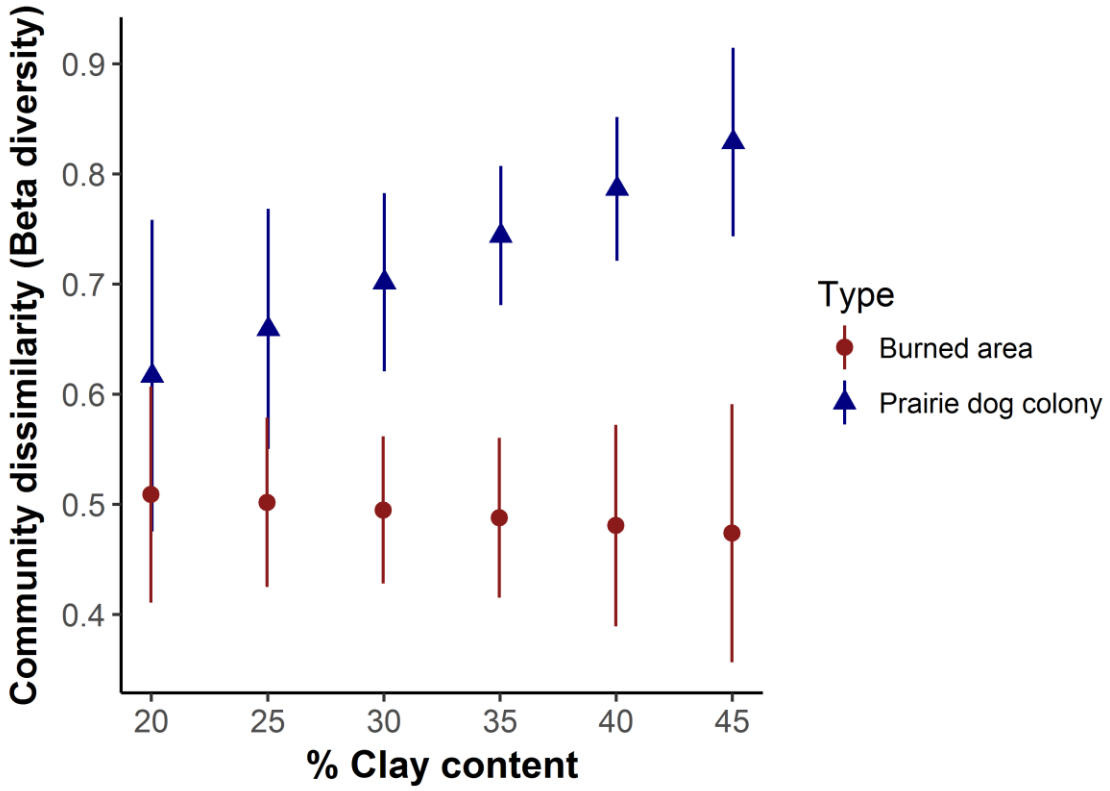

Figure 7. Interactive effects of clay content (%) within disturbed patch and disturbance type on community dissimilarity in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017.

Chapter 3. Threshold responses of grassland and sagebrush birds to patterns of disturbance created by an ecosystem engineer

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ABSTRACT

Context: Burrowing mammals play a role in rangeland disturbance worldwide, enhancing habitat for certain species while negatively affecting others. However, little is known concerning effects of disturbance spatial pattern on co-occuring fauna. In the North American Great Plains, colonial black-tailed prairie dogs (*Cynomys ludovicianus*) may enhance habitat for one suite of birds while degrading habitat for others.

Objectives: We examined the influence of prairie dogs on birds in a mosaic grassland-shrubland landscape. We evaluated how birds associated with shortgrass, midgrass, and sagebrush (*Artemisia* spp.) plant communities respond to spatial pattern of prairie dog disturbance and identified thresholds where abundance changes.

Methods: We surveyed bird abundance on prairie dog colonies of varying sizes and shapes, across colony edges into undisturbed habitat, and within undisturbed sagebrush in northeastern Wyoming. We modeled species responses to colony presence, distance to colony edge, and total area and edge density of colonies at four spatial scales (100 m, 225 m, 500 m, 1000 m).

Results: Sagebrush specialists like Brewer's sparrow (*Spizella breweri*) and sage thrasher (*Oreoscoptes montanus)* were 4.5 times more abundant in undisturbed shrublands. Conversely, the shortgrass-specialist mountain plover (*Charadrius montanus*) was abundant on colonies but showed a non-linear response to colony edge, increasing in abundance up to 600 m from edges then declining further towards colony cores.

Conclusions: While some species may be broadly intolerant to disturbance, disturbance-dependent birds can display a "goldilocks syndrome" relative to disturbance size. As such, management for multiple species of conservation concern can be optimized relative to other goals by identifying thresholds associated with the effect of disturbance.

KEYWORDS: mountain plover, grasshopper sparrow, Brewer's sparrow, sage thrasher, rangeland, community, ecotone;

INTRODUCTION

Rangeland ecosystems worldwide are shaped by disturbance processes including fire and grazing by mammalian herbivores (Fuhlendorf et al. 2012, Davidson et al. 2012). North American rangelands were drastically altered following European settlement as a result of conversion to rowcrops (Wright and Wimberly 2013), energy extraction (Allred et al. 2015), exurban development (Riebsame et al. 2014, Sala et al. 2017), introduction of exotic species (USDA 2010, DiTomaso et al. 2017), extirpation and control of undesirable native species (Miller et al. 2007, Sayre 2017), and alteration of historic disturbance regimes (Sayre 2017, Fuhlendorf et al. 2017). These changes have severely reduced habitat availability and quality for rangeland wildlife, making these species a key target for conservation. Restoration of historic disturbance regimes is especially important for rangeland wildlife that evolved in the context of these disturbances (e.g., Brawn et al. 2001, Fuhlendorf and Engle 2001). Throughout the Great Plains, disturbance caused by black-tailed prairie dogs (*Cynomys ludovicianus*), which are colonial, burrowing, herbivorous mammals, has been identified as a major driver of community structure in grasslands (Lomolino and Smith 2004, Augustine and Baker 2013). This oversized influence has led black-tailed prairie dogs to be labeled as both a keystone species (Kotliar et al. 1999) and an ecosystem engineer (Van Nimwegen et al. 2008). While the black-footed ferret (*Mustela nigripes*) is well known as a globally-imperiled species that is an obligate predator of prairie dogs (Dobson and Lyles 2000), many other species including herptiles (Shipley and Reading 2006), arthropods (Davidson and Lightfoot 2007), mammals (Lomolino and Smith 2004, Shipley and Reading 2006), and birds (Augustine and Baker 2013) rely on colonies for breeding habitat and food resources.

Despite the crucial role black-tailed prairie dogs play in these systems, they occupy less than 1% of their historic range (Miller and Cully 2001) and continue to experience lethal control because of potential competition with livestock (Derner et al. 2006, Miller et al. 2007). Prairie dog populations are further reduced by epizootics of sylvatic plague (*Yersina pestis*), which can lead to >95% dieoff within colony complexes (Cully et al. 2010). Prairie dog declines due to lethal control and plague epizootics have been directly linked with declines in imperiled grassland birds including the mountain plover (*Charadrius montanus*; Augustine et al. 2008, Dinsmore and Smith 2010) and burrowing owl (*Athene cunicularia;* Desmond et al. 2000).

Restoration of black-tailed prairie dogs has benefitted many species but may negatively affect disturbance-intolerant birds. The black-tailed prairie dog's propensity for pervasive vegetation clipping and burrow construction can be a detriment to species that rely on tall, dense grasses (Augustine and Derner 2015) or shrubs (Knick et al. 2005, Beck et al. 2012) for nesting and foraging. Specifically, sagebrush-associated birds may be affected if frequent prairie dog clipping and girdling kills sagebrush (Johnson-Nistler et al. 2004, Ponce-Guevera et al. 2016), which is slow to recover following disturbance (Baker et al. 2006, Porensky et al. 2018). Much of the sagebrush steppe lacks prairie dogs entirely or is inhabited by white-tailed (*Cynomys leucurus*) or Gunnison's (*Cynomys gunnisoni*) prairie dogs, which are less inclined to clip vegetation, live at far lower densities, and have smaller colony sizes than black-tailed prairie dogs (Hoogland 1995). However, the eastern portion of sagebrush distribution, where these shrubs coexist with grasses characteristic of the mixed-grass prairie (Porensky et al. 2018), overlaps with the distribution of black-tailed prairie dogs (Fig. 1). At this ecotone between the Great Plains and the sagebrush steppe, black-tailed prairie dogs engineer habitats that may benefit certain grassland species, but negatively impact sagebrush-associated birds.

Although previous research indicates that prairie dog disturbance affects sagebrush and shortgrass bird species differently (Augustine and Baker 2013), we do not yet understand at what scales these species respond, and whether there are thresholds beyond which habitat becomes unsuitable. Identification of these thresholds is of crucial import in rangelands where multiple bird guilds coexist with livestock grazing, because they imply that small changes to management or disturbance regimes in such landscapes may have large impacts on avian diversity.

We sought to address these issues by examining the influence of black-tailed prairie dog disturbance on priority bird species on the Thunder Basin National Grassland (TBNG). This mosaic grassland-sagebrush landscape is managed by the U.S. Forest Service, representing a considerable opportunity for the management and conservation of declining grassland and sagebrush birds. However, because National Grasslands are managed as multiple-use landscapes, understanding the role of fine-scale changes in disturbance amount and configuration is important for sustaining all uses, including livestock grazing and habitat for wildlife. The TBNG encompasses one of the largest contiguous tracts of public land managed for both wildlife conservation and livestock production in central North America, and the size and distribution of black-tailed prairie dog colonies has been monitored for the past two decades (Cully et al. 2010), creating a unique opportunity to examine how such variation influences the abundance of rangeland bird species.

We explored the relationship between disturbance and rangeland birds with three objectives in mind. First, we asked how both vegetation structure and composition changed as a function of spatial and temporal variation in the history of prairie dog disturbance, in particular evaluating whether these changes varied with distance to disturbed patch edge or were more marked in areas of long-term disturbance **(Q1)**. Second, we examined the direct response of

rangeland birds to prairie dog disturbance **(Q2)**. Specifically, we were interested in the responses of shortgrass ('disturbance-dependent') species versus responses of species relying on less disturbed habitat (midgrass and sagebrush birds). Finally, we wanted to understand how these same species responded to both the composition and configuration of prairie dog disturbance at multiple spatial scales **(Q3)**. We predicted that vegetation structure would differ substantially between disturbed and undisturbed patches, and as a result that bird communities would differ on and off colonies; however, it was unclear how each species would respond to non-binary features of disturbance, like distance to colony edge, or percent colony cover at various spatial scales.

METHODS

Study area

Our study was conducted on public lands within the U.S. Forest Service (USFS)–Thunder Basin National Grassland in Converse, Weston, and Campbell counties, Wyoming, USA (Fig 1). Mean annual precipitation ranges from 25-35 cm (Porensky et al. 2018) mainly falling as rain in the spring and summer. During our study (2015–2017) annual precipitation was 34 cm, 20 cm and 32 cm respectively (NOAA 2018). Summer high temperatures average around 27 degrees Celsius (80 degrees Fahrenheit), but can exceed 38 degrees.

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 lower densities in this region than elsewhere in the sagebrush steppe (Chambers et al. 2016), but reached >30% canopy cover in some areas (Porensky et al 2018). Other common species

included greasewood (*Sarcobatus vermiculatus*), broom snakeweed (*Gutierrezia sarothrae*), plains pricklypear (*Opuntia polyacantha*), and other sagebrush species (*Artemisia* spp.).

The entirety of our study area in the southern portion of the Thunder Basin represents over 1,000 km^2 (100,000 ha) of sagebrush, grassland, and prairie dog colonies, as well as some badlands and riparian areas. Black-tailed prairie dog colonies expanded over the duration of the study, with mean colony size increasing from 2015 through 2017 as colonies expanded (2015 = 0.7 km^2, 2016 = 0.88 km^2, 2017 = 2.68 km^2). In 2017, the total extent of prairie dog colonies on public lands within our study area was >160 km^2, which at the time represented the largest known colony complex in the world. Individual colonies within the complex were up to 40 km^2 in size, which is an order of magnitude larger than the size of prairie dog colonies typically found on National Grasslands in the western Great Plains over the past two decades (see Cully et al. 2010; Johnson et al. 2011). This wide range in prairie dog colony size over space and time within our study area provided a unique opportunity to examine how colony distribution and size influenced the grassland bird community.

Study Design

To assess bird responses to prairie dog disturbance in this landscape, we used a point-transect-based sampling design (Fig. 1). Because TBNG is a patchwork of cover types, and our objective was to sample a wide range of locations that varied in terms of colony size and distance from the location to colony edges, we established transects using 3 different criteria. First, colony core transects (n = 10, 8 points per transect) were randomly placed with the constraint that transects fell entirely within prairie dog colonies. Second, colony edge transects (n = 41, 5–8 points per transect depending on colony size) were randomly located with the requirement that transects crossed the edge of a prairie dog colony with four points located outside the colony and one to

four within the colony, depending on colony size. Third, sagebrush transects (*n* = 10, 8 points per transect) were located non-randomly in 10 known areas of extensive sagebrush habitat, which were identified during past surveys of greater sage-grouse (*Centrocercus urophasianus*), to ensure our surveys included portions of the landscape supporting spatially extensive stands of sagebrush. All transects contained 5–8 points spaced 250 m apart, for a total of 61 transects containing 439 survey points. We conducted two rounds of avian surveys between mid-May and late June each year from 2015–2017, surveying between sunrise and 10:00 AM on days with low wind and no rain (Pavlacky et al. 2017). By traveling to many points via off-road vehicle we ensured more effective detection of mountain plovers, which display more cryptic behavior in response to observers on-foot (Dinsmore 2003). To adjust for detectability, we modeled avian abundance using Program DISTANCE (version 6.0) for seven focal species. We categorized species as either generalists or specialists within shortgrass, mid-grass, or sagebrush systems (Fig. 2), and compared models including time of survey, wind, temperature, observer, travel method (ATV vs. on foot), and visual obstruction. The latter was incorporated to specifically address potential detectability differences between sites, as prairie dog colonies typically have lower visual obstruction (Duchardt et al. 2018).

Vegetation and landscape composition

We collected vegetation data at each survey point following point counts. We recorded line-point intercept data every meter along 30-m transects radiating from each point, perpendicular to the axis of the point count transect (Herrick et al. 2009). These data consisted of basal and canopy hits for perennial grasses, annual grasses, cacti, forbs, and shrubs. Ground cover categories included bare ground, litter, biological soil crust (BSC), and lichen, in addition to basal cover of

vegetation classes. We measured visual obstruction, a metric incorporating both vegetation height and density, using a Robel pole (Robel et al. 1970) placed at 5-m increments along transects. 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 likely varies minimally over 1–2 years, we used these data to calculate percent cover of sagebrush and cactus at each point and used this value for all years.

Prairie dog colony boundaries in the Thunder Basin have been either partially or fully mapped by the USFS and partners since 2001 (Cully et al. 2010), mapping the perimeter of each colony using a GPS unit to walk between exterior active burrows (Sidle et al. 2012). .Because most colony growth occurs in summer and early fall (Garrett and Franklin 1988, Milne-Laux and Sweitzer 2006), and birds select breeding habitat in the spring, we used mapped boundaries from the previous year to represent colony habitat in a given year (i.e., bird data collected in spring 2016 were paired with colony boundaries from fall 2015). Using these data, we generated multiple metrics of colony disturbance including distance to colony edge (positive inside, negative outside) as well as a binary measure of disturbance presence/absence. Prairie dog disturbance, especially that engendered by black-tailed prairie dogs, differs from many other sources of biotic or abiotic disturbance in that it is continuous and additive—areas that have been colonized for ten years generally differ in terms of vegetation structure and composition from those only colonized for two (Garrett and Franklin 1988, Johnson-Nistler et al. 2004). Colonies have been expanding in Thunder Basin since 2006 (Cully et al. 2010), so those areas colonized for multiple years have experienced a longer period of grazing and burrowing pressure from prairie dogs than more recently colonized areas. As such, we also calculated the distance to edge

for each point count location in each year, and a binary metric representing whether the location was colonized prior to or after 2013 ("long-term" colony cover).

Because we were also interested in how disturbance may affect birds at scales beyond an individual colony, we examined whether abundance was related to the proportion of the landscape occupied by prairie dogs surrounding any given point (hereafter referred to as landscape occupancy) or the density of prairie dog colony edges within the vicinity of any given point (hereafter edge density) at four spatial scales (100 m, 225 m, 500 m, 1000 m). The 100 m and 225 m scales contain the average territory size of the smallest (grasshopper sparrow [*Ammodramus savannarum*; Vickery 1996] and largest (mountain plover [Knopf and Wunder 2006]) focal species, while the larger scales may capture sensitivity to patch size during spring settlement (e.g., Hutto 1985).

Data Analyses

To evaluate what vegetation characteristics best differentiate between prairie dog colonies and undisturbed habitat at a grassland-sagebrush ecotone (Q1), we used a logistic model to explain colony presence-absence as a function of a suite of characteristics of both vegetation structure (i.e., visual obstruction and bare ground) and composition (e.g., sagebrush cover). We modeled this same response for long-term colony cover and used a general linear model to examine distance to core colony.

To examine whether and how colony-associated birds responded to cover of their preferred habitat, and conversely how species preferring more dense vegetation (mid-grass and sagebrush birds) responded to prairie dog disturbance (Q2), we used a Generalized Additive Mixed Model framework in the gamm4 package in R (Wood and Scheipl 2017). Generalized additive models (GAMs) extend off generalized models using a non-parametric smoothing term

to fit the data (Hastie and Tibshirani 1986) and are well-suited to detecting threshold responses (e.g., Large et al. 2013), and a mixed-model framework (GAMM) can be used to incorporate random effects (Wood 2011). Furthermore, they are well-suited to examining ecological patterns, which are rarely linear in nature (e.g., Bestelmeyer et al. 2011).

We tested three main hypotheses concerning the abundance of rangeland bird species: that prairie dog disturbance would have no effect (**Q2H$_0$**), that current or long-term colony cover would explain variation in abundance but distance to edge (either inside or outside) would not (**Q2H$_{1C}$, Q2H$_{1LT}$,**), and finally that distance to either current or long-term edges would influence abundance (**Q2H$_{2LT}$, Q2H$_{2C}$**). We also compared both linear and non-linear models testing H2. We used an AIC model framework (Burnham and Anderson 2002) to evaluate the strength of these 7 models for each of our focal species, ranking models based on model weight. All models included a fixed effect of year and topographic roughness, as the latter has been shown to be important for habitat use for many of these species (Duchardt et al. 2018). We also incorporated a random effect of transect to address spatial autocorrelation (Legendre and Legendre 1998). We examined semivariograms and calculated Moran's I (Moran 1950) for model residuals to ascertain that this variable did significantly reduce autocorrelation in the dataset. For species with <2 observations in a given strata (i.e., inside or outside colony), we excluded data from that strata in our models.

We used an approach similar to that described above to compare hypotheses concerning avian response to landscape occupancy of prairie dogs and colony edge density at four spatial scales. Our hypotheses were that colony cover at broader spatial scales would have no effect beyond the presence or absence of disturbance, or distance to edge (**Q3H$_0$**), that the total area (composition) of colony cover would influence abundance beyond the presence or absence of

current (**Q3H$_{1c}$**) or long-term (**Q3H$_{1LT}$**) disturbance, and that current (**Q3H$_{2c}$**) or long-term (**Q3H$_{2LT}$**) edge density (configuration) would affect abundance. All models included a random effect of transect identity (see above) and a fixed effect of year and topographic roughness. We compared these models for each focal species using AICc (Burnham and Anderson 2002). We did not combine models representing Q2 and Q3, because correlation (*r*) between distance to edge and total colony cover in the landscape was high (0.6–0.73), which was unsurprising given larger colonies will have greater interior distance.

RESULTS

Q1. Colony vegetation composition and structure

Prairie dog colonies differed substantially from undisturbed habitat, and were characterized by lower visual obstruction, less sagebrush and grass cover, and more forb cover (Table 1, Appendix 1). Compared with undisturbed habitat, colonies also had substantially more bare ground and cactus cover. Areas of long-term prairie dog disturbance did not differ markedly from more recently colonized area in terms of bare ground but did have much lower visual obstruction and sagebrush cover. For survey points located on colonies, distance to the colony edge was not associated with variation in vegetation structure. Sagebrush and grass cover declined while forb cover increased within increasing distance from colony edge (i.e., as one moves toward the center of large colonies; Table 1).

Q2. & Q3. Avian abundance

Best-fitting models of detectability varied by species, with the basic hazard rate model describing detectability of sage thrashers and horned larks, while lark buntings were best described by the uniform function. Mountain plover detectability was explained by use of ATV on surveys and

wind. Western meadowlark detectability varied with observer, while grasshopper sparrows varied by observer and start time. Finally, Brewer's sparrow detectability varied with visual obstruction. The best model for each species had good fit based on a chi-squared test (P>0.1).

Horned larks, Brewer's sparrows, and western meadowlarks (*Sturnella neglecta*) were the three most common species based on distance-adjusted densities across habitats (Fig. 3). Horned larks were the most abundant species on colonies ($\bar{x}$ = 54 km^{-2}, 95% CI = 51.2–57.2) and Brewer's sparrows the most abundant in undisturbed habitat ($\bar{x}$ = 69 km^{-2}, 95% CI = 62.5–76.4). Distance-adjusted densities differed markedly between disturbed and undisturbed habitat for all species (Fig. 3). Mountain plovers occurred almost exclusively on colonies (3.4 km^{-2} on colonies [95% CI = 2.8 - 4.1], with only one observation off-colony). All other species were less abundant on versus off prairie dog colonies (Fig. 3), although western meadowlarks still reached moderate abundances on colonies (17 km^{-2}, 95% CI = 16.1–18.1).

Abundances of all seven species were well-explained by models representing prairie dog disturbance, especially distance to colony edge, and there was little uncertainty in selection of the most parsimonious model for each species (Table 2; Fig. 4). Sage thrashers (*Oreoscoptes montanus*) and Brewer's sparrows responded most strongly to long-term prairie dog disturbance with lower abundances on colonies (**Q2H$_{1LT}$**), whereas grasshopper sparrows showed lower abundance on current colonies (**Q2H$_{1C}$**). More generalist species showed a non-linear response to distance to colony edge, with lark buntings (*Calamospiza melanocorys*) declining with distance to current edge (**Q2H$_{2C}$**, Fig. 4), and western meadowlarks declining with increasing distance (from negative outside to positive inside) to historic edge (**Q2H$_{2LT}$).**

Models for shortgrass-associated bird species also showed strong support for a non-linear relationship with distance to colony edge **(Q2H$_2$**). Horned larks were more sensitive to historic

edges, and although they were abundant throughout the study area were 4.6 times more abundant within colonies. Plovers were so rare off colonies (only 1 detection in 3 years of surveys) that their abundance could only be modelled as a function of distance to edge within colonies; we found that plover density at first increased with distance to edge, reaching maximum density at approximately 500 m, and declining sharply beyond 800 m (Fig 4). Densities were generally high at distances of ~350–650m from an edge. This relationship predicts that for an approximately circular colony, mountain plover density was maximized on colonies ~ 1.1 km^2 (110 ha) in size and declined in abundance in the center of colonies >1.5 km^2.

Total long-term cover of prairie dog colonies (landscape occupancy) also affected abundance of five bird species, although no landscape occupancy models improved upon models from Question 2 for lark buntings or sage thrasher (Table 3). There was evidence of a linear positive effect of overall long-term colony cover for plovers at the 100 m and 225 m scale, correlating with territory size in this species (**$Q3H_{1LT}$**), and non-linear increases in horned larks at the 225 m scale. Grasshopper sparrows declined non-linearly with increasing long-term colony cover at the 500 m scale, while meadowlarks and Brewer's sparrows declined linearly, best described at 225 and 100 m scales, respectively. We did not find support for an effect of colony edge density on any species at any scale (**$Q3H_2$**).

DISCUSSION

Avian responses to prairie dog disturbance

We found that the presence versus absence of disturbance by prairie dogs was not enough to explain abundances of focal species in this system. Rather, landscape context of disturbance and disturbance duration influenced both sagebrush and grassland birds, albeit in different ways. For many of these species, this is the first example of landscape-scale response to prairie dog

disturbance. For others, it provides evidence of new spatial patterns of abundance that prior research had not identified. Most notably, studies throughout the western Great Plains have shown that mountain plovers increase in abundance on black-tailed prairie dog colonies (Dinsmore et al. 2005, Goguen 2012, Augustine and Baker 2013), and are more abundant on colonies >0.8km^2 in size, compared to colonies <0.8 km^2 (Goguen 2012, Augustine and Skagen 2014). This suggests that "bigger is always better" regarding the relationship between mountain plovers and prairie dog colonies. However, to our knowledge our study is the first to document a decline in mountain plover density towards the center of extremely large colonies, or a "goldilocks response" to distance to colony edge (Fig. 4). We note that "large" colonies in the previously mentioned studies varied from ~ 0.8–4.8 km^2 (80–480 ha) in size. *Average* colony size throughout our study in Thunder Basin fell within this range (see Methods), whereas "large" colonies were 10 times larger. Indeed, plover density in Thunder Basin was maximal in the range of 350–650 m from a colony edge, was similar near colony edges and areas ~800 m from edges and declined below this level over distances of 800 – 1200 m from edges.

How this result translates into a relationship between plover density and colony size will depend heavily on colony geometry, but as a first approximation a circular colony with radius of 650 m (i.e., within the range of maximum plover abundance) would be 1.32 km^2 in size, which corresponds to the mean size of large colonies supporting high plover densities in other localities (Dinsmore et al. 2005, Augustine et al. 2008, Goguen 2012, Augustine and Skagen 2014). In reality, colonies show high complexity in shape due to variation in vegetation and topography, so colonies with >650 m to nearest colony edge will generally be much larger. For example, in 2015 the colony with highest mountain plover density was 3.2 km^2 in size, but no point in the colony was greater than 650 m from an edge due to irregular colony shape. Thus, only when

colonies begin exceeding many hundreds of hectares will they contain substantial area that exceeds 800 m from a colony edge.

The unique nature of our study area allowed us to detect a threshold beyond which very large colonies supported reduced mountain plover density. Our data do not allow us to directly test drivers of this response, but we here consider three potential mechanisms. Vegetation structure at colony cores was distinct from edges (Table 1), and plovers may avoid areas that are too sparse, especially if insect biomass is lower in these areas (Schneider et al. 2006). We did not detect avoidance above certain levels of bare ground, nor have other researchers (e.g., Knopf and Miller 1994, Goguen et al. 2012), but s measures of insect biomass on colonies may shed light on this idea in the future. Distance to colony edge may be a driver if edges provide resources that colony cores do not (Ries et al. 2004). It is unlikely that >800 m is an infeasible distance for adults to travel for foraging opportunities given evidence plovers can move more than 1 kilometer to preferred foraging sites (Woolley 2016). More likely, edges represent better cover for brood-rearing (Schneider et al. 2006), and potential thermoregulatory benefits for both chicks and adults (Graul 1975, Shackford 1996), but increased distance to these resources increases risk associated with reaching them, especially for unfledged chicks. Such benefits have been tied directly with shrubs (Schneider et al. 2006), which were much more abundant outside of colonies ($\bar{x}$ =1.3–7.3% cover). We also found that plover density declined near colony edges relative to areas 100 – 650 m from an edge, which could potentially be related to increased predation risk close to edges.

The lack of shrub cover within colonies also explains sagebrush bird avoidance of areas of long-term prairie dog disturbance. Long-term disturbance leads to prolonged clipping and girdling of sagebrush by prairie dogs, explaining extremely low sagebrush cover on these sites ($\bar{x}$

= 0.6%) and resulting avoidance by sagebrush specialists like the Brewer's sparrow and sage thrasher. It's important to note that neither species responded to distance to colony edge, and only Brewer's sparrows decreased with increasing long-term cover at a 100 m scale. These results indicate that sagebrush specialists overall show low sensitivity to the spatial arrangement of colonies in the landscape, responding mainly to local availability of sagebrush.

We also note that densities of Brewer's sparrows and sage thrashers were lower in the TBNG (including undisturbed habitat) than many other areas throughout their range (Rotenberry et al. 1999, Reynolds et al. 1999, Aldridge et al. 2011). It would be challenging to untangle the ubiquitous presence of disturbance in this landscape from the fact that it represents range-edge for both species (Rotenberry et al. 1999, Reynolds et al. 1999). Species abundances are generally lower near range boundaries (Andrewartha and Birch 1954, Kirkpatrick and Barton 1997), and the fact that this is indeed a range edge for sagebrush birds is underscored by the absence of sagebrush sparrows (*Artemisiospiza nevadensis*) on these sites, a species that is found along with sage thrashers and Brewer's sparrow throughout many portions of the sagebrush steppe (Martin and Carlson 1998).

Generalists like western meadowlarks and lark buntings were sensitive to distance to colony edge (Fig 4). Because colonies grow and expand into undisturbed habitat, more central, "core" areas tend to be older, and locations radiating from the core represent a chronosequence of decreasing age (Johnson-Nistler et al 2004). The vegetational distinctiveness of these older areas helps explain the non-linear edge responses in many of Thunder Basin's birds. Although both will nest near shrubs or taller grasses, lark buntings and western meadowlarks are primarily ground nesters and foragers. As such, they are less sensitive to the absence of shrubs within

colonies and are tolerant of the low-intensity disturbance present at colony edges as long as some grass and litter cover is still present (Davis and Lanyon 2008, Augustine and Derner 2015).

While shortgrass birds increased with increasing long-term colony cover, midgrass and sagebrush birds mainly responded to long-term colony cover at more local scales, highlighting the importance of disturbance duration in this system. Conversely, few species responded to total colony cover at broader scales or to current colony cover, and none appeared sensitive to edge density. At broader scales, it appears that most avian species respond primarily to the extremely sparse cover of patches that have experienced multiple years of disturbance, and are less sensitive to short-term fluctuations in prairie dog disturbance.

Implications for prairie dog management

While few black-tailed prairie dog colony complexes reach the size of those observed in Thunder Basin (but see Ceballo et al. 2010), prairie dog conservation to this point has generally taken a "bigger is better" approach. Efforts to reintroduce endangered black-footed ferrets target complexes >2000 ha (20 km^2) in size (Roelle et al. 2005), with the underlying assumption that suitability for ferrets, and other colony associates, increases directly with size (Houston et al. 1986). Our results suggest that this may not be the case for the mountain plover, a species of conservation concern throughout its limited range (Birdlife International 2017). Further, our data show that sagebrush-associated birds are present but rare on prairie dog colonies – although these species may tolerate some large colonies within this landscape, their populations cannot be sustained without undisturbed sagebrush. The greater sage-grouse, another species of concern in this landscape, may also be negatively impacted if colonies become too large. Though sage-grouse have been observed using small colonies for lekking sites (D. Pellatz, personal communication), they rely on large patches of sagebrush for nesting, brood-rearing, and

overwintering (Connelly et al. 2011, Knick and Hanser 2011), and this habitat declines with long-term prairie dog disturbance. Given the past and ongoing conversion of rangelands to croplands in the Great Plains (Wright and Wimberley 2013), conservation of these multiple bird guilds on a declining land base highlights the need to carefully consider the size and spatial dispersion of prairie dog disturbance on the landscape.

Beyond the responses of individual species to large colonies, colony size may be related to transmission of sylvatic plague, and thus the sustainability of prairie dog colonies in this landscape (Collinge et al. 2005, Johnson et al. 2011). Plague was introduced to North America over 100 years ago (Antolin et al. 2002) and is now among the major drivers of prairie dog declines. Plague vaccines (Abbott et al. 2012) and dusting to kill fleas that carry plague (Seery et al. 2003) have had some success in controlling these outbreaks, but there is evidence that the probability and intensity of outbreaks is greater as colony size increases (Collinge et al. 2005). It is important to note that "large" colonies in Collinge et al.'s study were 0.4–0.5 km^2 in size, or two orders of magnitude smaller than large colonies in the Thunder Basin, and thus these effects may be magnified in the Thunder Basin landscape. While plague can be contracted by black-footed ferrets (Williams 1994), it does not directly affect colony-associated avifauna (Antolin et al. 2002). However, large epizootics can decimate local prairie dog populations, and birds relying on engineered habitat structure (Augustine et al. 2008, Dinsmore and Smith 2010) or prairie dogs as a food resource (Seery and Matiatos 2000), often decline or disappear as a result. Thus, in the long-term, an important management consideration is how to maintain colonies in a spatial pattern that mitigates the "boom-and-bust" cycle of colony growth and plague, which has been documented in Thunder Basin and other landscapes over the past several decades (Cully et al. 2010).

A final key consideration for managing colony size and distribution in this landscape is the potential impact on livestock production and the local ranching community (Derner et al. 2006). Other studies have shown that stakeholders that coexist with prairie dogs generally consider them as pests (Lybecker et al. 2002), and ranchers especially see them as a threat to cattle production (Reading and Kellert 1993, Miller et al. 2007). While most stakeholders acknowledge a need for some prairie dogs for maintenance of wildlife populations, there can be disagreement concerning management, and concern for a loss of control over livestock management (Reading and Kellert 1993). In the Thunder Basin, rapid colony growth over a three-year period led to significant concerns within the ranching community (Ruckelshaus Institute 2017), and an undermining of trust between public and private stakeholders. Our findings regarding the threshold responses of both sagebrush-associated birds and mountain plovers to the spatial pattern of prairie dog disturbances suggest that management to minimize the presence of colonies containing areas >800 m from colony edges is consistent with goals to conserve multiple avian guilds while also reducing conflict with livestock producers and reducing the potential for plague transmission across the landscape.

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Tables and Figures

Table 1. Parameter estimates (with standard errors) of covariates describing black-tailed prairie dog colony presence/absence, or distance to colony edge within the TBNG, eastern Wyoming, USA, 2015–2017 (Q1). Distance to edge models only included points that fell within a colony. Negative values indicate parameters were lower either inside a colony or moving towards colony core. Bolded parameter estimates indicate significance at alpha = 0.05.

		Vegetation Structure		Vegetation Composition (percent foliar cover)						
Colony Metric	**R - squared**	**Bare Ground (%)**	**Visual obstruction (cm)**	**C3 grass**	**C4 grass**	**Brome**	**Annual grass**	**Forbs**	**Sagebrush**	**Cactus**
In/out	0.40	**-1.69 (0.37)** **	**-0.08 (0.03)** **	**-2.09 (0.46)** **	**-4.85 (0.44)** **	-1.17 (0.79)	**-3.16 (0.86)** **	**6.15 (0.77)** **	**-15.71 (1.72)** **	**11.19 (2.07)** **
Long-term in/out	0.45	-0.21 (0.38)	**-0.22 (0.05)** **	0 (0.49)	**-2.93 (0.47)** **	-1.98 (1.03)	**-1.92 (0.94)** **	**6.12 (0.71)** **	**-30.35 (3.48)** **	**3.4 (1.45)** *
Dist edge	0.24	0.03 (0.03)	-0.003 (0.002)	**-0.1 (0.04)** **	**-0.26 (0.03)** **	-0.08 (0.06)	**-0.23 (0.07)** **	0.33 (0.06)	**-0.58 (0.11)** **	**0.61 (0.11)** **
Long-term dist edge	0.18	0.02 (0.02)	-0.003 (0.002)	-0.01 (0.03)	**-0.1 (0.03)** **	-0.08 (0.05)	**-0.12 (0.05)** *	**0.24 (0.05)** **	**-0.46 (0.08)** **	**0.21 (0.08)** *

Asterisks represent significance at alpha=0.05 (*) and alpha=0.01 (**), respectively.

Table 2. Top models explaining avian abundance as a function of different aspects of prairie dog disturbance within the TBNG, eastern Wyoming, USA, 2015–2017. Only top models explaining >98% of total model weights are shown (bold), along with a base model. "LT" represents areas of long-term prairie dog disturbance. See Fig. 2 for avian 4-letter alpha codes.

Species		Q2 Hypothesis	Model	AICc	ΔAICc	K	Weight
Shortgrass	MOPL	**H_{2C}- Nonlinear**	**Year + Roughness + Dist edge**	1407.4	**0**	**7**	**1.00**
		H_0	*Year + Roughness*	*1458*	*50.6*	*5*	*0.00*
	HOLA	**H_{2LT}- Nonlinear**	**Year + Roughness + Dist edge $_{LT}$**	**9283**	**0**	**7**	**1.00**
		H_0	*Year + Roughness*	10827.8	1544.7	*5*	*0.00*
Midgrass	WEME	**H_{2LT}- Nonlinear**	**Year + Roughness + Dist edge $_{LT}$**	**6993.4**	**0**	**7**	**1.00**
		H_0	*Year + Roughness*	7300.7	307.3	5	0.00
	GRSP	**H_{1C}**	**Year + Roughness + In/out**	1163.9	0	6	0.78
		H_{1LT}	**Year + Roughness + In/out$_{LT}$**	1166.7	2.8	6	0.20
		H_0	*Year + Roughness*	1298.5	134.6	5	0.00
Sagebrush	LARB	**H_{2C}- Nonlinear**	**Year+ Roughness + Dist edge**	**5547.6**	**0**	**7**	**1.00**
		H_0	*Year + Roughness*	6156.3	608.7	*5*	*0.00*
	BRSP	**H_{1LT}**	**Year + Roughness + In/out$_{LT}$**	10583.3	0	6	**1.00**
		H_0	*Year + Roughness*	12087.3	1504	5	*0.00*
	SATH	**H_{1LT}**	**Year + Roughness + In/out$_{LT}$**	1686	0	6	**1.00**
		H_0	*Year + Roughness*	1719.5	33.5	5	*0.00*

Table 3. Top models explaining avian abundance in response to composition and configuration of colonies in the TBNG, eastern Wyoming, USA, 2015–2017. Top models explaining >98% of total model weights are shown, along with a base model and the best model from Table 2. Bolded models indicate competitive landscape models. "LT" represents areas of long-term prairie dog disturbance. See Fig. 2 for avian 4-letter alpha codes.

Species		Q3 Hypothesis	Model	AICc	ΔAICc	K	Weight
Shortgrass	MOPL	**H_{1LT} 225m**	**Year + Roughness + PD Occupancy @ 225 m_{LT}**	**1396.9**	**0**	**6**	**0.94**
		H_{1LT} 100m - nonlinear	**Year + Roughness + PD Occupancy @100 m_{LT}**	**1402.9**	**5.9**	**7**	**0.05**
		H_0 *No addl. landscape effect*	Year + Roughness + Dist edge	1407.4	10.5	7	0.004
		Base model	*Year + Roughness*	1458	61.11257	5	0.00
	HOLA	**H_{1LT} 225m - nonlinear**	**Year + Roughness + PD Occupancy @ 225 m_{LT}**	**9250.5**	**0**	**7**	**1.00**
		H_0 *No addl. landscape effect*	Year + Roughness + Dist edge LT	9283	32.6	**7**	0.00
		Base model	Year + Roughness	10827.8	1577.3	5	0.00
Midgrass	WEME	**H_{1LT} 225m**	**Year + Roughness + PD Occupancy @ 225 m_{LT}**	**6921.9**	**0**	**6**	**1.00**
		H_0 *No addl. landscape effect*	Year + Roughness + Dist edge $_{LT}$	6993.4	71.5	7	0.00
		Base model	Year + Roughness	7300.7	378.8	5	0.00
	GRSP	**H_{1LT} 500m –nonlinear**	**Year + Roughness + PD Occupancy @ 500 m $_{LT}$**	**1110.4**	**0**	**7**	**1.00**
		H_0 *No addl. landscape effect*	Year + Roughness + In/out	1163.9	53.5	6	0.00
		Base model	Year + Roughness	1298.5	188.1	5	0.00
Sagebrush	LARB	H_0 *No addl. landscape effect*	Year + Roughness + Dist edge	5547.6	0	7	1.00
		H_1 225m, - nonlinear	Year + Roughness + PD Occupancy @ 225 m	5636.9	89.3	7	0.00
		Base model	Year + Roughness	6156.3	608.7	5	0.00
	BRSP	**H_{1LT} 100m**	**Year + Roughness + PD Occupancy @ 100 m**	**10555.2**	**0**	**6**	**1.00**
		H_0 *No addl. landscape effect*	Year + Roughness + In/out$_{LT}$	10583.3	28.1	6	0.00
		Base model	Year + Roughness	12087.3	1532.1	5	0.00
	SATH	H_0 *No addl. landscape effect*	Year + Roughness + In/out$_{LT}$	1686	0	7	0.99
		H_{1LT} 225m non-linear	Year + Roughness + PD Occupancy @ 225 m_{LT}	1695.5	9.5	7	0.01
		Base model	Year + Roughness	1719.5	33.5	5	0.00

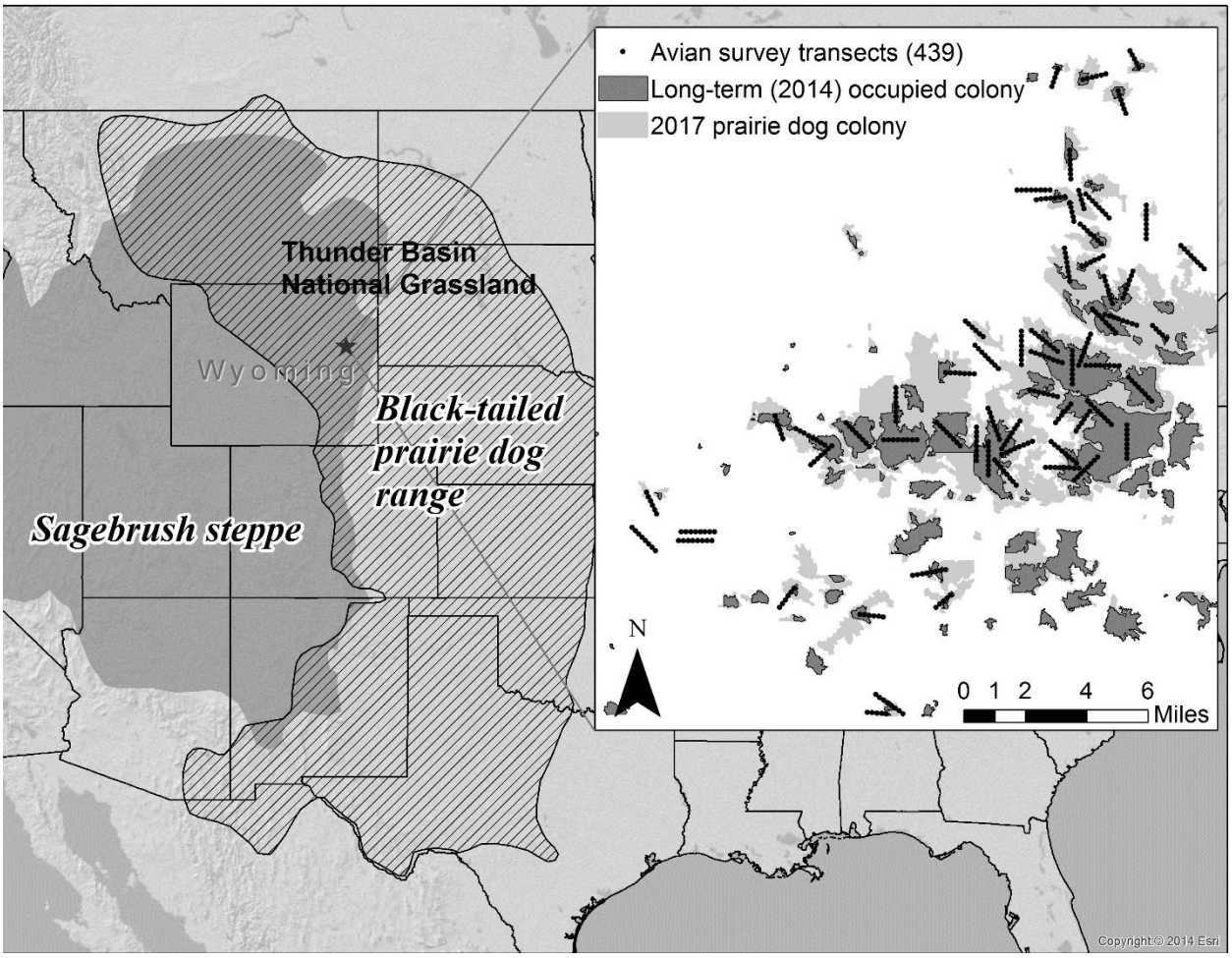

Figure 1. Location of the TBNG within eastern Wyoming, USA, where the range of the black-tailed prairie dog overlaps the sagebrush steppe. Inset: Avian point count locations (*n* = 439) within sagebrush and across long-term and new prairie dog colony habitat in the Thunder Basin, surveyed between 2015–2017.

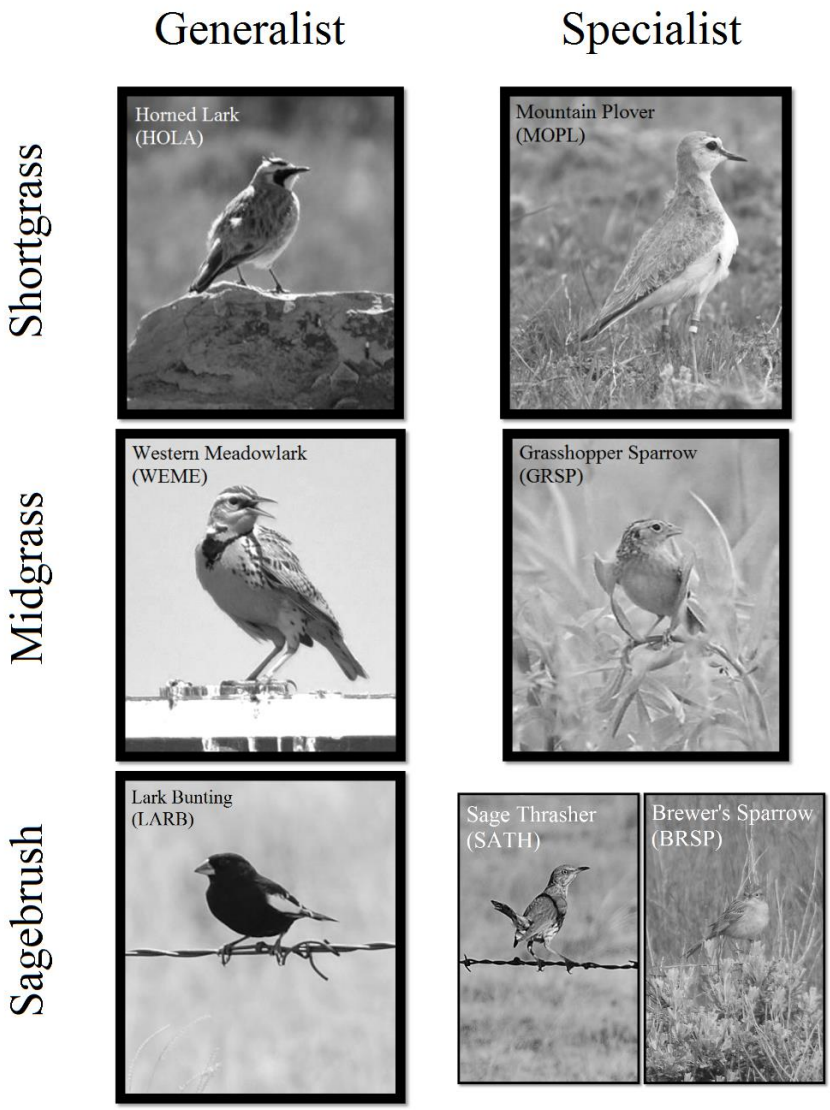

Figure 2. Species names and four-letter alpha codes for shortgrass, midgrass, and sagebrush bird species in the TBNG, eastern Wyoming, USA, 2015–2017. “Generalists” in this sense display wider niche breadth and tolerances of other habitat types (e.g., lark bunting utilized both midgrass and sagebrush), whereas specialists were found only within that habitat. Superscripts indicate Wyoming species of Conservation Need (A, WGFD 2010) and U.S. Forest Service Sensitive Species (B, U.S. Forest Service 2017)

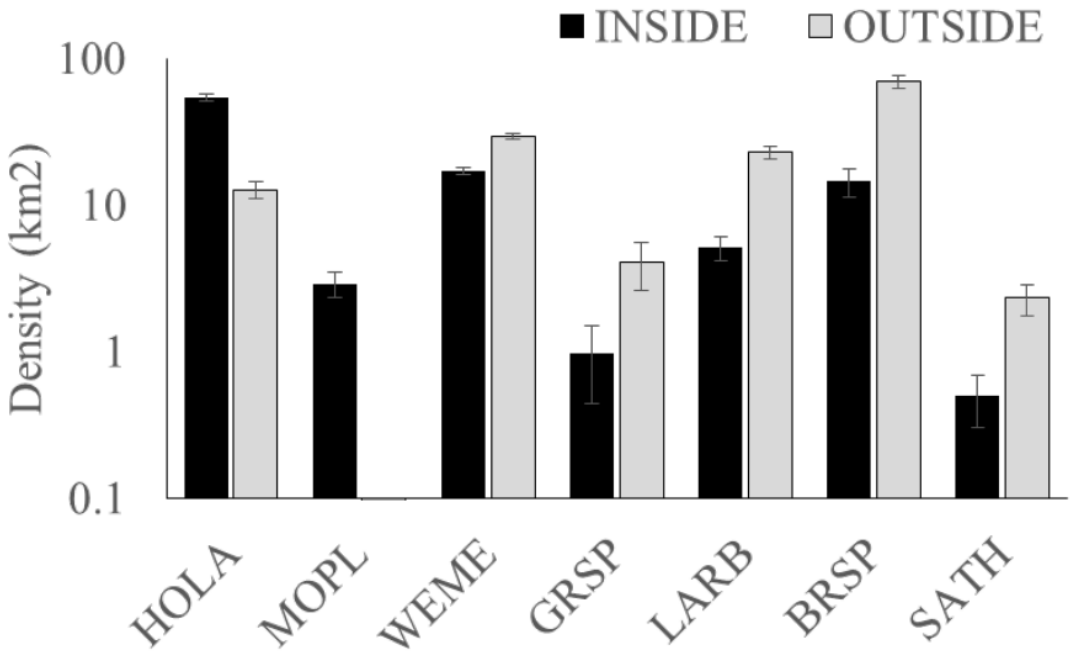

Figure 3. Avian densities (log scale) inside and outside current prairie dog colonies across three years in the TBNG, eastern Wyoming, USA, 2015–2017. Bars represent 95% confidence intervals.

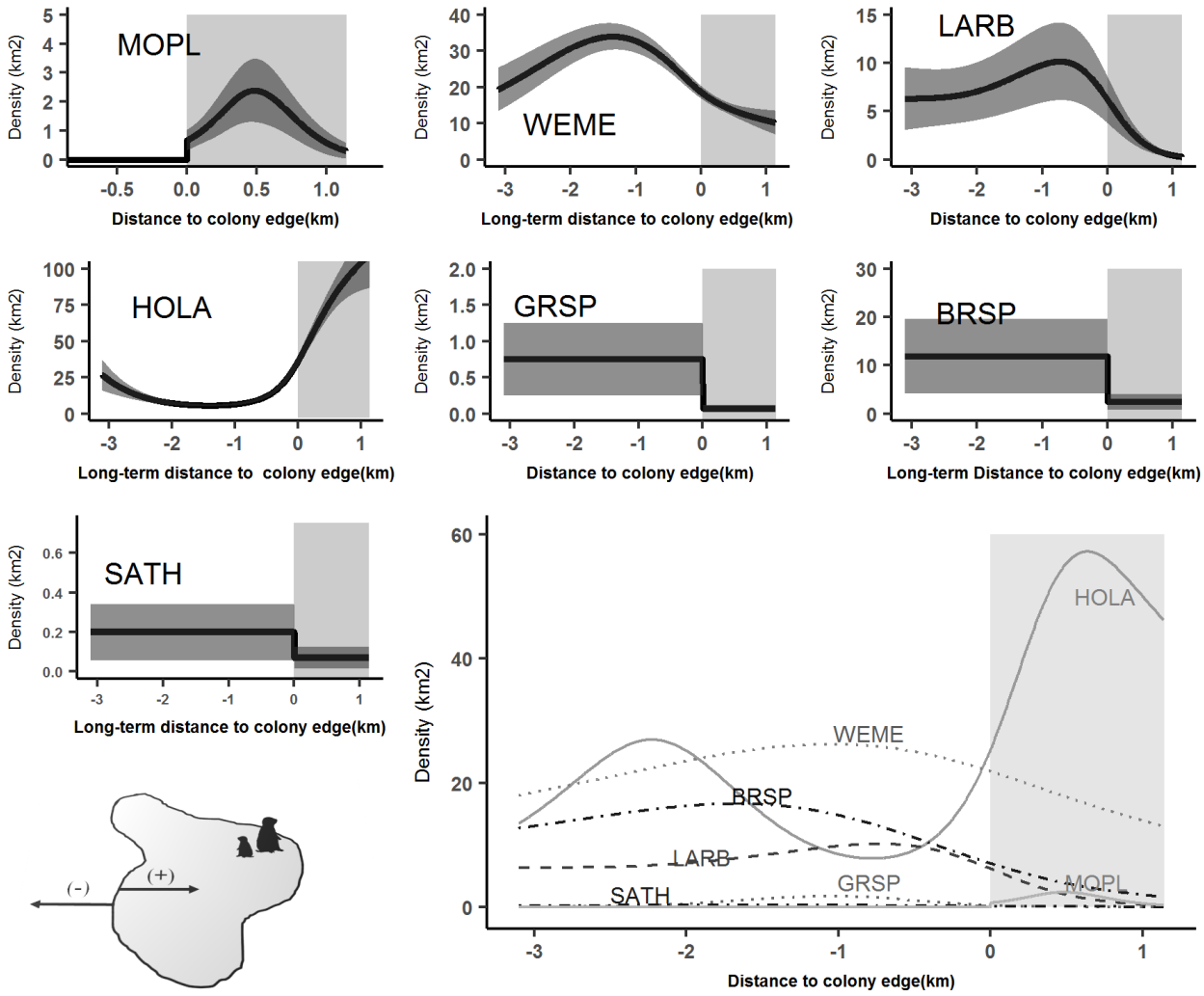

Figure 4. Top models of avian abundance (transformed to density per km^2) in response to distance to current colony edge or historic colony edge of seven species in TBNG, eastern Wyoming, USA, 2015–2017. Envelopes in single-species figures represent 95% confidence envelopes. Grey shading indicates prairie dog colony. Bottom right figure combines models of abundance in response to current edge for all seven species (even where this was the second-best model). See Table 1 for alpha codes.

Chapter 4. Drivers of mountain plover habitat selection and nest survival on large prairie dog colonies

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Abstract

Habitat loss and altered disturbance regimes have led to declines in many species of grassland and sagebrush birds, including the imperiled Mountain Plover (*Charadrius montanus*). In certain parts of their range Mountain Plovers rely almost exclusively on Black-Tailed Prairie Dog (*Cynomys ludovicianus*) colonies as nesting habitat. Previous studies have examined Mountain Plover nest and brood survival on prairie dog colonies, but little is known about how colony size and shape influence these vital rates or patterns of habitat selection. We examined how 1) adult habitat utilization, 2) nest-site selection, and 3) nest success responded to a suite of local- and site-level variables on large prairie dog colony complexes in northeastern Wyoming. Abundance of adult Mountain Plovers was highest on points within older, "medium"-sized (100–500 ha) colonies with high cover of annual forbs and bare ground (5.8 birds/km^2), but lower on extremely large (>2000 ha) colonies (2.1 birds/km^2). Nest sites were characterized by high proportions of annual forbs and bare ground and low cactus cover and vegetation height. Nest survival was higher for older nests, and nests with lower cactus cover, and decreased with increasing temperatures. Uncertainty was high for models of daily nest survival, potentially because of two competing sources of nest failure: nest depredation and nest abandonment or inviability of eggs. Drivers of these two sources of nest failure differed, with inclement weather and higher temperatures associated with nest abandonment or egg inviability. We highlight how prairie dogs alter vegetation structure and bare ground heterogeneously across the landscape, and

how this in turn influences bird abundance and nest distribution at different temporal and spatial scales. Furthermore, our work reveals how partitioning the causes of nest failure during nest survival analyses enhances understanding of survival rate covariates.

Keywords

Black-tailed prairie dog, disturbance, grassland, bird, nest survival, habitat selection, conservation, Charadrius, breeding ecology

Introduction

Among the numerous conservation challenges facing North American wildlife are precipitous declines in grassland and sagebrush bird populations (Brennan and Kuvlesky 2005, Sauer et al. 2017, Rosenberg et al. 2019). These declines are driven in large part by habitat loss via conversion to row crop agriculture (Wright and Wimberly 2013), energy extraction (Allred et al. 2015), and exurban development (Sala et al. 2017), and have led to the loss of between 70–99% of grassland habitat in many regions of the United States (Samson and Knopf 1994). On grasslands that remain, many species are negatively affected by the absence of disturbance, since many of these species evolved with natural disturbance regimes (Brawn 2001; Fuhlendorf and Engle 2001). Fire, ungulate grazing, and burrowing mammals play integral roles as ecosystem engineers in grasslands (Davidson et al. 2012, Fuhlendorf et al. 2017), but throughout North America these disturbance regimes have been severely altered, potentially leading to reduced biodiversity (Fuhlendorf et al. 2006). Conversely, where historic disturbance regimes have been restored, avian biodiversity has increased (Coppedge et al. 2008, Augustine and Derner 2015, Duchardt et al. 2016).

The Mountain Plover (*Charadrius montanus*) is a declining disturbance-associated bird currently listed as near-threatened on the IUCN Redlist (Knopf 1996, Birdlife International 2018). The species is sexually monomorphic, socially monogamous, and employs a simultaneous multiple-clutch system, (e.g., Beck et al. 2005), where females lay two separate three-egg clutches, the first nest typically tended by the male and the second by the female (Knopf and Wunder 2006). The species breeds mainly within the Intermountain West and western Great Plains, overwintering in the southern U.S. and Mexico with localized breeding areas within the winter range. Mountain Plovers are patchily distributed throughout their

relatively small breeding range (Figure 1), and typically breed on relatively flat landscapes (Graul 1975) with extensive bare ground exposure (often >30%; Knopf and Miller 1994), as well as short (Graul 1975, Olson and Edge 1985, Augustine and Derner 2012) and sparse (Knopf and Wunder 2006) vegetation. Individual studies have also noted potential associations with shrubs (Schneider et al. 2006) or forb cover (Olson and Edge 1985).

These conditions can occur on high-elevation sites (e.g., South Park, Colorado; Wunder et al. 2003) or in desert shrublands (Wyoming, Plumb et al. 2005); however, in grasslands throughout the western Great Plains of North America, Mountain Plovers often breed in highly disturbed areas including cropfields (Shackford et al. 1994, Wooley 2016), recently burned sites (Augustine and Derner 2012), and heavily grazed areas (Plumb et al. 2005, Uresk 2017). Throughout much of their range, Mountain Plovers are especially dependent on Black-Tailed Prairie Dogs (*Cynomys ludovicianus*) to engineer suitable habitat through soil disturbance and vegetation clipping (Dinsmore et al. 2005, Augustine and Derner 2012, Duchardt et al. 2018). Although all species of prairie dog consume vegetation and cause some level of soil disturbance by burrowing, Black-tailed Prairie Dogs actively clip vegetation to maintain visibility for predators and live at extremely high densities. These activities lead to substantial soil and vegetation disturbance (Hoogland 1995); this combination of traits make Black-tailed Prairie Dog colonies ideal habitat for Mountain Plovers.

The association of Mountain Plovers with prairie dog colonies across much of their range (Figure 1) may be another factor contributing to declines in Mountain Plover populations. Widely recognized as both an ecosystem engineer and keystone species (Kotliar et al. 1999, Van Nimwegen et al. 2008), Black-Tailed Prairie Dogs can also compete with cattle for forage (Derner et al. 2006; Augustine and Springer 2013) and as such are often subject to lethal control

via poisoning and shooting on lands managed for livestock (Miller et al. 2007). In addition to lethal control, outbreaks of Sylvatic Plague (*Yersina pestis*) regularly lead to drastic local population reductions (>95% mortality in Black-Tailed Prairie Dogs; Cully and Williams 2001). These factors have severely reduced Black-Tailed Prairie Dog populations (occupying <3% of their historic range; Mulhern and Knowles 1997), pushing colony associates like the Black-Footed Ferret (*Mustela nigripes*) to the brink of extinction (Dobson and Lyles 2000). Given the observed impacts on other colony-associates, Mountain Plover populations that rely on prairie dogs for breeding habitat may be especially vulnerable.

Many aspects of Mountain Plover breeding biology on prairie dog colonies have been studied (Dinsmore et al. 2005, Dreitz and Knopf 2007, Augustine et al. 2008, Goguen 2012, Augustine and Skagen 2014), but these studies have occurred in landscapes with a limited range of colony sizes (5–480 ha), and with smaller total area of colony complexes (a "complex" is a cluster of colonies within the same landscape; Hoogland 2006). Within certain landscapes, plovers occupy colonies >4000 ha in size in colony complexes exceeding 15,000 ha (Duchardt et al. 2019), but little is known about Mountain Plover breeding ecology on large colonies. To address this gap in knowledge, we studied Mountain Plover habitat selection and nest survival in the Thunder Basin National Grassland of northeastern Wyoming, USA (Figure 1), where we focused on four questions: 1) How does variation in prairie dog colony size and within-colony variation in vegetation structure influence adult abundance (density) during the nesting season? 2) How does fine-scale variation in habitat structure influence Mountain Plover nest placement? 3) What are the effects of habitat structure, weather, and predation on Mountain Plover nest survival? and 4) Can we separate drivers of different sources of nest loss for Mountain Plovers?

METHODS:

Study area

We conducted our field sampling from 2015–2017 on and around prairie dog colonies on public lands within the Thunder Basin National Grassland, located in Campbell, Converse, and Weston counties, Wyoming (Figure 1). The study area was composed of rangeland with low to moderate stocking rates (0.1–0.4 Animal Unit Months [AUM]/ha; Connell et al. 2019) of both domestic sheep and cattle. Elevation within our study area ranged between 1200–1500 m. Mean annual precipitation averaged 25–35 cm per year, with most precipitation occurring in spring and summer. Shrublands in this system were dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), greasewood (*Sarcobatus vermiculatus*), broom snakeweed (*Gutierrezia sarothrae*), and other sagebrush species including silver sagebrush (*A. cana*). Common perennial grass species included blue grama (*Bouteloua gracilis*), threadleaf sedge (*Carex filifolia*), needle-and-thread (*Hesperostipa comata*), and cheatgrass (*Bromus tectorum*), an invasive annual. Prairie dog colonies were characterized by a high proportion of bare ground and dominated by western wheatgrass (*Pascopyrum smithii*), plains pricklypear (*Opuntia polyacantha*), and various forb species. Dominant land uses in our study area included livestock grazing, energy extraction, and recreation.

Perimeters of Black-Tailed Prairie Dog colonies in the study area were mapped by the U.S. Forest Service and researchers from 2014–2016 (Cully et al. 2010, Parker et al. 2019). Prairie dog colonies ranged in size from 6–1700 ha in 2015. Colony expansion in 2016 and 2017 led to colony sizes exceeding 4000 ha; the largest colonies in Thunder Basin were nearly an order of magnitude larger than where Mountain Plovers have been studied in Montana (Olson

and Edge 1985; Dinsmore et al. 2005), Colorado (Augustine and Skagen 2014), and New Mexico (Goguen 2012).

Adult Mountain Plover Density

Data collection

We surveyed point transects located entirely within colonies (*n* = 10, 8 points per transect), and across colony edges into adjacent undisturbed habitat (*n* = 41, 5–8 points per transect) during 2015–2017 as a part of a larger study assessing grassland and sagebrush bird responses to prairie dogs (Figure 1). All transects contained 4–8 points spaced 250 m apart, and no point in any transect was closer than 250 m to another point. Although the complete dataset included some points outside of colonies, previous analyses indicated that plovers are almost entirely restricted to colony habitat in this system (Duchardt et al. 2018); therefore we only used points located within colonies for the following analyses. However, this study design allowed us to capture more points each year due to colony growth over the study period, because many points that were located outside colonies in 2015 were within colonies by 2017. As such, this dataset includes 196, 236, and 280 points surveyed each year, respectively.

We conducted two rounds of avian surveys on these transects between mid-May and late June each year from 2015–2017, surveying between sunrise and 10:00 AM on days with low wind and no rain (Pavlacky et al. 2017). We conducted discrete six-minute point counts at each point within transects, recording all birds detected within the survey period at an unlimited distance. By traveling to many points via off-road vehicle we ensured more effective detection of Mountain Plovers, which display more cryptic behavior in response to observers on foot (Dinsmore 2003).

We collected habitat data each year along 30-m transects radiating from each point. We measured visual obstruction, a metric incorporating both vegetation height and density, using a Robel pole (Robel et al. 1970) placed at 5-m increments along transects. We also measured vegetation cover and bare soil exposure using the line-point intercept method at 1-m increments (Herrick et al. 2009). We recorded basal and canopy contacts for perennial C3 and C4 grasses, annual grasses, and forbs. Ground cover categories included bare ground and litter, in addition to basal cover of plant functional groups. Shrub and cactus canopy cover were only measured in 2015 using the line-intercept method (measuring gaps in shrub and cactus canopy along the transect; Canfield 1941, Herrick et al. 2009) because we reasoned that these cover measurements would remain relatively static over the course of our study. Because both topography and soil type may also influence habitat use, we used a digital elevation model to generate a topographic roughness index within a 100-m buffer around each point (Gesch 2007, Porensky et al. 2018) and the SSURGO database (NRCS 2017) to characterize average soil texture (percent clay, silt, and sand) from 0 to 30 cm depth at each point.

Modeling Framework

We began our overall modeling process by identifying variables likely to be important to Mountain Plover habitat selection (Table 1). These included structural variables often tested in the literature (e.g., bare ground and visual obstruction, Knopf and Miller 1994), topography and soil type, which have been shown previously to be important for shortgrass bird habitat use in this system (Duchardt et al. 2018), as well as a number of variables related to prairie dog disturbance. These included aspects of disturbance itself (colony size, duration of disturbance at a given point [i.e., colony age], and distance to colony edge), as well as proportions of cover in different vegetation classes (C3 perennial grasses, C4 perennial grasses, annual forbs). We

included the latter because while it is widely recognized that black-tailed prairie dogs alter vegetation composition (Winter et al. 2002, Johnson-Nistler et al. 2004), it is unclear whether these effects impact habitat quality for Mountain Plover.

To adjust for detectability, we modeled Mountain Plover abundance (truncated to within 200 m of a point) using Program DISTANCE (version 6.0), comparing models including hazard rate and half-normal key functions along with covariates including sky cover, wind, temperature, visual obstruction, and use of ATV; the best model explaining detectability included an effect of wind and use of off-road vehicle (see Appendix 2 and Duchardt et al. 2019 for more detail concerning distance sampling methods).

Counts of Mountain Plovers were zero-inflated, so we employed a zero-inflation Poisson model in the package glmmTMB in R (Brooks et al. 2017) to model variation in abundance. Each model included variables specified under the traditional conditional model ("conditional model") as well as variables expected to predict structural zeroes in the dataset ("zero-inflated model"). Because Program DISTANCE output is in the form of density estimates, we modeled instead the response of raw plover abundance with an offset variable in all models to include the effect of species detectability (Aldridge et al. 2011, Timmer 2017). We also included a random effect of transect to account for spatial autocorrelation within transects (Duchardt et al. 2019) and calculated Moran's I to ensure independence (Moran 1950).

We examined univariate models of each target variable specified in either the conditional (c) or zero-inflated (zi) portion of the model, and compared these models to a base model (in this case, a model including the random effect of spatial autocorrelation and detectability offset term), selecting those models with an Akaike's Information Criterion for small samples (AIC_c; Burnham and Anderson 2002) smaller than the base model to be incorporated into a global

model. Where multiple highly correlated variables were all better than the null, we selected the variable from the model with the lowest AIC_c for inclusion in the global model. This global model was then reduced by manually removing variables that appeared to be statistically less important (85% confidence intervals overlapping zero, beginning with the greatest overlap) until the AIC_c was minimized, resulting in a "best reduced" model. We then compared all univariate models and the global and reduced models with a "literature model" including visual obstruction and bare soil, two variables consistently identified as important traits of plover habitat in the literature (Knopf and Miller 1994, Knopf and Wunder 2006).

Nest-site selection

Data collection

Following point counts we returned to colonies where Mountain Plovers had been detected, either that year or historically, and conducted nest searches at these sites following the method of Dinsmore et al. (2002), utilizing all-terrain vehicles to survey the entire colony. Upon detecting a Mountain Plover, we observed the bird until we either located its nest or determined that it likely was not tending a nest based on behavioral cues. Once a nest was located, we recorded its geographic coordinates using a global positioning system device (Trimble GeoXT, Sunnyvale, CA), and placed cow pats 5 m to the north and south of the nest to facilitate revisits to the nest site to determine nest fate, while avoiding detection of the nest by predators. We also floated one egg from each nest to determine nest age (Dinsmore et al. 2002; University of Wyoming IACUC Protocol Approval *[#20150518JB00168-01*], Wyoming Game and Fish Department Chapter 33 Permit *1017,* USFWS Permit *MB95551B-0*). We visited each nest every 5–7 days during the incubation period (approximately 30 days) to determine nest fate.

To assess patterns of nest-site selection we compared habitat data collected at survey points with data collected at the nest site and area around the nest. At the nest, we used a 40 cm x 40 cm point intercept grid, centered on the nest (Augustine and Derner 2012). We measured ground cover (including basal vegetation) and canopy (measured as pin hits) at 25 systematically-positioned points within this grid for the following cover classes: C4 perennial grasses, C3 perennial grasses, annual grasses, forbs, shrubs (to spp.), litter, and bare ground. We also overlaid two 30-m transects oriented N-S and E-W centered on the nest (i.e., representing a 15-m radius around the nest). Along each transect, we collected visual obstruction data using Robel pole readings in four directions at the nest, and at 5-m and 10-m from the nest. Along the E-W transect, we collected line intercept data on shrubs and cactus. We also collected point intercept data for the same vegetation categories as above at 1-m intervals along the E-W transect for a total of 30 points. These measurements were conducted from May to July each year, typically within 5 days of nest failure or fledging.

Modeling framework

We used logistic regression to model nest-site selection in Mountain Plovers (Keating and Cherry 2002). We implemented a use versus non-use framework, randomly selecting "unused" sites from among previously sampled point count locations within colonies, using only points where no plovers were detected during surveys in that year and no nests were observed. Because we were interested in selection of nest-sites at the within-colony scale, we limited our selection to an equal number of unused points per colony per year (e.g., where 4 nests were found on a colony in a given year, 4 random points were selected from that colony for that year).

As in analyses of adult density described above, we examined univariate models of each variable considered to be important for Mountain Plover nest-site selection (Table 1). Where data

were available at the scale of both the nest site (15-m radius around the nest) and nest cup, we examined univariate models at both scales and selected the model at the scale with the lowest AICc (because the two scales were generally too correlated to include in the same model). We then selected all variables from univariate models that were >2AICc less than the null model, and combined these in a global model. When variables were highly correlated ($|r|$ >0.7), we selected the variable with the lowest univariate AIC_c. Finally, this global model was then reduced by manually removing statistically unimportant variables (i.e., 85% CI overlapping zero) until AIC_c was minimized, resulting in a "best reduced" model. We then compared all univariate models and the best global and reduced models with a "literature model" including visual obstruction and bare soil, two variables typically identified as important in the literature (Knopf and Miller 1994.

Nest survival

Modeling framework

To investigate the effects of vegetation, topoedaphic factors, and weather on nest survival, we estimated daily survival rates (DSR) using the logistic exposure method (Shaffer 2004) in program R (Herzog and Bolker 2014). Because temporal variables (Table 1) have been identified as extremely important in predicting nest survival in this species (e.g., Dinsmore et al. 2002, Dreitz et al. 2012), we used a hierarchical approach to build models of nest survival. We began by examining all univariate temporal models (see Table 1). However, because nest survival is commonly influenced by interactions between temporal variables, in this step we also examined 2-way interactions between year, nest age, and day of season, as well as between year, nest age, and quadratic day of season to capture potential non-linear effects. We then built a global model

with all temporal variables better than the null. This temporal global model was reduced by manually removing statistically unimportant (i.e., 85% confidence interval overlapping zero) variables until the AIC_c was minimized, resulting in a "best reduced" temporal model. In step two of this approach, we used this best temporal model as a base to examine all variables related to vegetation structure and composition, building a complete global model with both temporal and structural variables, and again removing statistically unimportant variables until the AIC_c was minimized. We also included a literature-based model of nest survival including nest age and day of season.

We obtained weather data including temperature, precipitation, and inclement weather from a local weather station administered by the National Oceanic and Atmospheric Administration (NOAA; data requested from www.ncdc.noaa.gov/oa/climate/stationlocator.html). Inclement weather measures included days with hail and days of thunder (Carver et al. 2017) We generated weather variables for the midpoint of the exposure interval of each nest (Table 1).

We observed that, in addition to predation events, both nest abandonment and egg inviability (i.e., adult continued to tend eggs that never hatched) sometimes were causes of nest failure. We hypothesized that among all failed nests, different factors affected the probability of predation as compared to abandonment and inviability. We further explored these effects by predicting the source of nest failure, either in the form of depredation or abandonment/egg inviability. We used logistic regression with a reduced dataset only including failed nests to examine drivers of abandonment (1) versus predation (0). We compared models including any competitive vegetation variables from above (>2 AIC_c better than the null), as well as all weather variables and year. Weather variables associated with causes of nest failure were either summed

("“precipitation,” “hail,” “thunder”) or modeled as the maximum of these variables (“min temp” and “max temp”) over the duration of the nesting cycle.

RESULTS

Adult Mountain Plover Density

Adult Mountain Plover density on prairie dog colonies in the Thunder Basin National Grassland averaged 2.9 birds/km^2 (SE = 0.28). Density varied substantially across years, with the highest densities observed in 2015 (3.8 birds/km^2, SE = 0.67), but also varied with colony age and size (Figures 2a-b), with highest densities on colonies between 100–500 ha (5.82 birds/km^2, SE = 1.0). Overall, six variables in addition to colony area, distance to colony edge, and colony age were included in multivariate model exploration, including aspects of vegetation structure, composition, and topoedaphic features (Table 2, Appendix 3; see Appendix 1 for average covariate values for plover presence vs. absence).

The best multivariate model predicting Mountain Plover density had an $R^2 = 0.12$ and a model weight of 0.99 (Table 2). Most variables played a stronger role in predicting plover presence versus absence on colonies, including maximum vegetation height ($\beta_{MAXHEIGHT} = -0.1$, SE = 0.04), cover of annual forbs ($\beta_{AF} = 3.19$ SE = 1.1), cover of C3 annual grasses ($\beta_{C3P} = -5.81$, SE = 3.31), quadratic effects of colony age ($\beta_{AGE} = 0.55$ SE = 0.3; $\beta_{AGE}^2 = -0.04$, SE =0.02) and distance to colony edge ($\beta_{DIST} = 0.52$ SE = 0.3; $\beta_{DIST}^2 = -0.06$, SE =0.03). Bare ground ($\beta_{BARE} = 0.81$, SE = 0.3), soil clay content ($\beta_{CLAY} = 2.35$, SE = 0.6), colony age ($\beta_{AGE} = 0.08$, SE = 0.03) and colony area (km; $\beta_{AREA} = -0.026$, SE = 0.007) were included in the conditional portion of the model.

Nest-Site Selection

During 2015–2017, we located and monitored 144 Mountain Plover nests on colonies ranging from 15–4000 ha in size. Because nest fate was uncertain in some cases, and in others vegetation data were not collected, we conducted nest-site selection analyses on 138 nests paired with 138 unused points. After comparing all univariate models (Appendix 4) nine variables were included in exploration of multivariate models. The best multivariate model (R^2 = 0.58; Table 3) included a negative response to vegetation height at the nest bowl (β_h= -0.42, SE = 0.07; Fig. 4b) and to presence of shrubs (β_{shrub}= -1.79, SE = -0.49), cactus (β_{cactus}= -23.0, SE = 5.81; Fig. 4d), topographic roughness (β_{rough}= -0.84, SE = 0.48) at the nest site, as well as a marginal response to colony age (β_{colage} = -0.15, SE = 0.09). The model also included a positive response to annual forbs at the nest (β_{af} = 4.45, SE = 1.4), and bare ground (β_{bare} = 2.45, SE = 0.94) at the nest site, as well as marginal effects of soil clay content (β_{clay} = 0.1, SE = 0.03), and cover of C4 perennial grasses at the nest (β_{C4} = -3.75, SE = 2.42; Figure 3).

Nest Success

Nesting began between 24 April–28 April each year, but average nest initiation date was 19 May (range: 24 Apr–20 Jun) because many individuals re-nested in late May or June following nest failure. Fifty-three of 136 nests with complete survival data were successful (apparent survival = 39%), while 54 nests were depredated and 29 failed due to other causes (e.g., nest abandonment, egg inviability, egg damage). Daily nest survival across years was estimated at 0.96, with an estimated 30-day survival rate of 34%. Univariate models with year, thunder, maximum temperature, and the interaction between nest age and day of season were all better supported

than the null model (Appendix 5). The reduced temporal model included the effects of thunder, maximum temperature, and the interaction between nest age and day of season (Table 4).

Second-stage models examining each habitat variable along with the best temporal variables indicated that cactus cover, shrub cover, C4 perennial grasses at the nest, and C3 perennial grasses at the site, and a quadratic effect of colony age all influenced nest survival. The final reduced model included the effect of maximum temperature (β = -0.036, SE = 0.01), cactus cover (β = -13.53 SE = 4.8), thunder (β = -0.54, SE = 0.3), shrub cover (β = -1.0, -0.4), nest age (β = 0.10, SE = 0.03), day of season (β = 0.044, SE = 0.02), and the interaction between nest age and day of season (β = -0.002, SE = 0.0008; Figure 4). This model also included a marginal effect of colony age (β = -0.23, SE = 0.2) and the quadratic effect of colony age (β = 0.03, SE = 0.02).

Our simple approach to separating the drivers of nest predation from other sources of nest failure across the duration of the nesting cycle enhanced our ability to detect and understand factors related to nest survival rates (Table 5, Appendix 6). After combining all variables better than the null into a multivariate global model, and then reducing from the global model, the resulting best model included the effects of maximum precipitation (2.67, SE = 1.03), hail (2.21, SE = 1.0), maximum temperature (0.10, SE = 0.06), and an effect of C4 perennial grasses at the nest site (-19.9, SE =9.2). Thus nests experiencing higher temperatures, hail, and more intense precipitation events were more likely to fail due to factors other than predation.

Discussion

Our findings reinforce the importance of Black-tailed Prairie Dogs as engineers of Mountain Plover habitat, but also identified novel responses of plovers to large prairie dog colonies. Prairie

dog disturbance explained a large amount of variation in selection of breeding and nesting habitat, reinforcing the role of prairie dogs as identified in studies from other portions of the species' range (Dinsmore et al. 2005, Tipton et al. 2009, Augustine 2011, Gougen 2012). Aspects of prairie dog colonies directly influenced habitat suitability for adult plovers, with birds preferring older portions of moderately-sized colonies, and habitat characteristics influenced by prairie dogs (e.g., vegetation height, bare ground exposure, and annual forb abundance; Appendix 1) were quantitatively linked to habitat suitability both at the breeding site and nest site scales. Plover densities on moderately-sized (100–500 ha) prairie dog colonies or at moderate distances from colony edges in the Thunder Basin were comparable with other identified hotspots in Wyoming (Plumb et al. 2005) and elsewhere in their range (Childers and Dinsmore 2008, Tipton et al. 2009, Augustine 2011, Pierce 2017). Nest survival rates for the Thunder Basin plover population also fell centrally within ranges reported in the literature (e.g., Dinsmore et al. 2002, Augustine and Skagen 2014, Pierce et al. 2019). As such, we posit that the Thunder Basin National Grassland, and specifically its prairie dog colonies, are an important resource in terms of range-wide Mountain Plover conservation.

Despite the importance of prairie dog colonies as breeding habitat, we found that not all colonies are equal in terms of habitat quality. Areas of longer-term prairie dog disturbance on colonies had higher mountain plover densities, likely because long-term disturbance is linked with increased bare ground exposure and lower vegetation height, as well as more annual forbs (Whicker and Detling 1988, Johnson-Nistler et al. 2004). More surprising was that extremely large colonies had lower average densities of adult Mountain Plovers and probability of site use declined near cores of large colonies. We had observed a similar trend in abundance responding to distance to colony edge previously (Duchardt et al. 2019), but this is the first direct evidence

that colony size may negatively influence plover density. Observed densities were lowest on colonies >500 ha in size, while they were highest on colonies between 100-500 hectares in size (Figure 2), although we note there was substantial variation in densities within this size class.

Similar findings are likely absent in the literature because most remaining Black-Tailed Prairie Dog colonies are comparatively small in size; maximum colony sizes in previous studies did not exceed approximately 480 ha (Dinsmore et al. 2005, Augustine et al. 2008, Goguen 2012, Augustine and Skagen 2014). In contrast, the largest colonies in Thunder Basin exceeded 4,000 ha in the final year of our study. While we did not directly examine mechanisms driving the response of plovers to colony size and distance to colony edge, one potential driver may be complementary resources (Ries et al. 2004). We have observed directly that vegetation height and shrub cover are higher outside of prairie dog colonies (Duchardt et al. 2019), which may be especially important for adults with broods; taller vegetation may provide protection from predators [Schneider et al. 2006], while vegetation and shrubs may provide better opportunities for thermoregulation, especially important for chicks in a region where daytime temperatures may exceed 100 F (38 C) (Shackford 1996). These resources are lacking within colonies, and it may be easier for adults to travel with chicks if they nest nearer a colony edge than traveling > 1km from a colony core. However, our results indicated that while distance to colony edge was a strong driver of plover presence, total colony area influenced the abundance of birds – thus there are likely factors associated directly with colony size in addition to complementary resources (e.g., predator abundances or food resources may vary with colony size).

Local-scale habitat attributes including reduced vegetation height and increased exposure of bare ground have been linked to enhanced Mountain Plover habitat quality in the literature (Knopf and Miller 1994, Dinsmore 2003, Augustine and Derner 2012) and were also important

in our study. We note that we quantified two metrics of vegetation height/structure: the first was visual obstruction, or height at which the vegetation is sufficiently dense to obscure a 2.5-cm wide pole when viewed from a 1 m height (Robel 1970). The second was maximum vegetation height, or the height of the tallest vegetation visible in front of a 2.5-cm wide pole, regardless of that vegetation's density. Because these two measurements covary strongly (r = 0.82), we did not consider models with both predictors. Our model comparison analysis found that maximum vegetation height was the better of the two in explaining variation in plover habitat use. Our selected model indicated that plovers avoided nesting in areas with a maximum vegetation height >11 cm, corresponding with an average visual obstruction of greater than 5 cm. We suggest that the presence of sparse vegetation in the range of 3–5 cm, which is typically associated with a shorter layer (1–1.5 cm) of more dense vegetation, is ideal habitat because the short, dense layer can provide some concealment to a sitting plover's body, and the taller but sparse pieces of vegetation break up the outline of a plover while still affording them the ability to scan for and detect approaching ground predators (Knopf and Wunder 2003). Our models also identified high levels of bare soil exposure as an important component of plover habitat (Table 2), likely because plovers blend in especially well with bare soil when viewed by aerial predators.

Although cactus cover has been examined in the literature, responses of plovers to this variable have been mixed, with some reports of avoidance (Knopf and Miller 1994), but no apparent sensitivity in other systems (Augustine and Derner 2012). Our results show avoidance of cactus at the nest site, combined with lower nest survival in areas of unusually high cactus cover (Figure 4). Perhaps the reason this has not been detected in the past is the especially high cactus density in some portions of Thunder Basin, compared with more moderate cover in other locales, but this is difficult to assess because maximum percent cover of cactus is not generally

reported in the literature (e.g., Knopf and Miller 1994, Augustine and Derner 2012). We found that probability of plovers nesting in a locality declined most notably where cactus exceeded 10% cover. It is important to note that while we observed avoidance of extensive cactus cover at the nest site, low or moderate cactus cover may be beneficial to Mountain Plovers for crypsis at broader spatial scales, or during the brood-rearing period.

In addition to cactus cover, a number of other variables influenced nest survival, including nest age (Figure 4). Unlike altricial species, increased nest age in precocial species is often associated with increased probability of survival (Klett and Johnson 1982). We observed this trend, but it was paired with an interaction with day of season, such that older nests were less likely to survive late in the season. This may be related to stress on adults to complete the nesting season, or increased temperatures later in the nesting season. We found support for the latter proposed mechanism, as higher temperatures were also associated with lower nest survival. Temperature has been previously linked with Mountain Plover nest survival (Dreitz et al. 2012, Pierce et al. 2019), but the role of extreme minimum or maximum temperatures may vary because Mountain Plovers inhabit a fairly wide climatic envelope given their limited geographic range (Knopf and Wunder 2006). In the Thunder Basin and other lower-elevation sites, maximum temperature is likely to limit nest survival. In the Thunder Basin National Grassland, maximum temperatures exceeded 37 degrees C (100 degrees F) for multiple days in all years, and high temperatures were often accompanied by altered adult behavior at the nest (e.g., drastically reduced flight initiation distance, panting while shading eggs), indicating increased stress associated with shading eggs at high temperatures.

Models of nest survival did not support the importance of precipitation as indicated in the literature (Dreitz et al. 2012), but precipitation was identified as important when partitioning

between depredated and abandoned/inviable nests. We identified several key differences in weather variables associated with nest depredation versus nest abandonment or egg inviability, including higher precipitation associated with abandoned nests. We note that during field monitoring of nests, it can be difficult to determine whether a nest was inviable or just abandoned early during the incubation period, leading to a cessation of development in eggs. However, in at least one case we know that eggs were inviable and not noticeably damaged or abandoned; in 2017 we observed the same individual (identified by color bands outfitted by collaborators) attending a nest for at least 72 days, failing to abandon even after we determined eggs were inviable on day 35. We grouped these two sources of failure (nest abandonment and nest inviability) together because they can sometimes be difficult to discern from one another, and because they are likely influenced by similar drivers. Indeed, abandoned or inviable nests were characterized by exposure to higher temperatures and intense precipitation events. Dreitz et al. (2012) observed a similar trend in overall nest survival for Mountain Plovers in eastern Colorado, with higher rates of nest survival during drought and periods of cooler temperatures, although the authors did not indicate what proportion of nests failed due to predation as compared to other causes.

Management actions in many upland systems, especially for gamebirds, often focus on predator control (e.g., Schroeder and Baydack 2001, Fletcher et al. 2010), but this may not be appropriate if substantial numbers of nests are lost due to other causes. In the case of the Mountain Plover and other ground-nesting species exposed to climatic extremes, we encourage future research to explore the drivers of different sources of nest failure. Our own approach to this issue was relatively simple and was constrained by our dataset and research foci, but new methods are emerging for partitioning sources of variation in nest success (e.g., Darrah et al.

2017), providing opportunities to further explore this concept both for Mountain Plovers, and other grassland and sagebrush bird species.

Conservation Implications

Mountain Plovers are strongly dependent on prairie dog colonies for nesting habitat in the Thunder Basin National Grassland, as evidenced by their near-absence off-colonies during the nesting season (Duchardt et al. 2019). However, our analyses of Mountain Plover adult distribution during the nesting season indicates that extremely large colonies are likely suboptimal in terms of habitat value for this species. While the mechanisms driving these responses warrant further exploration, this finding has important and immediate management implications. In addition to reduced habitat quality for Mountain Plovers, large prairie dog colony complexes can impact livestock production on rangelands (Derner et al. 2006; Augustine and Springer 2013), creating tensions between land managers, livestock producers, and conservation organizations. Future management of Black-Tailed Prairie Dog colonies to support Mountain Plover conservation may be optimized by aiming to sustain complexes that include moderately-sized colonies (100–500 ha). In addition to benefitting mountain plover, this strategy would also sustain many other ecosystem services (e.g., sagebrush wildlife habitat, livestock forage) associated with off-colony plant communities.

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Table 1. Variables used in models predicting Mountain Plover habitat use, nesting habitat use, and nest survival for data collected in the Thunder Basin National Grassland, USA, 2015–2017.

	Adult habitat use	**Nesting habitat**	**Nest survival**
Response variable	*Abundance, adjusted for detectability*	*Nest site use v. non-use*	*Daily Survival Rate*
Data source	*Point counts*	*Nest searching*	*Nest monitoring*
Modeling framework	*Zero-inflated Poisson model*	*Logistic model*	*Logistic exposure model*
Covariates			
Prairie dog colony - direct			
	Colony size^2	---**	Colony size^2
	Colony age^2	Colony age^2	Colony age^2
	Distance to colony edge^2	Distance to colony edge^2	Distance to colony edge^2
Vegetation Structure			
	Visual obstruction*	Visual obstruction (Nest, 5 m, 10 m)*	Visual obstruction (Nest, 5 m, 10 m)*
	Maximum vegetation height*	Maximum vegetation height (Nest, 5 m, 10 m)*	Maximum vegetation height (Nest, 5 m, 10 m)*
	Bare ground	Bare ground (Nest, Nest site)	Bare ground (Nest, Nest site)
Vegetation Composition			
	Shrub cover (0/1)	Shrub cover (0/1)	Shrub cover (0/1)
	Sub-shrub cover (0/1)	Sub-shrub cover (0/1)	Sub-shrub cover (0/1)
	Cactus cover	Cactus cover	Cactus cover
	Annual Forb	Annual Forb (Nest, Nest site)[t]	Annual Forb (Nest, Nest site)
	C3 perennial grass cover	C3 perennial grass cover (Nest, Nest site)	C3 perennial grass cover (Nest, Nest site)
	C4 perennial grass cover	C4 perennial grass cover (Nest, Nest site)	C4 perennial grass cover (Nest, Nest site)
	C3 annual grass cover	C3 annual grass cover (Nest, Nest site)	C3 annual grass cover (Nest, Nest site)
Topo-edaphic			
	% Clay*	% Clay*	% Clay*
	% Silt*	% Silt*	% Silt*
	% Sand*	% Sand*	% Sand*
	Topographic Roughness	Topographic Roughness	Topographic Roughness
Periodic/Temporal			
	Year	Year	Year
			Day of Season
			Day of Season^2
			Nest Age
			Precipitation [tt]
			Thunder [tt]
			Hail [tt]
			Maximum Temperature [tt]

* Indicates variables that were highly (>0.6) correlated with at least one other variable; in multivariate model building, only the variable with the lowest AICc was used in building more complex models

**Because available paired points for nest site selection analyses were located within the same colony, colony size was identical between used and available points at this scale.

[t] Data were available at the nest cup and nest site for most composition variables, and at the nest cup, 5 m distant and 10 m distant for measurements of VO and vegetation heights. Because of high correlation between measurements at different scales, for each variable the scale with lowest AICc was used in building more complex models.

[tt] Weather variables were calculated as the value at the midpoint of the exposure period.

Table 2. Results of model-building and model comparison predicting adult Mountain Plover habitat utilization in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. The conditional and zero-inflated portions of the model are specified by (c) and (zi), respectively. The "Model" column indicates whether the model represents univariate model exploration from step one of our modeling approach, the global model built from competitive variables, the reduced global model, or an *a priori* model based on literature. Shown are the global and reduced model, as well as top univariate and quadratic models. For full model list see Appendix 3.

Model	**Model**	**AIC_c**	**ΔAIC_c**	***K***	**w_i**
(c) Clay + Colony area + Bare ground + Colony age *(zi) Max. vegetation height + Colony age^2 + Distance to colony edge^2 + Annual forb +C3 Annual Grasses*	***Best Reduced***	869.30	0	15	0.99
(c) Clay + Colony area + Bare ground + Colony age$^{2\,+}$ Distance to colony edge^2 + Max. vegetation height *(zi) Max. vegetation height + Colony age^2 + Distance to colony edge^2 + Annual forb +C3 Annual Grasses + Topographic Roughness + Bare ground*	***Best Global***	878.05	8.75	21	0.01
(zi) Colony Age^2	Quadratic	917.83	48.53	6	0
(zi) Colony Age	Univariate	920.17	50.87	5	0
(zi) Distance to edge^2	Quadratic	927.90	58.60	6	0
(c) Colony Age^2	Quadratic	929.53	60.23	6	0
(zi) Maximum vegetation height	Univariate	931.90	62.59	5	0
(zi) Visual obstruction + Bare ground	**Best a priori model**	933.59	64.28	6	0
(zi) Annual forb	Univariate	943.18	73.88	5	0
(zi) Bare ground	Univariate	943.38	74.07	5	0
Null	---	959.48	90.18	4	0

Table 3. Summary results of model-building and model comparison predicting Mountain Plover nest-site selection in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017, including the global model, reduced model, an *a priori* literature model, top univariate model, and null model. Full model set including all univariate models can be found in Appendix 4

.

Model	**Model**	**AIC$_c$**	**ΔAIC$_c$**	***K***	***w$_i$***
Max. vegetation height (nest) + C4 perennial grass (nest) + cactus + Shrub + Bare (nest site) + Annual forb (nest) + Clay + Topographic roughness + Colony age	Reduced model	181.27	0.00	10	0.89
Max. vegetation height (nest) + C4 perennial grass (nest) + cactus + Shrub + Bare (nest site) + Annual forb (nest) + C3 perennial grass (nest) + Clay + Topographic roughness +Colony age^2	Global model	185.52	4.24	12	0.11
Max. vegetation height (nest)	Univariate	267.93	86.66	2	0.00
Visual obstruction (5m) + Bare ground (site)	Literature Model	299.10	117.83	3	0.00
Null	Null	384.63	203.36	1	0

Table 4. Top models predicting daily nest survival for Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. Full model set including all univariate models can be found in Appendix 5.

Model	**Model type**	**AIC_c**	**ΔAIC_c**	***K***	w_i
Cactus+ Shrub + Nest Age*Day of season + Colony age^2 + Max Temp + Thunder	Temporal + structure (reduced)	460.20	0	10	0.65
Cactus+ Shrub + Colony Age^2 + C3 perennial grass (Site) + C4 perennial grass (nest) + Nest Age*Day of season + Max Temp + Thunder	Temporal + Structure (global)	462.38	2.18	12	0.22
Cactus + Age*Day of season + Max. Temp + Thunder	Temporal + Cactus	464.02	3.83	7	0.10
Shrub + Age*Day of season +Max. Temp + Thunder	Temporal + Shrub	467.97	7.77	7	0.01
Age*Day of season +Max. Temp + Thunder	Best temporal model	471.99	11.29	6	0
Null	---	479.78	19.58	1	0
Max. Temp + Age + Day of season + Precipitation	Literature Model	480.64	20.45	5	0

Table 5. Top univariate models differentiating between nest failure by abandonment and nest failure by predation for Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017, and the final combined global model, where positive parameter estimates indicate greater probability of abandonment.

Univariate model	**AIC$_c$**	**ΔAIC$_c$**	**K**	**w$_i$**	**Parameter estimate (SE)**	***R*^{2}**
Max. Precipitation + Max. Temperature + Hail + C4 perennial grasses (nest site)	*61.01*	*0*	*5*	*1*	β_{precip} *= 2.67 (1.03)* $\beta_{maxtemp}$ *= 0.10 (0.06)* β_{c4p2} *= -19.9 (9.3)* B_{hail} *=2.20 (1.04)*	*0.42*
Hail	77.95	16.93	2	0	2.13 (0.6)	0.15
Max. Precipitation	82.08	21.06	2	0	1.61 (0.56)	0.1
Max. Temperature	84.28	23.27	2	0	0.08 (0.03)	0.08
Visual obstruction at nest	85.25	24.23	2	0	0.52 (0.23)	0.07
C4 perennial grass (nest site)	86.05	25.04	2	0 0	-9.89 (5.7)	0.06
Thunder	86.43	25.42	2	0	1.87 (1.07)	0.05
Null	89.04	28.03	1	0	---	

Figures

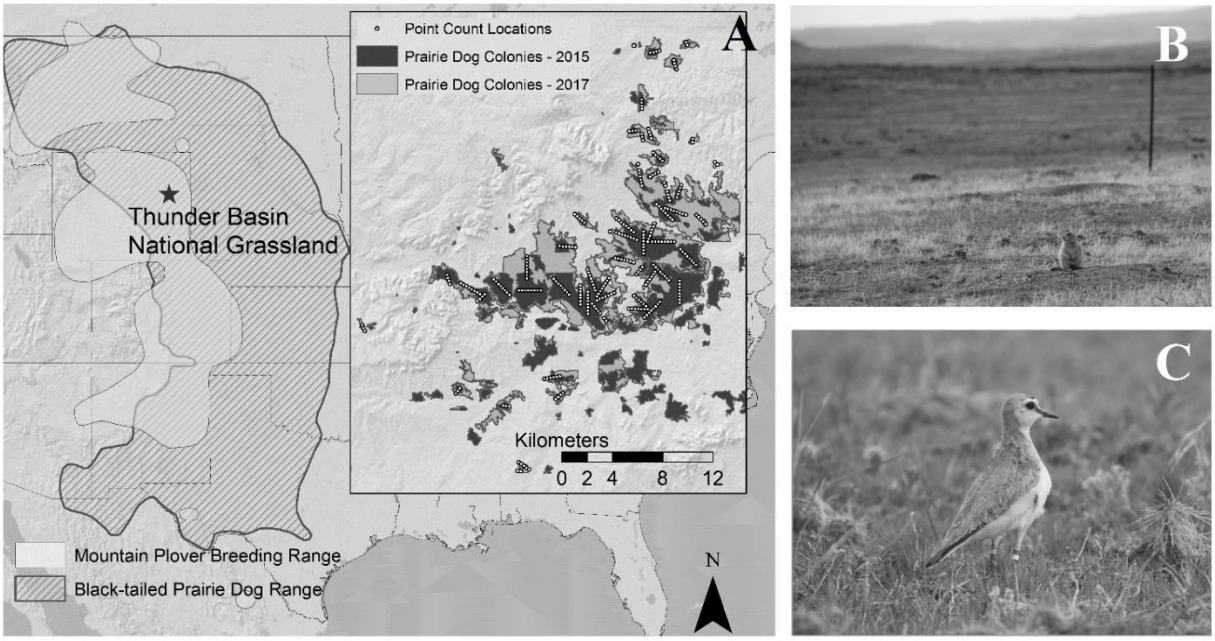

Figure 1. Location of the Thunder Basin National Grassland in eastern Wyoming in relation to breeding range of Mountain Plover and annual range of Black-Tailed Prairie Dog, with inset representing study area (**A**). Black-Tailed Prairie Dog colony (**B**) and Mountain Plover (**C**) in Thunder Basin National Grassland.

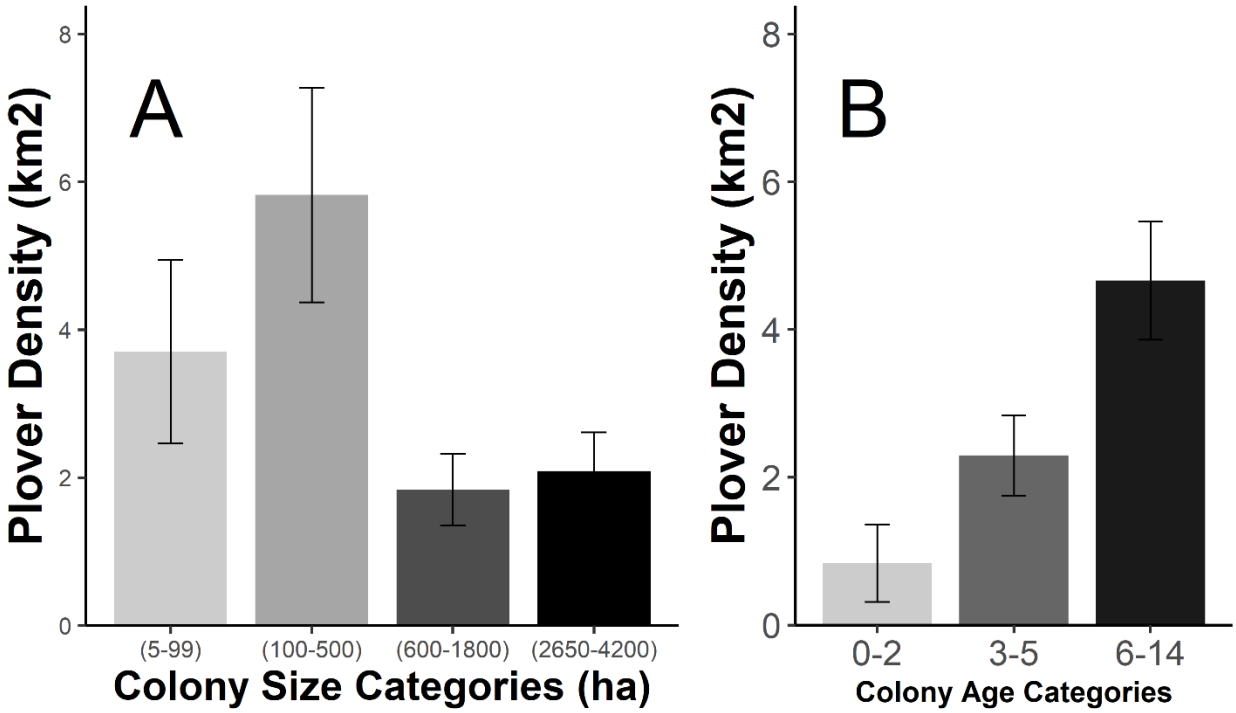

Figure 2. Mountain Plover density as a function of prairie dog colony size (**A**) and age (**B**) in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. The first two size categories (5–99 ha and 100–500 ha) represent small and large colonies in previous studies (e.g., Dinsmore et al. 2005, Augustine et al. 2008, Gougen 2012), respectively. Colony sizes above 500 ha are unique relative to previous studies of breeding Mountain Plovers. Colony ages represent old (6–14), intermediate (3–5) and young (0–2) colonies. Error bars represent 85% confidence intervals. Values above bar plots are number of colonies in each size category. Note: these are observed distance-adjusted densities and not model-generated predictions.

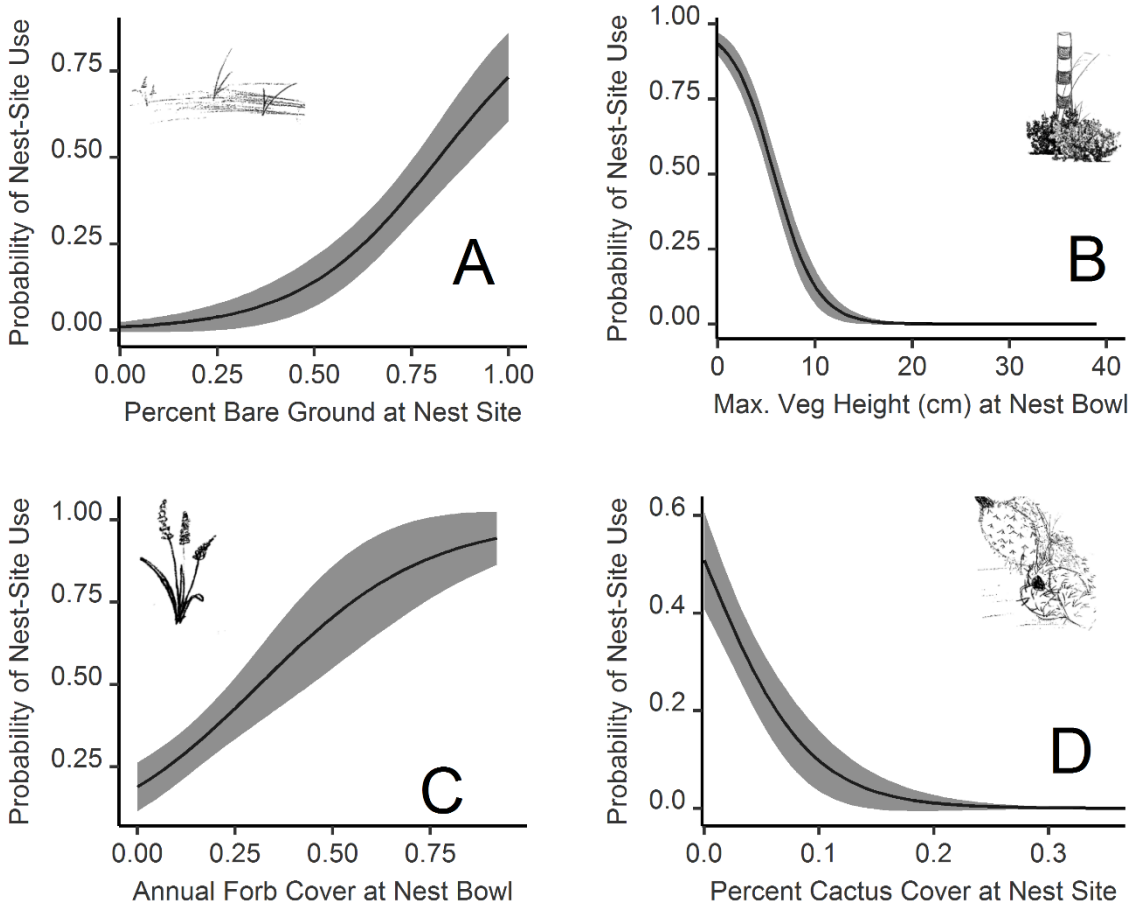

Figure 3. Probability of nest site use by Mountain Plovers as a function of percent bare ground (**A**), maximum vegetation height (**B**), annual forb cover (**C**), and cactus cover (**D**) in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017. Grey envelopes represent 85% confidence intervals.

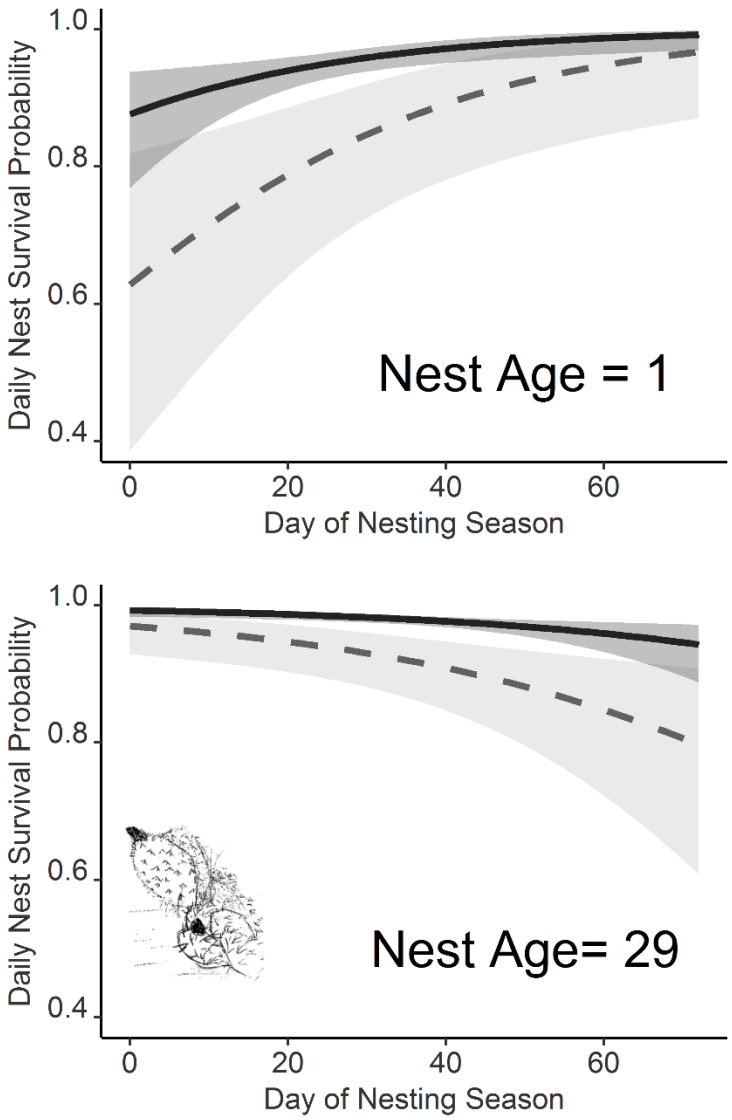

Figure 4. Daily nest survival for Mountain Plovers in the Thunder Basin National Grassland, Wyoming, USA, 2015–2017 increases across the nesting period for young nests (top), but decreases across the season for older nests (bottom). Solid and dashed lines represent 0% and 10% cactus cover, respectively. Grey envelopes represent 85% confidence intervals.

Chapter 5: Sagebrush bird responses to natural and anthropogenic disturbance at the eastern edge of the sagebrush steppe

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ABSTRACT

Among North American avifauna, sagebrush (*Artemisia* spp.) birds are experiencing some of the steepest 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 due to natural disturbance by ecosystem engineers including the black-tailed prairie dog (*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 both natural (i.e., prairie dog) and anthropogenic disturbance. We used a combination of field data collection, state-level and national datasets for the Thunder Basin National Grassland of eastern Wyoming to determine which factors drive lek attendance by sage-grouse and habitat use by two passerines in this system. For all three species, models including big sagebrush were the most competitive among univariate models, supporting the paradigm that sagebrush is key for these species. Overwhelmingly models including anthropogenic disturbance (well density, road density) outcompeted models of prairie dog disturbance alone, although long-term disturbance by prairie dogs did reduce abundance of sagebrush songbirds. Although long term prairie dog disturbance has the potential to reduce habitat quality for sagebrush birds, such events are likely rare due to outbreaks of plague (*Yersina pestis*) and lethal control on borders with private land. Conversely, anthropogenic disturbance is slated to increase in this system in the future.

INTRODUCTION

Aridland avifauna have suffered some of the steepest declines of any bird guild in North America (Sauer et al. 2017). Birds associated with sagebrush (*Artemisia spp.*) ecosystems are especially vulnerable, as sagebrush was historically reduced to increase forage availability for livestock on grazing lands (Vale 1974, Beck et al. 2000, Welch and Criddle 2003). While this practice has become less common, sagebrush ecosystems still 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 juniper (*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, 2017).

Severe reductions in habitat availability and quality have led to severe declines in many sagebrush-obligate birds, most notably in sage-grouse (*Centrocercus* spp.). The Gunnison sage-grouse (*C. minimus*), currently limited in extent to southwestern Colorado and southeastern Utah, is federally threatened (USFWS 2010), while the more widespread and abundant greater sage-grouse (*C. urophasianus*) was considered warranted for federal listing in 2010 under the Endangered Species Act, but was later determined to be not warranted due to extensive conservation efforts throughout its range (USFWS 2015). Although conservation efforts continue, in many areas greater sage-grouse populations continue to decline (Knick and Connelly 2011). This is often directly in response to human activity as oil and gas development disturbance has been especially detrimental to both sage-grouse (Walker et al. 2006, Doherty et al. 2008, Gregory and Beck 2014, Heinrichs et al. 2019) and sagebrush songbirds (Gilbert et al. 2011, Hethcoat and Chalfoun 2015). The sage thrasher (*Oreoscoptes montanus*) and Brewer's

sparrow (*Spizella breweri*), have also declined in recent decades (Sauer et al. 2017), and are key targets for conservation throughout the sagebrush steppe. While management focusing on sage-grouse as umbrella species for other sagebrush songbirds has received much attention to date (Hanser and Knick 2011, Gamo et al. 2012), recent research indicates that this umbrella may not always be adequate, and that 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, for multiple reasons. First, this region has experienced unprecedented energy development in recent decades, which has reduced net primary productivity across rangelands, in turn impacting ecosystem services including availability of livestock forage, biodiversity, and wildlife habitat (Allred et al. 2015). Another recent factor contributing to sagebrush habitat loss within the northwestern Great Plains has been conversion of intact rangelands to tillage agriculture (Chambers et al. 2016, Smith et al. 2016).

Where avian conservation is concerned, management is somewhat complex because managers must consider not only the needs of imperiled sagebrush species but also declining grassland birds (Duchardt et al. 2018). A pivotal character in this is the black-tailed prairie dog (*Cynomys ludovicianus*). This species is a critical ecosystem engineer for grassland birds including the mountain plover (*Charadrius montanus*) and burrowing owl (*Athene cunicularia*), but long-term prairie dog disturbance could potentially reduce habitat availability for sagebrush birds in some areas (Duchardt et al. 2019). Another issue is that vegetation structure within sagebrush habitat in systems along the eastern edge of sagebrush range differs markedly from elsewhere in the sagebrush steppe (Chambers et al. 2016), exhibiting a much denser grass understory, often mixed with annual grasses, where much less research exists (Porensky et al

2018). More broadly, wildlife populations are generally lower and more variable at range-edge (Andrewartha and Birch 1954; Kirkpatrick and Barton 1997). Despite these complications sagebrush bird populations along this ecotone warrant additional research in their own right, but may also become more important if predicted loss of sagebrush due to climate change occurs in the hotter, southerly range or lower elevations within the sagebrush steppe (Bradley et al. 2010, Chambers et al. 2016, Renwick et al. 2017).

To better understand sagebrush bird habitat use along a sagebrush-grassland ecotone, we examined sagebrush bird responses to vegetation, and to anthropogenic and natural disturbance, in the Thunder Basin National Grassland (TBNG) of eastern Wyoming. The TBNG is composed of a mosaic of grassland and sagebrush habitat managed by the United States Department of Agriculture–Forest Service (USFS) and represents a considerable opportunity for the management and conservation of declining grassland and sagebrush birds. The size and distribution of black-tailed prairie dog colonies in this landscape have been monitored for the past two decades (Cully et al. 2010), creating a unique opportunity to examine how such variation influences the abundance of rangeland bird species. Previous research indicates that sagebrush 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 two species.

Understanding the interplay of natural disturbance and anthropogenic disturbance is critical 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 (but see Herman-Brunson et al. 2009, Swanson 2012). Further, because this region must provide

habitat for both sagebrush and prairie dog-associated species, and because this region is likely to experience a rapid increase in energy development in the coming years (Allred et al. 2015), understanding potential impacts of disturbance is especially important. Therefore, we asked the following questions related to the role of natural and anthropogenic disturbance in affecting habitat quality 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? Based on the literature, we anticipate that anthropogenic disturbance associated with energy extraction will reduce habitat quality for all three species, though only weak effects have been observed for sage thrashers in the past (Ingelfinger and Anderson 2004, Gilbert and Chalfoun 2011). Previous research in this system indicates that natural disturbance in the form of prairie dog occupation likely affects sagebrush songbirds only so far as sagebrush is reduced, while little sensitivity has been observed at landscape scales (Duchardt et al. 2019).

METHODS

Study Area

Our study was conducted within the U.S. Forest Service (USFS)–Thunder Basin National Grassland in Campbell, Converse, Weston, and Niobrara counties, Wyoming, USA (Fig 1). Mean annual precipitation ranged from 25–35 cm (Porensky et al. 2018) mainly falling as rain in the spring and summer. Elevation ranged between 1100–1600 m. 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 can reach >30% canopy cover in some areas (Porensky et al 2018).

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 U.S. Forest Service staff and collaborators since 2001. As in many other portions of their range, prairie dogs in the TBNG experience outbreaks of sylvatic plague, but boom-and-bust cycles of colony growth and die-off in this region are particularly severe (e.g., Cully et al. 2001), making this dataset extremely valuable and providing a unique opportunity to examine how colony distribution and size potentially influence sagebrush birds.

Greater-sage grouse lek data

We obtained greater sage-grouse lek survey count data between 1999–2018 from the State of Wyoming (T. Christiansen, WGFD Sage-Grouse Program Coordinator, personal communication, 2018). Because we wanted to focus specifically on dynamics in the area of the TBNG, we selected all leks within a 5 x 7 township grid centered on the TBNG (Figure 1), bounded roughly by Bill, Wyoming to the south and Wright, Wyoming to the north. This method yielded 58 leks which would have been considered “occupied” (Wyoming Game and Fish Department Sage Grouse definitions 2010; Hess and Beck 2012) during at least some portion of the study period. While six of these leks did not have observed males within the study period (1999–2018), they did have observations of males in the mid-1990s.

For the analyses below, we examined dynamic models of 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, 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 from 2–4 years, and final intervals were as follows: 1999–2001, 2002–2004, 2005–2008, 2009–2011, 2012–2014, 2015–2016, 2017–2018. This yielded 287 data points. Within this dataset we also included leks discovered after the starting point of 1999 (32 leks).

Songbird data

As part of a larger study between 2015–2017, we surveyed both sagebrush and grassland habitat using a point-transect based sampling design. Because TBNG is a patchwork of cover types, we established transects using 3 different criteria. First, colony core transects (n = 10, 8 points per transect) were randomly placed with the constraint that transects fell entirely within prairie dog colonies. Second, colony edge transects (n = 41, 5–8 points per transect depending on colony size) were randomly located with the requirement that transects crossed the edge of a prairie dog colony with four points located outside the colony and one to four within the colony, depending on colony size. Third, sagebrush transects (n = 10, 8 points per transect) were located non-randomly in 10 known areas of extensive sagebrush habitat, which were identified during past surveys of greater sage-grouse, to ensure our surveys included portions of the landscape supporting spatially extensive stands of sagebrush. All transects contained 5–8 points spaced 250 m apart, for a total of 61 transects containing 439 survey points. We conducted two rounds of surveys between mid-May and late June each year from 2015–2017, surveying between sunrise and 10:00 AM on days with low wind and no rain (Pavlacky et al. 2017). To adjust for detectability, we modeled Brewer's sparrow and sage thrasher abundance using Program

DISTANCE (version 6.0), comparing models including time of survey, wind, temperature, observer, travel method (ATV vs. on foot), and visual obstruction (See Duchardt et al. 2019 for further detail on DISTANCE methods).

Following point counts, we collected vegetation data at each survey point. We measured visual obstruction, a metric incorporating both 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 hits for grasses, forbs, cacti, and shrubs. Ground cover categories included bare ground, litter, biological soil crust (BSC), and lichen, in addition to basal cover of vegetation classes. 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 likely 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.

Landcover data

Sagebrush cover was calculated using available LANDFIRE Existing Vegetation Type (2014) 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) as well as 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 data. We used

these data to calculate percent sagebrush cover at multiple radii from both 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 both territory and landscape scales. We applied a larger radius 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 quality, we used a digital elevation model to generate a topographic roughness index (Gesch 2007, Porensky et al. 2018) within 100 m of both point count and lek locations.

Natural and anthropogenic disturbance data

Perimeters of black-tailed prairie dog colonies in the study area were mapped on the ground by the U.S. Forest Service and partners each year between 2001–2018 using a handheld GPS device. Mapping efforts were focused on public lands, and although colonies on private lands were occasionally mapped as well, total colony area in a given year likely represents minimum coverage throughout the grassland. To maintain consistency, we only included areas that were 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 recolonization and population growth post-plague. Minimum colony area in 2007–2008 amounted to approximately 1400 ha, while maximum area exceeded 30,700 ha in 2017. We used these data to generate values of colony cover at multiple scales and distance to colony for sage-grouse (Table 1). We only examined presence/absence of prairie dog disturbance, either current or long term (>4 years) for songbirds, as past research indicates other aspects of prairie dog disturbance are relatively unimportant (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/), and calculated density of all roads at two sets of spatial scales corresponding to sage-grouse and sagebrush passerines, as discussed above.

Well pad location and production data were obtained from the Wyoming Oil and Gas Conservation Commission (2019). 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 one 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 two sets of spatial scales corresponding to sage-grouse and sagebrush passerines. Finally, we assessed the potential effect of mining disturbance on both species. The North Antelope Rochelle Mine (Peabody Energy, Incorporated, Saint Louis, Missouri) is one of the largest active coal mines in the country, located in Campbell County, Wyoming near Wright. Because we anticipated mine disturbance may 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 grew during the study period, we used distance to mine center, which has not changed substantially. While mine expansion reduces habitat, at least temporarily, non-destructive effects (e.g., noise, traffic, etc.) are less well understood, and should be captured by this metric.

Analyses

We assessed the response of maximum lek attendance over time using generalized estimating equations (GEE; Yan and Fine 2004) in the package “geepack” (Hojsgaard et al.

2006). This method is well-suited to longitudinal data and is robust to missing data points (Hojsgaard et al. 2006), allowing us to track leks over time including leks not discovered until partway through the study period. Models included an autoregressive correlation structure with leks as clusters. We applied a two-step approach to modeling, examining all potential combinations of variables within three different modeling categories (Landscape, Anthropogenic Disturbance, Natural Disturbance (Table 1)). We note that because the literature has indicated potential quadratic effects of roads and topography (Doherty et al. 2008, Aldridge et al. 2012), we included these effects as well. Because well density was relatively low in this area we created a categorical variable of well density class (similar to Harju et al. 2010, but note classes were defined differently; Table 1) and therefore did not consider a quadratic of this effect. We then took the top model from each category and examined all possible combinations of these top models and compared with a null model. Highly (>0.7) and moderately (>0.5) correlated variables were not used within the same models to avoid collinearity.

We used generalized linear mixed models to investigate drivers of songbird habitat use in this system. Because both sage thrashers and Brewer's sparrows are considered obligate sagebrush nesters (Reynolds et al. 1999, Rotenberry et al. 1999), we removed any points that had occurred in areas without sagebrush cover at a 250-m radius in LANDFIRE, to help avoid zero-inflation. This process removed 45 out of 439 points in each year. We applied an information-theoretic approach, using Akaike's information criterion (AIC_c; Burnham and Anderson 2002) to compare models of the effects of local and landscape-scale vegetation, natural disturbance, and anthropogenic disturbance (Table 1) on both sage thrashers and Brewer's sparrows, examining the same models for both species. We note that in some cases we used binary or categorical variables instead of continuous ones, especially where data were extremely unevenly distributed,

as was the case with well data surrounding point count locations (Table 1). Similar to the approach described above, we applied a two-step approach to modeling, examining all potential combinations of variables within four different modeling categories (Landscape, Anthropogenic Disturbance, Natural Disturbance, local habitat (Table 1)), and then examined all possible combinations of these top models and compared with a null model. Highly (>0.7) and moderately (>0.5) correlated variables were not used within the same models to avoid collinearity.

We modeled Brewer's sparrow abundance using a Poisson distribution. For sage thrasher, we modelled presence-absence using logistic regression because when this species was present at a point, we typically only detected one individual. To address potential spatial autocorrelation within transects, we also included a random effect of transect and calculated Moran's I to assess spatial independence (Moran 1950). 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 to determine which best described habitat use in each species. Highly (>0.7) and moderately (>0.5) correlated variables were not used within the same models.

RESULTS

Greater sage-grouse

Step 1 of our modeling process generated top models of landscape aspects as well as both natural and anthropogenic disturbance (Table 2). Top univariate models included a positive relationship with sagebrush cover within 5 km of the lek, and negative relationship with distance to mine (Appendix 1a). After examining all potential combinations of top models from Step 1, Step 2

yielded a top model including aspects of both disturbance types and landscape (Table 2). The strongest variables included a positive effect of sagebrush cover within 5 km ($\beta = 3.73$, SE = 0.92) and distance to mine ($\beta = 0.04$, SE = 0.009), as well as a quadratic effect of road density at 1km ($\beta_{rd} = 0.47$, SE = 0.2, $\beta_{rd2} = -0.06$, SE = 0.02; Figure 2). There was also a marginal effect of well density class (Figure 2). Other variables included non-significant quadratic effects of topographic roughness and prairie dogs at 500 m (Appendix 1a)

Sagebrush songbirds

Both local and broad-scale variables were important in explaining sagebrush songbird habitat use, but the role of disturbance varied by species. For Brewer's sparrow, Step 1 examining all combinations of variables within local habitat, landscape, natural disturbance, and anthropogenic disturbance generated top models in each category, with the best univariate model including a positive effect of sagebrush cover within 250 m (Appendix 1b. After examining all potential combinations of top models from step 1, the full model had the lowest AIC_c and an $R^2 = 0.24$ (Table 3). Within this model, local variables included positive effects of sagebrush cover ($\beta = 2.27$, SE = 0.12), herbaceous canopy cover ($\beta = 0.48$, SE = 0.09), and cactus cover ($\beta = 0.58$, SE = 0.19), and broad-scale effects of sagebrush cover at 250 m ($\beta = 1.78$, SE = 0.11), a negative effect of litter cover ($\beta = -0.27$, SE = 0.07) a quadratic effect of topographic roughness ([$\beta_{rough} = 0.01$, SE 0.05, $\beta_{rough}^2 = -0.02$, SE 0.01]) and a year effect. Aspects of both anthropogenic (negative effect of well presence within 500 m [$\beta_{well500} = -0.63$, 0.09] and a quadratic effect of total road density within 1 km [$\beta_{road1k} = 1.63$, SE 0.19, $\beta_{road1k}^2 = -0.19$, SE 0.02]) and natural (long-term prairie dog disturbance $\beta = -0.98$, SE = 0.05) disturbances reduced Brewer's sparrow density as well (Fig. 3).

Sage thrasher presence/absence was also explained by variables at the local and landscape scale and by natural disturbance, but no anthropogenic disturbance model was better than the null (Appendix 1c). The best univariate model explaining sage thrasher presence was local cover of Wyoming big sagebrush (Appendix 1c). 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 (Table 3). The model included local effects of sagebrush cover (β = 7.13, SE = 1.41), litter (β =1.35, SE = 0.69), broad-scale effects of sagebrush cover at 1 km (β =4.14, SE = 1.43), a marginal effect of topography (β =-0.19, SE = 0.05) and year (Fig. 4), with an R^2 = 0.104. The best disturbance model included only a negative effect of long-term prairie dog disturbance, but this variable was not included in the final model. No aspect of anthropogenic disturbance was competitive (Table 3).

DISCUSSION

We identified a number 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 and anthropogenic disturbance than prairie dog disturbance alone. We observed a strong effect of a number of covariates related to human disturbance (well density, road density) on both greater sage-grouse and Brewer's sparrow in this system. A number of studies support the potential for energy development to have severe impacts on greater sage-grouse (Gregory and Beck 2014), and sagebrush 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 Management Zone I (Doherty et al. 2008). Although Doherty (2008) examined a dataset 10 years prior to ours, he also identified a threshold where well density became extremely important for sage-grouse lek

attendance beyond one well per 1 mile^2, which translates to approximately 0.39 wells/km^2; this is consistent with our threshold for high well density (0.4/km^2), which was associated with the lowest level of lek attendance (Figure 2). Other researchers have linked oil and gas disturbance to reduced sage-grouse chick survival (Aldridge and Boyce 2007) and yearling survival (Holloran et al. 2010). Furthermore, Sanders and Chalfoun (2019) showed that populations of a main nest predator of sagebrush passerines (deer mouse; *Peromyscus maniculatus*) increased with oil and gas disturbance. Fewer studies have noted impacts of coal mining, but we note here that the effects we observed were likely largely due to direct loss of habitat via mine expansion, and less to indirect effects of disturbance.

Other studies have noted negative impact of roads either directly (Ingelfinger and Anderson 2004), or indirectly (Blickley et al. 2012), an effect which we identified for both grouse and Brewer's sparrows. However, the relationship we identified was quadratic, with lowest abundances at low and high road density. We do not know of any other research indicating this quadratic road effect, which may in fact be a threshold response. Although interesting, 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 at smaller scales). Gilbert and Chalfoun (2011) proposed either an insensitivity to disturbance or high site fidelity as potential mechanisms of response—because we did note some level of sensitivity to prairie dog disturbance in this study, and to fire in a previous study (Duchardt et al. 2018), we are inclined to support the site fidelity hypothesis in this system.

Overall, although prairie dog disturbance explained some variation in abundance for all three species, these models were weaker than models including effects of habitat or anthropogenic disturbance (Table 2, Table 3). Despite extensive discussion in this system about

the potential for prairie dogs to negatively impact 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 because very few leks fell within this category), while at the 5- km scale only "high" (>10%) prairie dog cover was associated with reduced maximum lek attendance. In fact, very few leks have been located within or near core prairie dog habitat since leks were first surveyed in the area (~1970s), which pre-dates the expansion of prairie dog colonies during the 2000s. The lack of suitable habitat for sage grouse in the core of our study area may be due to long-term (multiple decades), heavy prairie dog disturbance, but 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. during 2014 – 2017) did not occur in prior decades . (USDA-Forest Service 2009; Cully et al. 2010). Alternatively, it may be associated with increased tree cover near riparian areas and along the edges of the Red and Rochelle hills, as tree cover has been identified as an important driver of decreased habitat quality, especially within Management Zone I (Doherty et al. 2016).

Among sagebrush passerines, prairie dog disturbance was more important than other habitat or landscape features, especially when considering disturbance within a given year. Other research in this system indicates that while long-term occupancy of prairie dogs may reduce sagebrush bird abundance, prairie dog occupancy within a given year had a much smaller effect (Duchardt et al. 2019). This is likely because the clipping and girdling actions of prairie dogs only kill sagebrush after multiple years of grazing pressure (Ponce-Guevara et al. 2016) In fact, 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 (USDA-Forest Service 2009, *Personal observation*), and are often followed by plague outbreaks which decimate populations (e.g. Augustine et al. 2008; Cully et al. 2010)?. After these outbreaks, prairie dogs typically regroup in areas with naturally shorter vegetation (CD and DJA, personal observation) and often do not reoccupy the same areas occupied during prior population lows (Augustine et al. 2008); as such, multi-year clipping by prairie dogs on sagebrush may be rare.

Least surprising among our results was the strong positive relationship between these species and sagebrush cover. The most important sagebrush variables scaled with body size, as sagebrush cover was most important at 250 m, 1 km, and 5 km, for Brewer's sparrow, sage thrasher, and greater sage-grouse. Topography also played a role, with a marginal negative effect on sage thrasher presence and quadratic effect for Brewer's sparrow and sage-grouse, which has been reported for sage-grouse previously (Chambers et al. 2016). At the local scale, we noted interesting relationships between sagebrush bird abundance/presence and aspects of the sagebrush understory, which has received much less attention than aspects of sagebrush cover (but see Peterson and Best 1991). Both species responded to litter cover, but in opposing ways; this may be linked to the differing foraging strategies of the two 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 impact the foliage-gleaning Brewer's sparrow. Two other studies have also identified this link to litter cover with the sage thrasher (Peterson and Best 1991, Timmer 2017). However, the link between Brewer's sparrow abundance and increased herbaceous understory and cactus cover is novel to our knowledge; we posit that the former may aid in nest concealment (Martin 1992), while the latter

may elicit ground predator avoidance where stands of cactus are especially thick: however, were unable to identify any studies that have examined this potential effect.

Management Implications

While our results support the idea that sagebrush birds as a group are disturbance intolerant, anthropogenic disturbance plays a far larger role in their abundance than disturbance by black-tailed prairie dogs. This finding is especially salient given recent proposals to revise to local land management plans (USDA-Forest Service 2019), widespread increases (and planned increases) to oil and gas development in the area (Allred et al. 2015), and recent discussion of rolling back sage-grouse protections throughout their range. We suggest that while managers should consider the potential for long-term prairie dog occupation to impact sagebrush bird habitat suitability, such impacts may be limited relative to the current expansion of anthropogenic disturbance within the eastern edge of the sagebrush steppe.

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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	DEM - U.S. Geological Survey
Sagebrush cover		
	(5km)	LANDFIRE, 2014. 1.1.0 Existing Vegetation Type Layer. U.S. Geological Survey
(1km)	(1km)	
(500m)	(500m)	
(250m)		
Anthropogenic disturbance		
Well density		
---	Density class [0-3][1] (5km)	
Presence/absence (1km)[1]	Presence/absence(1km)	The Wyoming Oil and Gas Conservation Commission (2019).
Presence/absence (500m)	Presence/absence (500m)	
Presence/absence (250m)		
Road density		
	Road density (5km) ^q	
Road density (1km) ^q	Road density (1km) ^q	Wyoming Geospatial Hub (https://geospatialhub.org/)
Road density (500m) ^q	Road density (500m) ^q	
Road density (250m) ^q		
	Distance to mine ^q[2]	2008 NAIP Imagery
Prairie dog disturbance		
Long term prairie dog disturbance (0,1)		
Prairie dog disturbance (0,1) [3]	Prairie dog disturbance (0,1) [3]	U.S. Forest Service digitized boundaries 1999-2018
	Distance to nearest prairie dog colony	
Local Habitat[4]		
Big sagebrush cover		
shrub cover		
Visual obstruction		
Litter		Field Measurements (see Duchardt et al. 2019)
Bare ground		
Brome cover		
Herbaceous canopy		
Cactus cover		

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/absence variable for these analyses. At the 5km scale we assigned density classes as follows: “3” >0.4, “2” <0.4 & >0.1, “1” <0.1 &>0, “0” = 0.

2. The North Rochelle Mine was a similar distance from most of the songbird study area (Fig. 1), so we did not include this variable in the analyses

3. Colony cover at multiple spatial scales was found to be relatively unimportant to sagebrush songbirds (Duchardt et al. 2019), and was thus not included. We examined prairie dog cover for lek data, but found these data to be extremely zero inflated (only 6 leks were within 1km of prairie dog colonies at any time during the study). Therefore, we examined a categorical variable of prairie dog cover within 5km, with three categories (None = 0, Low = 0.01%-10%, High>10%)

4. Local vegetation data were collected as part of another study, and were therefore only available for songbirds.

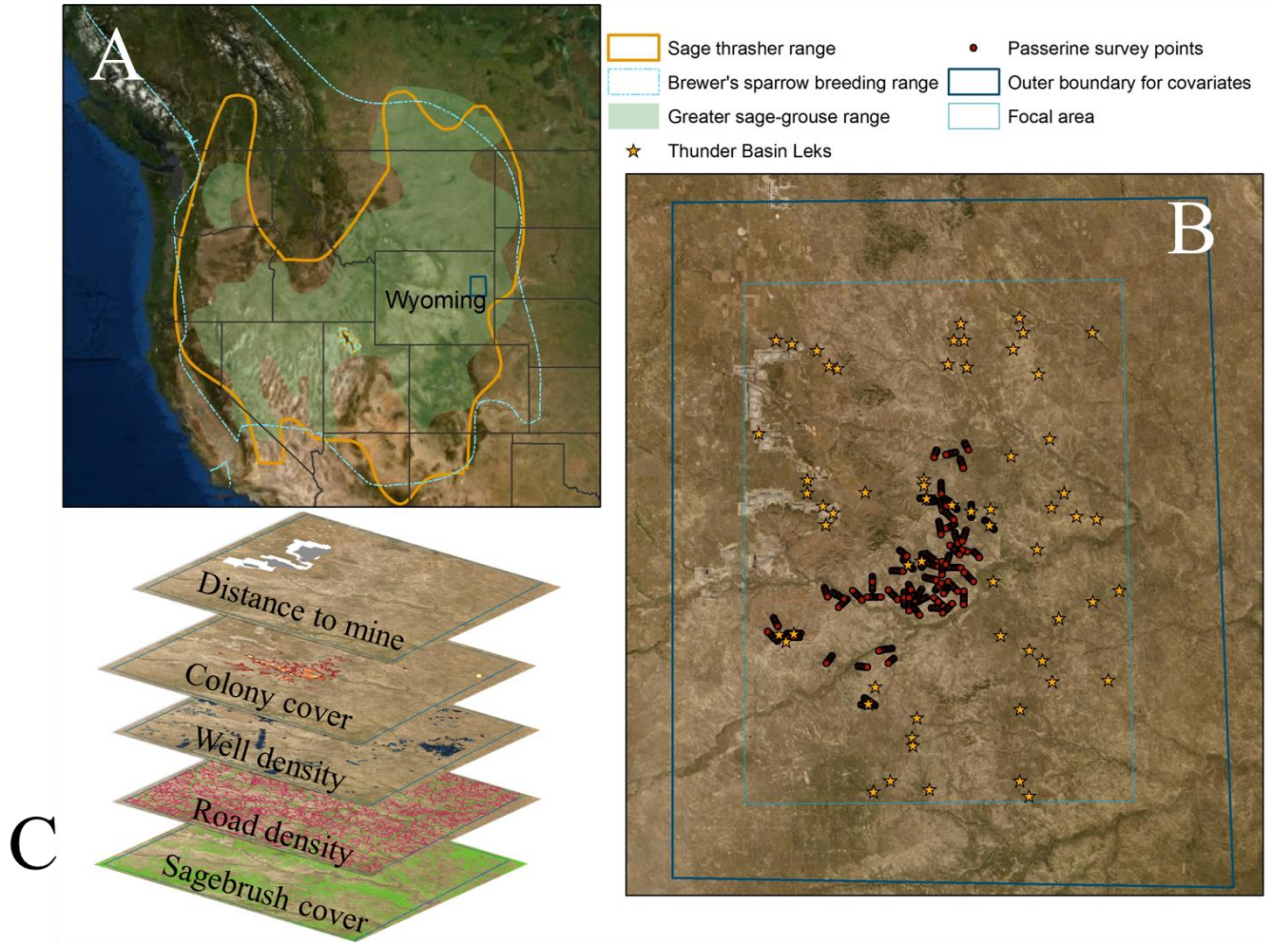
Table 2. Results of model selection process for models predicting greater sage-grouse lek attendance within the Thunder Basin National Grassland, Wyoming, USA, 1999–2018. We present the top three models among all combinations of landscape variables, anthropogenic disturbance variables, and natural disturbance variables (Step 1), as well as the best model generated from examining all possible combinations of Step 1 top models (Step 2).

Model	QIC	ΔQIC	w
Step 1			
Top Landscape			
Sagebrush cover (5km)+Topographic roughness^2	-5726.29	0	1
Sagebrush cover (5km)+Topographic roughness	-5682.65	43.64	0.00
Sagebrush cover (5km)	-5666.35	59.94	0.00
Top Anthropogenic Disturbance			
Distance to mine +Road1km^2 + Well Density Class 5k[0,1,2,3]	-6099.61	0	1
Road1km^2 +Well Density Class 5k[0,1,2,3]	-6050.36	49.24	0.00
Distance to mine + road5km^2 +Well Density Class 5k[0,1,2,3]	-6002.26	97.34	0.00
Top Natural Disturbance			
pdog 500m[0,1]	-5517.34	0	0.81
pdog5km[0,1,2]	-5514.42	2.92	0.23
Null	-5501.97	15.37	0.00
Step 2			
Sagebrush cover (5km)+Topographic roughness^2+Pdog 500m[0,1]t+Distance to mine + Road1km^2+Well Density Class 5k[0,1,2,3]	**-6506.56**	**0**	**1.00**

Table 3. Results of model selection process for models predicting Brewer's sparrow abundance and sage thrasher presence within the Thunder Basin National Grassland, USA, 2015–2017. We present the top three models among all combinations of local variables, landscape variables, anthropogenic disturbance variables, and natural disturbance variables (Step 1), as well as the best model(s) generated from examining all possible combinations of Step 1 top models (Step 2).

Brewer's Sparrow					**Sage Thrasher**				
Model	AICc	ΔAICc	K	*weight*	Models	AICc	ΔAICc	K	*weight*
Step 1					*Step 1*				
Local					*Local*				
Sagebrush + Litter + Herbaceous canopy + Cactus	10462.8	0.0	6	0.85	Sagebrush + Litter	520.4	0.0	4	0.26
Sagebrush + Litter + Herbaceous canopy	10466.3	3.5	5	0.15	Sagebrush + Bare	521.8	1.5	4	0.12
Sagebrush + Bare + Herbaceous canopy + Cactus	10519.2	56.3	6	0.00	Sagebrush + Litter +Canopy	522.1	1.8	5	0.11
Landscape					*Landscape*				
Sagebrush cover (250m) + Topographic roughness^2 + Year	10614.6	0.0	7	1.00	Sage cover (1km) + Topographic roughness	548.1	0.0	6	0.26
Sagebrush cover (250m) + Topographic roughness+ Year	10638.6	24.1	6	0.00	Sage cover (500m)+ Topography	549.0	0.9	6	0.16
Sagebrush cover (250m) + Year	10639.9	25.4	5	0.00	Sage cover (250m)+ Topographic roughness	549.3	1.2	6	0.14
Anthropogenic Disturbance					*Anthropogenic Disturbance*				
Wellcat(500m) + Roads(1km)^2	11905.2	0.0	5	0.99	Null	558.2	0.0	2	0.13
Wellcat(500m) + Roads(1km)	11915.3	10.1	4	0.01	Roads (250m)	558.7	0.5	3	0.10
Wellcat(500m) + Roads(500)^2	11933.1	27.9	5	0.00	Wellcat(500m)	559.5	1.3	3	0.07
Natural Disturbance					*Natural Disturbance*				
Long term prairie dog disturbance (0,1)	10975.8	0.0	3	1.00	Long term prairie dog disturbance (0,1)	550.3	0.0	3	0.95
Current prairie dog disturbance (0,1)	11477.3	501.4	3	0.00	Prairie dog disturbance (0,1)	557.4	7.1	3	0.03
Null	12157.4	1181.5	2	0.00	Null	558.2	7.9	2	0.02
Step 2					*Step 2*				
Long term prairie dog disturbance (0,1) + Wellcat(500m) + Roads(1km)^2+ Sagebrush cover (250m) + Topographic roughness^2 + Year + Sagebrush + Litter + Herbaceous canopy + Cactus	**9323.5**	**0.0**	**15**	**1.00**	**Sagebrush cover (1km) + Topographic roughness+Year +Sagebrush+Litter+**	**510.9**	**0.0**	**8**	**0.67**
					Long term prairie dog disturbance (0,1)+Sagebrush cover (1km) + Topographic roughness+Year +Sagebrush+Litter+	512.4	1.5	9	0.32

Figure 1. Study area and design focusing on sagebrush birds within the Thunder Basin National Grassland (TBNG). (A) Range of three focal sagebrush species, including location of the TBNG. (B). Location of passerine survey points and sage grouse leks within the TBNG. (C) Overlaying spatial layers used in assessing sagebrush bird habitat use.



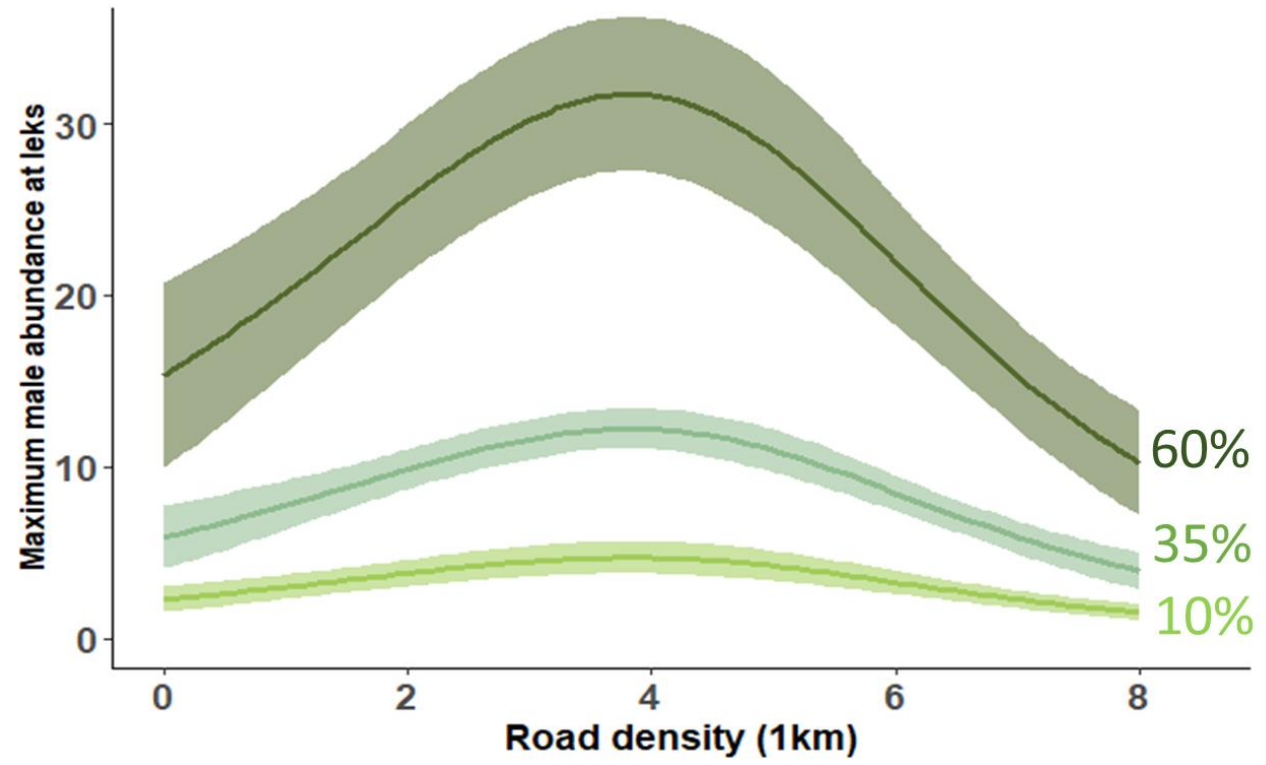


Figure 2. Trends in maximum lek attendance as a function of road density within 1 km of a lek and three levels of sagebrush cover at 5km in the Thunder Basin National Grassland 1999–2018

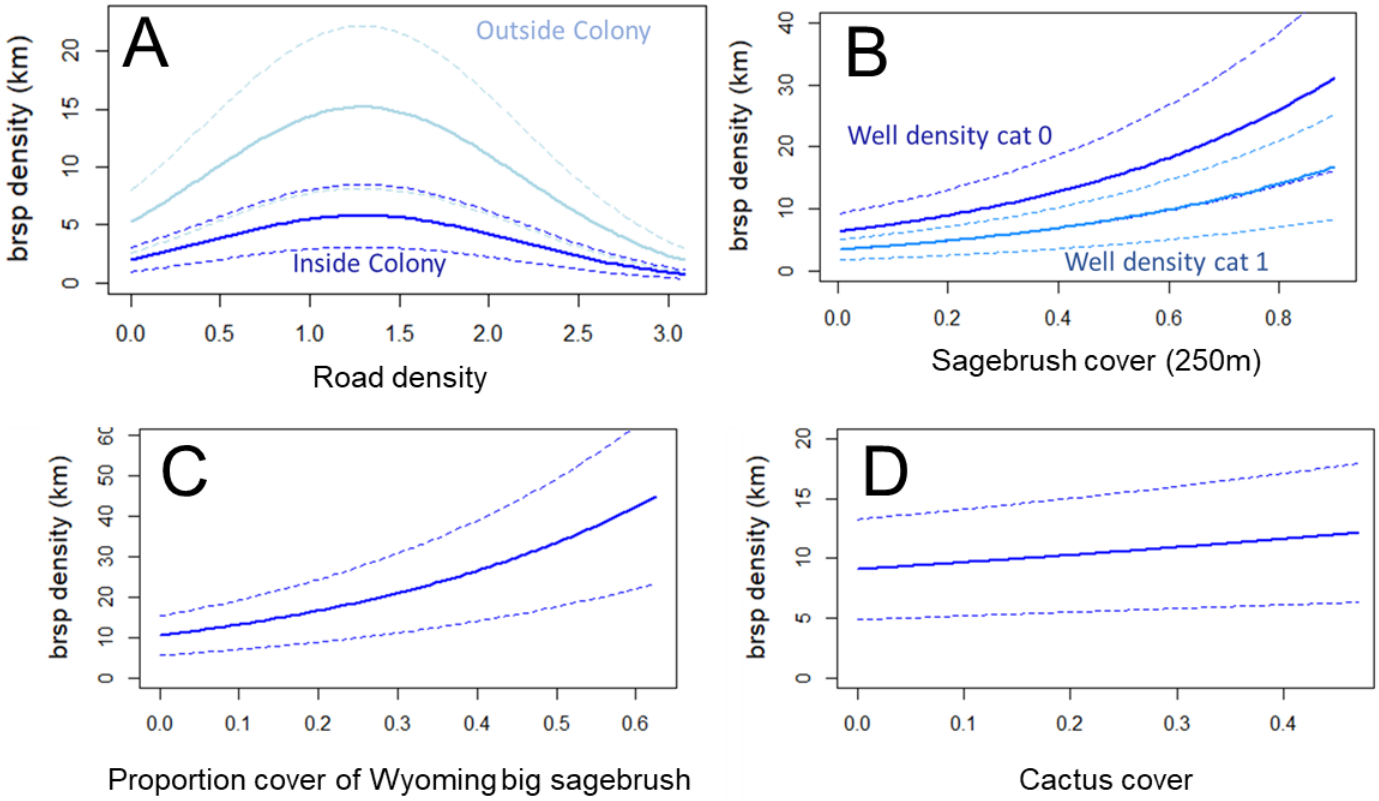


Figure 3. Effects of prairie dogs and road density (A), well density and landscape sagebrush cover (B), local cover of big sagebrush (C) and cactus cover (D) on Brewer's sparrow density within the Thunder Basin National Grassland, USA, 2015–2017.

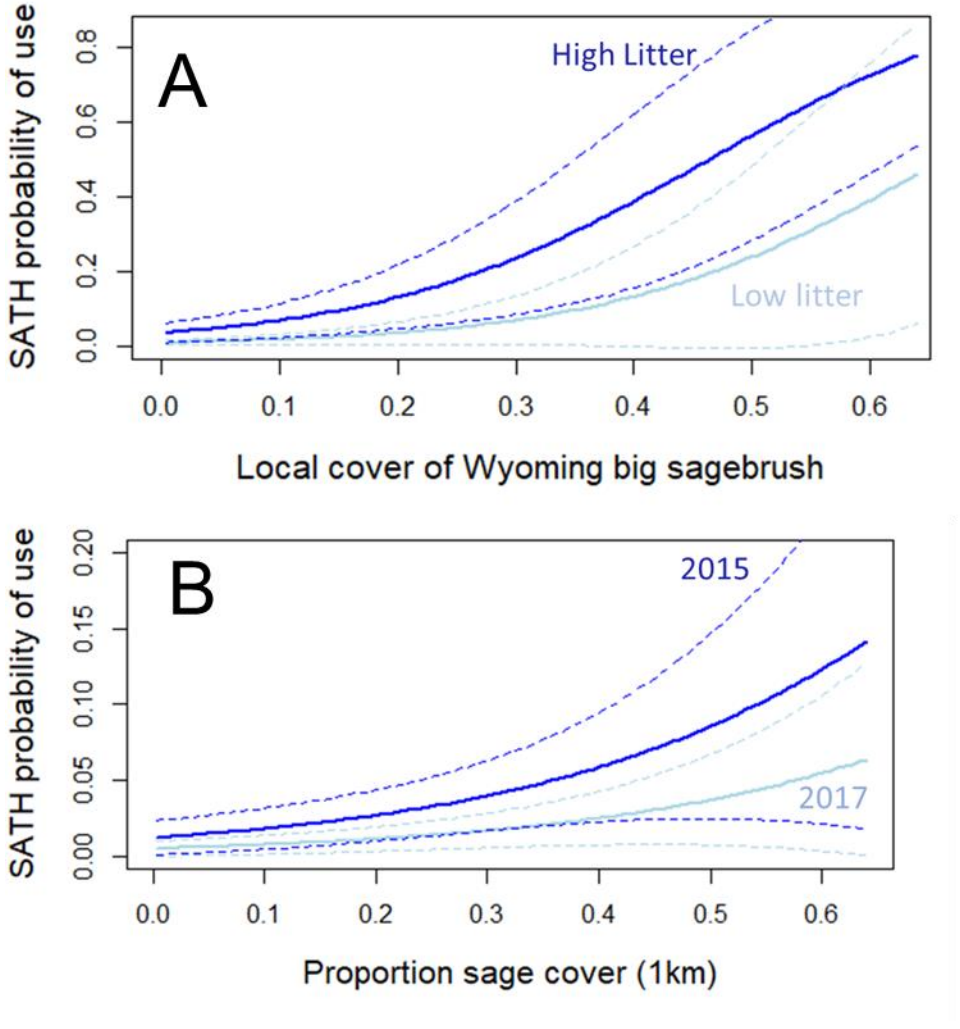


Figure 4. Effect of local sagebrush and litter cover (A) and sagebrush within 1 km and year (B) on sage thrasher presence/absence within the Thunder Basin National Grassland, USA, 2015–2017.

Chapter 6. CONCLUSIONS

As stated in the initial summary of this document, my dissertation was intended to provide a better understanding of the habitat requirements and disturbance tolerances of both grassland and sagebrush birds within the ecotonal landscape of the U. S. Forest Service–Thunder Basin National Grassland of northeastern Wyoming. The proximate application of this research was to inform both managers and citizens in the region of habitat requirements and tolerances of each avian species, with a goal of managing the landscape for long-term sustainability of all target populations.

In many ways this research has already achieved a number of these goals. One of the driving questions in this system concerned the nature of potential conflict between grassland and sagebrush (*Artemisia* spp.) birds. While we found that locally (and only with sustained pressure) prairie dogs decrease habitat suitability for sagebrush songbirds, landscape aspects of black-tailed prairie dog (*Cynomys ludovicianus*) disturbance appear to be comparatively less important. Further, because of very limited overlap between greater sage-grouse (*Centrocercus urophasianus*) and prairie dogs in this system, we found little evidence of reduced grouse habitat quality with increasing prairie dogs. Even more surprisingly, we found that a disturbance-obligate bird, the mountain plover, may actually prefer to breed on colonies of a moderate size as compared to extremely large (>1000 ha) colonies. Complexes of multiple colonies of this size would benefit mountain plover and still provide adequate habitat if black-footed ferrets (*Mustela nigripes*) are reintroduced in the future, while maintaining adequate uncolonized areas to benefit both sagebrush birds and grazing.

Although we found less impacts of prairie dogs than expected, we were unable to account for any potential effects from long-term (>20 years) prairie dog inhabitation in the region. It is possible that core prairie dog areas can support sagebrush, but have been clipped so consistently

that sagebrush is now relatively rare. One potential way to examine this would be to generate sagebrush suitability models throughout the Thunder Basin; although protection of existing sagebrush is the highest priority, reintroduction of sagebrush in certain areas may be considered in the future, and an understanding of suitability across the landscape may be useful.

Finally, although not detailed within my dissertation, following data collection in 2017 prairie dogs experienced an extreme plague event in this system. Only one year later, bird communities changed drastically (unpublished data). By 2019, many sites had experienced complete avian community turnover. Our work through 2017 gave us a better sense of avian community structure on functioning black-tailed prairie dog colonies—future work will focus on how quickly this community structure is altered following plague, and broadly aid in our understanding of keystone disturbance processes in rangeland ecosystems.

APPENDIX

CHAPTER 2

Table S1. Raw counts of 50 species observed on point counts in the Thunder Basin National Grassland, Wyoming, USA, 2016–2017. Species used for modeling are in bold. Asterisks indicate Wyoming-designated Species of Greatest Conservation Need. Parentheses represent the number of points surveyed

		2016				**2017**			
		Colony		Fire		Colony		Fire	
Common name	Scientific name	Inside (40pts)	Outside (40pts)	Inside (37 pts)	Outside (37 pts)	Inside (40pts)	Outside (40pts)	Inside (37 pts)	Outside (37 pts)
American Kestrel**	*Falco sparverius*			1		2	4	2	3
American Robin	*Turdus americanus*								1
Bald Eagle**	*Haliaeetus leucocephalus*								1
Barn Swallow	*Hirundo rustica*			1	2				1
Black-billed Magpie	*Pica hudsonia*		7			1		2	1
Brown-headed Cowbird	*Molothrus ater*		1	1	11			1	
Brewer's Blackbird	*Euphagus cyanocephalus*	9	2	5	3	10	9	13	5
Brewer's Sparrow**	***Spizella brewerii***	**6**	**23**	**3**	**41**	**6**	**53**	**14**	**57**
Bullock's Oriole	*Icterus bullockii*					1	2		
Burrowing Owl**	*Athene cunicularia*					2			
Canada Goose	*Branta canadensis*								1
Chipping Sparrow	*Spizella passerina*					1		1	
Cliff Swallow	*Petrochelidon pyrrhonota*	2			1		1	6	6
Common Grackle	*Quiscalus quiscula*		3			3	3	4	
Common Nighthawk**	*Chordeiles minor*		7	6	3		3	1	
Eastern Kingbird	*Tyrannus tyrannus*			1			3	1	1
European Starling	*Sturnus vulgaris*					1	4	3	1
Ferruginous Hawk**	*Buteo regalis*	1	1	1		1	2	1	1
Gadwall	*Anas strepera*				4				
Golden Eagle**	*Aquila chrysaetos*		1	2		1	4	2	1
Grasshopper Sparrow**	***Ammodramus savannarum***		**2**	**8**	**4**		**4**	**11**	**6**
Horned Lark	***Eremophila alpestris***	**90**	**13**	**50**	**36**	**136**	**27**	**41**	**16**

Killdeer	*Charadrius vociferus*	3		1	5	7	5	1	1
Lark Bunting	***Calamospiza melanocorys***	**4**	**11**	**28**	**42**	**19**	**41**	**73**	**75**
Lark Sparrow	***Chondestes grammacus***		**19**	**1**	**3**		**25**		**5**
Long-billed Curlew**	*Numenius americanus*					1			
Loggerhead Shrike**	***Lanius ludovicianus***		**4**	**2**		**5**	**9**	**2**	**3**
Mallard	*Anas platyrhynchos*					3		2	1
McCown's Longspur**	*Calcarius mccownii*			2	1			3	3
Mountain bluebird	*Sialia currucoides*			1	2			3	
Mourning Dove	***Zenaida macroura***	**4**	**4**	**3**	**8**	**7**	**6**	**2**	**2**
Mountain Plover**	***Charadrius montanus***	**8**				**42**			
Northern Flicker	*Colaptes auratus*	3	4	2	5		3	3	1
Northern Harrier	*Circus cyaneus*			1	1		3		
Northern Mockingbird	*Mimus polyglottos*						1		
Red-headed Woodpecker**	*Melanerpes erythrocephalus*	1							
Rock Wren	*Salpinctes obsoletus*		1				3		
Red-tailed Hawk	*Buteo jamaicensis*			2			2	2	
Red-winged Blackbird	*Agelaius phoeniceus*				1	4	1	1	
Say's Phoebe	*Sayornis saya*		1	1				2	1
Sage Thrasher**	***Oreoscoptes montanus***	**3**	**4**	**1**			**8**	**1**	**3**
Short-eared Owl**	*Asio flammeus*				1				
Swainson's Hawk**	*Buteo swainsoni*			1	1				
Tree Swallow	*Tachycineta bicolor*			1			1	3	
Turkey Vulture	*Cathartes aura*						1		1
Upland Sandpiper**	*Bartramia longicauda*							2	1
Vesper Sparrow	***Pooecetes gramineus***		**9**	**2**	**5**	**1**	**16**	**4**	**10**
Western Kingbird	*Tyrannus verticalis*		2		3	2	3	3	
Western Meadowlark	***Sturnella neglecta***	**32**	**73**	**78**	**69**	**113**	**214**	**91**	**71**
Western Wood-pewee	*Contopus sordidulus*								1

Table S2. Relative abundance and conservation ranking of 11 species included in analysis of Thunder Basin bird community 2016-2017. International Union for Conservation of Nature (IUCN) Red List species, Wyoming Species of Greatest Conservation Need (SGCN), U.S. Forest Service Sensitive Species, and multiple metrics from Partner's in Flight. Partners in Flight metrics include species of regional concern, common birds in steep decline, and the percentage of each species breeding range within the Thunder Basin bird conservation region (region 17).

Common name	Relative abundance across all point counts (%)	IUCN Red List	WY Species of Greatest Conservation Need	U.S. Forest Service Sensitive Species	Partners in Flight Rankings			
					Regional Concern	*% Breeding range in BCR 17 Badlands and Prairies*	*Common bird in steep decline*	*Est. Global pop.*
Brewer's Sparrow	*10.6%*		Y	Y	Y	3.3%	Y	16 mil
Grasshopper Sparrow	*1.8%*		Y	Y	Y	17.4%	Y	32 mil
Horned Lark	*21.4%*					5.3%	Y	140 mil
Lark Bunting	*15.3%*				Y	48.2%	Y	10 mil
Lark Sparrow	*2.8%*				Y	8.7%		11 mil
Loggerhead Shrike	*1.3%*		Y	Y		5.7%	Y	4.9 mil
Mourning Dove	*1.9%*					4.4%		150 mil
Mountain Plover	*2.6%*	Near-Threatened	Y	Y	Y*	NA*		20 thou
Sage Thrasher	*1.0%*		Y		Y	0.7%		6.6 mil
Vesper Sparrow	*2.5%*				Y	11.0%		34 mil
Western Meadowlark	*38.8%*					47.4%		98 mil

**Partners in flight does not have regional-level data for non-passerine species*

CHAPTER 3

Appendix 1. Average values (and standard errors) for nine variables representing vegetation structure and composition on and off current and historic colonies in the Thunder Basin National Grassland.

Variable	Inside Colony (SE)	Outside Colony (SE)	Inside Colony 2014 (SE)	Outside Colony 2014 (SE)
Percent Bare Ground	53.57 (0.96)	45.23 (1.08)	57.08 (1.04)	44.75 (0.96)
Visual Obstruction	2.72 (0.12)	6.28 (0.21)	2.17 (0.09)	5.84 (0.18)
Percent C3P Grass	23.12 (0.71)	30.57 (0.73)	23.3 (0.83)	28.73 (0.65)
Percent C4P Grass	14.08 (0.65)	28.88 (0.85)	12.52 (0.73)	26.54 (0.74)
Percent *Bromus* spp.	3.23 (0.37)	8.74 (0.6)	1.98 (0.33)	8.33 (0.52)
Percent C3A Grass	2.83 (0.32)	6.21 (0.51)	2.3 (0.3)	5.8 (0.44)
Percent Forb	16.91 (0.69)	7.02 (0.36)	19.82 (0.81)	7.31 (0.37)
Percent Sagebrush	1.51 (0.17)	8.4 (0.37)	0.63 (0.1)	7.41 (0.31)
Percent Cactus	5.14 (0.28)	2.65 (0.14)	5.15 (0.27)	3.22 (0.21)

CHAPTER 4

Appendix 1. Average raw variable values at point count locations where mountain plovers were absent or present in the Thunder Basin National Grassland, USA, 2015–2017.

Variable	Average absent (SE)	Average present (SE)
Maximum vegetation height (cm)	10.58 (0.30)	7.13 (0.43)
Visual obstruction (cm)	2.88 (0.13)	1.85 (0.16)
Bare ground (%)	0.51 (0.01)	0.63 (0.02)
Colony age	4.59 (0.12)	6.43 (0.24)
Colony area (ha)	1794.38 (63.37)	1385.2 (118.03)
Topographic roughness	0.94 (0.02)	0.73 (0.04)
Annual forb (%)	0.11 (0.01)	0.18 (0.02)
C3 perennial grass (%)	0.24 (0.01)	0.21 (0.02)
Clay (%)	0.77 (0.01)	0.84 (0.01)
Cactus cover (%)	0.05 (0.002)	0.04 (0.01)
C3 Annual grass (%)	0.03 (0.004)	0.01 (0.004)
Shrub cover (%)	0.02 (0.002)	0.01 (0.002)
C4 perennial grass (%)	0.15 (0.01)	0.1 (0.01)
Distance to colony edge (m)	312.28 (12.56)	360.93 (20.20)
Silt (%)	0.48 (0.005)	0.5 (0.01)
Sand (%)	0.54 (0.01)	0.48 (0.01)

Appendix 2. Comparison of models adjusting for detectability of mountain plovers in the Thunder Basin National Grassland (2015-2017). The best model was determined to include a half-normal key function incorporating the effect of travel to the point using ATV and wind; although this model did not have the lowest AIC value, it had the lowest AIC value among models with acceptable goodness of fit (GOF Chi-p). Models with unacceptable GOF are shown in bold.

Covariates	Key Function	Expansions examined	# params	Delta AIC	AIC	ESW/ EDR	GOF Chi-p
ATV (0,1) + Wind + Sky (clear, partly cloudy, mostly cloudy, overcast)	Hazard rate	Cosine, Simple polynomial	7	0	1110.63	142.85	**0.02**
ATV (0,1) + Wind + Sky (clear, partly cloudy, mostly cloudy, overcast)	Half-normal	Cosine, Hermite polynomial	6	1.14	1111.77	123.98	**0.02**
Wind + Sky (clear, partly cloudy, mostly cloudy, overcast)	Hazard rate	Cosine, Simple polynomial	6	2.17	1112.80	140.93	**0.07**
Wind + Sky (clear, partly cloudy, mostly cloudy, overcast)	Half-normal	Cosine, Hermite polynomial	5	4.17	1114.80	125.23	**0.05**
ATV (0,1) + Wind	Half-normal	Cosine, Hermite polynomial	3	4.27	1114.90	126.35	0.19
Wind	Half-normal	Cosine, Hermite polynomial	2	5.48	1116.11	127.01	0.29
Sky (clear, partly cloudy, mostly cloudy, overcast)	Hazard rate	Cosine, Simple polynomial	5	6.93	1117.56	144.46	0.10
Sky (clear, partly cloudy, mostly cloudy, overcast)	Half-normal	Cosine, Hermite polynomial	4	7.71	1118.34	126.70	0.12
ATV (0,1)	Half-normal	Cosine, Hermite polynomial	2	11.58	1122.21	128.51	0.30
	Hazard rate	Cosine, Simple polynomial	2	11.98	1122.61	141.13	0.69
	Half-normal	Cosine, Hermite polynomial	1	13.17	1123.80	129.22	0.40

Visual obstruction	Hazard rate	Cosine, Simple polynomial	3	14.45	1125.08	136.68	0.49
Wind	Hazard rate	Cosine, Simple polynomial	3	14.45	1125.08	136.68	0.49
Visual obstruction	Half-normal	Cosine, Hermite polynomial	3	14.45	1125.08	136.68	0.49
Temperature	Hazard rate	Cosine, Simple polynomial	3	14.45	1125.08	136.68	0.49
ATV (0,1)	Hazard rate	Cosine, Simple polynomial	3	14.45	1125.08	136.68	0.49
Temperature	Half-normal	Cosine, Hermite polynomial	2	15.07	1125.70	129.18	0.30
ATV (0,1) + Wind	Hazard rate	Cosine, Simple polynomial	4	16.45	1127.08	136.68	0.35

Appendix 3. Model rankings of all univariate and "literature" models of Mountain Plover density – univariate and quadratic models include both zero-inflated and conditional models ("c" indicates the conditional portion of the model while "zi" represents the zero inflated portion). Variables were examined in each portion of the model separately.

Model	**Model Type**	**AICc**	**ΔAICc**	**k**	***weight***
Colony Age^2(zi)	Quadratic	917.83	0	6	0.76
Colony Age (zi)	Univariate	920.17	2.34	5	0.24
Distance to colony edge ^{2} (zi)	Quadratic	927.90	10.07	6	0
Colony age^2 (c)	Quadratic	929.53	11.70	6	0
Max. Vegetation Height (zi)	Univariate	931.90	14.06	5	0
Visual obstruction + Bare ground (zi)	Literature model (zi)	933.59	15.75	6	0
Colony Age	Univariate	937.70	19.86	5	0
Visual obstruction + Bare ground (c)	Literature model (c)	939.95	70.64	6	0
Distance to colony edge^2 (c)	Quadratic	942.05	24.22	6	0
Max. vegetation height (c)	Univariate	942.56	24.73	5	0
Annual forb (zi)	Univariate	943.18	25.34	5	0
Visual obstruction (zi)	Univariate	943.21	25.38	5	0
Bare ground (zi)	Univariate	943.38	25.54	5	0
Clay (c)	Univariate	944.10	26.27	5	0
Sand (c)	Univariate	945.87	28.03	5	0
Visual obstruction (c)	Univariate	948.10	30.27	5	0
Bare Ground (c)	Univariate	948.19	30.36	5	0
C3 annual grass (c)	Univariate	948.50	30.67	5	0
Topographic roughness (zi)	Univariate	949.70	31.86	5	0
C3 annual grass (zi)	Univariate	949.94	32.10	5	0
Sand (zi)	Univariate	950.20	32.36	5	0
Colony Area (c)	Univariate	950.97	33.13	5	0
Topographic roughness (c)	Univariate	951.42	33.58	5	0
Clay (zi)	Univariate	951.99	34.15	5	0
Colony Area^2(c)	Quadratic	952.54	34.71	6	0
C4 perennial grass (zi)	Univariate	953.11	35.28	5	0
Annual forb (c)	Univariate	953.67	35.83	5	0
C4 perennial grass (c)	Univariate	955.23	37.40	5	0
Year (c)	Univariate	956.05	38.22	6	0
Shrub (c)	Univariate	956.47	38.64	5	0
Distance to colony edge (zi)	Univariate	957.30	39.46	5	0
Silt (zi)	Univariate	957.48	39.65	5	0
C3 perennial grass (c)	Univariate	958.36	40.53	5	0
Shrub (zi)	Univariate	958.75	40.91	5	0

Sub-shrub (zi)	Univariate	958.85	41.02	5	0
Silt (c)	Univariate	959.39	41.55	5	0
C3 perennial grass (zi)	Univariate	959.41	41.58	5	0
Null	Null	959.48	41.65	4	0
Colony Area (zi)	Univariate	959.94	42.11	5	0
Cactus (c)	Univariate	960.06	42.23	5	0
Cactus (zi)	Univariate	960.69	42.86	5	0
Sub-shrub (c)	Univariate	960.84	43.01	5	0
Distance to colony edge (c)		961.04	43.21	5	0
Colony area^2 (zi)	Quadratic	961.95	44.11	6	0
Year (zi)	Univariate	962.78	44.94	6	0

Appendix 4. AICc ranking of univariate and quadratic models explaining nest-site selection in Mountain Plovers. Numbers following model names indicate whether the variable represents the nest cup (1) or nest "site" (2). For measures of vegetation height and density, they represent nest cup (1), 5 m from the nest and 10 m from the nest.

Univariate model	**AICc**	**ΔAICc**	**k**	**w_i**
Maximum vegetation height (nest)	267.93	0	2	1
Maximum vegetation height (5m)	289.66	21.73	2	0
Maximum vegetation height (10m)	289.66	21.73	2	0
Visual obstruction (5m)	316.80	48.87	2	0
Visual obstruction (10m)	316.80	48.87	2	0
C4 perennial Grass (Nest)	328.88	60.95	2	0
Visual obstruction (Nest)	331.81	63.88	2	0
Shrub	344.65	76.72	2	0
Cactus	346.61	78.69	2	0
Bare ground (Nest Site)	349.65	81.72	2	0
C4 perennial grass (Nest Site)	351.81	83.88	2	0
C3 perennial grass (Nest)	352.06	84.13	2	0
Annual forb (Nest)	356.72	88.79	2	0
Annual forb (Nest Site)	363.24	95.31	2	0
Colony age^2	369.02	101.09	3	0
Bare ground (Nest)	372.69	104.76	2	0
Colony age	373.53	105.61	2	0
Topographic roughness	374.11	106.18	2	0
Sand	375.31	107.38	2	0
Clay	375.93	108.01	2	0
C3 perennial grass (Nest Site)	378.57	110.64	2	0
Distance to colony edge^2	380.88	112.95	3	0
Null	384.63	116.70	1	0
Silt	385.26	117.33	2	0
Sub-shrub	386.14	118.21	2	0
Distance to colony edge	386.58	118.65	2	0
Year	388.70	120.80	3	0

Appendix 5. AICc ranking of all models explaining nest success in mountain plovers. Table includes all univariate and quadratic temporal models predicting nest survival ("univariate") used in step 1, both global and reduced temporal models used in step 2, models including the best temporal model + single covariates of structure, a global model of structure and temporal variables, and finally a reduced model of temporal and structural variables. We also include a "literature model", as described in the text.

Model	Model type	AIC_c	ΔAIC_c	k	w_i
Cactus + Shrub + Colony age^2 + Nest age*Day of season + Maximum temperature + Thunder	Temporal + Structural (reduced)	460.20	0	10	0.64
Cactus + Shrub + Colony age ^{2}+ C3P (Site) + C4P (Nest) + Nest age*Day of season + Maximum temperature + Thunder	Temporal + Structural (global)	462.38	2.18	12	0.22
Cactus	Temporal + Cactus	464.02	3.83	7	0.09
Shrub	Temporal + Shrub	467.97	7.77	7	0.01
Colony age^2	Temporal + Colony age^2	470.76	10.57	8	0
C4 perennial (Nest site)	Temporal + C4 Perennial (Nest site)	471.49	11.29	7	0
C3 perennial (Nest site)	Temporal + C3 Perennial (Nest site)	471.63	11.44	7	0
Colony age	Temporal + Colony age	471.74	11.54	7	0
Nest age*Day of season + Maximum temperature + Thunder	Temporal reduced	471.99	11.79	6	0
Colony area^2	Temporal + Colony age^2	472.22	12.03	8	0
Visual obstruction (10m)	Temporal + Visual obstruction (10m)	472.25	12.06	7	0
Visual obstruction (Nest)	Temporal + Visual obstruction (Nest)	472.40	12.21	7	0
Visual obstruction (Nest Site)	Temporal + Visual obstruction (Nest Site)	472.54	12.34	7	0
Visual obstruction (5m)	Temporal + Visual obstruction (5m)	472.57	12.37	7	0
Maximum vegetation height (nest)	Temporal + Maximum vegetation Height (nest)	472.66	12.46	7	0
Colony area	Temporal + Colony area	472.71	12.51	7	0
C4 perennial (Nest)	Temporal + C4 Perennial (Nest)	472.91	12.71	7	0

Distance to colony edge	Temporal + Distance to colony edge	472.98	12.78	7	0
C3 perennial (Nest)	Temporal + C3 Perennial (Nest)	473.61	13.41	7	0
Sand	Temporal + Sand	473.91	13.72	7	0
Sub-shrub	Temporal + sub-shrub	473.95	13.75	7	0
Maximum vegetation height (5m)	Temporal + Maximum vegetation height (5m)	473.95	13.76	7	0
Silt	Temporal + Silt	473.98	13.78	7	0
Clay	Temporal + Clay	473.99	13.80	7	0
Annual forb (Nest)	Temporal + Annual Forb (Nest)	474.01	13.81	7	0
Maximum vegetation height (10m)	Temporal + Maximum vegetation height (10m)	474.01	13.81	7	0
Topographic roughness	Temporal + Topographic roughness	474.03	13.84	7	0
Year + Nest age*Day of season + Maximum temperature +Thunder	Temporal global	474.17	13.97	8	0
Distance to colony edge^2	Temporal + Distance to colony edge^2	474.26	14.06	8	0
Year	Univariate	474.86	14.67	3	0
Nest age * Day of season	Temporal interaction	476.18	15.98	4	0
Nest age * Day of season^2	Temporal interaction	477.17	16.97	4	0
Year * Day of season	Temporal interaction	477.57	17.37	6	0
Thunder	Univariate	477.66	17.46	2	0
Nest age*Year	Temporal interaction	478.49	18.29	6	0
Maximum temperature	Univariate	478.82	18.63	2	0
Day of season^2*Year	Temporal interaction	479.29	19.09	6	0
Null	Null	479.78	19.58	1	0
Day of season^2	Quadratic	480.39	20.19	2	0
Maximum temperature + Nest age + Day of season + Precipitation	Literature Model	480.64	20.45	5	0
Day of season	Univariate	480.66	20.47	2	0

Precipitation	Univariate	481.06	20.87	2	0
Nest age	Univariate	481.35	21.15	2	0
Hail	Univariate	481.78	21.58	2	0

Appendix 7. Univariate models differentiating between causes of nest failure, as well as global and reduced models of nest failure, ranked using AICc. Dataset includes only failed nests.

Model	**AICc**	**ΔAICc**	**k**	**w_i**
Maximum precipitation + Maximum temperature + Hail + C4 perennial grasses (nest site)	61.01	0	5	0.83
Maximum precipitation + Maximum temperature + Hail + Visual obstruction (nest) + Thunder + C4 perennial grasses (nest site)	64.26	3.24	7	0.17
Hail	77.95	16.93	2	0
Precipitation	82.08	21.06	2	0
Maximum temperature	84.28	23.27	2	0
Visual obstruction (nest)	85.25	24.23	2	0
C4 perennial (nest site)	86.05	25.04	2	0
Thunder	86.43	25.42	2	0
C3 perennial (nest site)	87.69	26.68	2	0
Annual forb (nest site)	88.29	27.27	2	0
Maximum vegetation height (nest)	88.99	27.98	2	0
Null	89.04	28.03	1	0
Colony age	89.17	28.16	2	0
C4 perennial (nest)	89.52	28.51	2	0
Colony size	89.54	28.53	2	0
Distance to colony edge^2	89.77	28.76	3	0
Visual obstruction (5m)	89.92	28.9	2	0
Cactus	89.96	28.95	2	0
Annual forb (nest)	89.98	28.97	2	0
C3 perennial grass (nest)	90.01	29	2	0
Date found	90.46	29.45	2	0
Visual obstruction (10m)	90.64	29.63	2	0
Bare ground (nest site)	90.73	29.71	2	0
Bare ground (nest)	91.11	30.1	2	0
Colony age^2	91.12	30.1	3	0
Maximum vegetation height (10m)	91.14	30.12	2	0
Maximum vegetation height (5m)	91.15	30.13	2	0
Distance to colony edge	91.15	30.14	2	0
Colony size^2	91.19	30.18	3	0
Shrub	91.42	30.4	2	0

CHAPTER 5

Appendix 1A. Results of model selection process for models predicting greater sage-grouse lek attendance within the Thunder Basin National Grassland, Wyoming, USA, 1999–2018.

Model	QIC	ΔQIC
Step 2		
Well density cat (5km) + Distance to mine + Road density^2 +Sagebrush cover (5km) + Topographic roughness^2 +Prairie dog colony cat 0.5km	-6506.56	0.00
Well density cat (5km) + Distance to mine + Road density^2 + Sagebrush cover (5km) + Topographic roughness^2	-6494.42	12.14
Prairie dog colony cat 0.5km+ Well density cat (5km) + Distance to mine + Road density^2	-6136.25	370.31
Well density cat (5km) + Distance to mine + Road density^2	-6099.61	406.95
Sagebrush cover (5km) + Topographic roughness^2 + Prairie dog colony cat 0.5km	-5733.74	772.82
Sagebrush cover (5km) + Topographic roughness^2	-5726.29	780.27
Prairie dog colony cat 0.5km	-5517.34	989.22
Null	-5501.97	1004.59
Step 1		
Anthropogenic Disturbance		
Well density cat (5km) + Distance to mine + Road density 1km^2	-6099.61	0.00
Well density cat (5km) + Road density 1km^2	-6050.36	49.24
Well density cat (5km) + Distance to mine + Road density 5km^2	-6002.26	97.34
Well density cat (5km) + Distance to mine^2 + Road density .5km	-5991.91	107.69
Well density cat (5km) + Distance to mine^2	-5975.03	124.57
Well density cat (5km) + Distance to mine^2 + Road density 1km	-5974.48	125.13
Well density cat (5km) + Distance to mine + Road density 5km	-5970.68	128.93
Well density cat (5km)+ Road density 5km^2	-5919.26	180.35

Well density cat (5km)+Distance to mine + Road density 1km	-5900.43	199.17
Well density cat (5km)+Distance to mine + Road density 0.5km	-5895.21	204.39
Well density cat (1km)+Distance to mine + Road density 5km^2	-5894.58	205.02
Well density cat (5km)+Distance to mine + Road density 0.5km^2	-5887.30	212.31
Well density cat (5km)+Distance to mine	-5883.26	216.35
Well density cat (5km)+Distance to mine + Road density 5km	-5880.40	219.20
Distance to mine + Road density 5km^2	-5870.40	229.20
Well density cat (1km)+Distance to mine + Road density 1km^2	-5870.23	229.37
Well density cat (5km)+ Road density 0.5km	-5854.47	245.14
Well density cat (5km)+ Road density 1km	-5854.47	245.14
Well density cat (5km)+ Road density 5km	-5854.47	245.14
Road density 1km+ Distance to mine	-5849.12	250.48
Well density cat (5km) + Road density 0.5km^2	-5846.88	252.72
Well density cat (0.5km) + Distance to mine +Road density 1km^2	-5843.92	255.69
Well density cat (0.5km)+Distance to mine^+ Road density 5km^2	-5843.09	256.52
Well density cat (5km)	-5842.26	257.34
Well density cat (1km)+ Road density 1km^2	-5743.59	356.01
Well density cat (1km)+Distance to mine^2 + Road density 0.5km	-5737.13	362.47
Road density 0.5km+ Distance to mine^2	-5726.96	372.65
Well density cat (1km)+ Road density 5km^2	-5723.47	376.14
Well density cat (1km)+Distance to mine	-5720.68	378.93
Well density cat (1km)+Distance to mine^2+Road density 5km	-5720.49	379.11
Distance to mine ^2	-5719.61	380.00

Road density 1km+ Distance to mine^2	-5718.53	381.08
Well density cat (1km)+Distance to mine^2 + Road density 1km	-5717.21	382.39
Road density 5km+ Distance to mine^2	-5716.43	383.18
Well density cat (1km)+Distance to mine + Road density 0.5km^2	-5709.91	389.69
Road density 0.5km^2	-5701.27	398.34
Well density cat (0.5km)+Distance to mine^2 + Road density 0.5km	-5699.68	399.92
Well density cat (1km)+Distance to mine + Road density 5km	-5689.26	410.35
Well density cat (1km)+Distance to mine	-5688.33	411.27
Well density cat (0.5km)+Distance to mine^2	-5682.53	417.07
Well density cat (0.5km)+Distance to mine^2 + Road density 5km	-5682.47	417.13
Well density cat (0.5km)+Distance to mine^2+ Road density 1km	-5679.84	419.77
Road density 1km+ Distance to mine	-5679.57	420.03
Road density 0.5km^2+ Distance to mine	-5676.75	422.85
Road density 0.5km+ Distance to mine	-5675.58	424.02
Distance to mine	-5669.64	429.96
Road density 0.5km^2	-5669.03	430.58
Road density 5km+ Distance to mine	-5666.00	433.61
Well density cat (0.5km)+Distance to mine + Road density 0.5km	-5658.05	441.55
Well density cat (0.5km)+ Road density 5km^2	-5657.72	441.88
Well density cat (0.5km)+Distance to mine + Road density 0.5km	-5657.06	442.54
Well density cat (0.5km)+Distance to mine^2 + Road density 1km	-5644.92	454.68
Well density cat (0.5km)^2	-5639.90	459.71
Well density cat (0.5km)+Distance to mine + Road density 5km	-5638.50	461.10
Well density cat (0.5km) + Road density 1km^2	-5611.68	487.93
Well density cat (1km)+ Road density 0.5km	-5597.67	501.93

Well density cat (1km)+ Road density 1km	-5597.67	501.93
Well density cat (1km)+ Road density 0.5km^2	-5592.34	507.27
Well density cat (1km)	-5568.46	531.15
Well density cat (0.5km)+ Road density 5km	-5564.12	535.49
Road density 1km	-5549.75	549.86
Well density cat (0.5km) + Road density 0.5km	-5512.87	586.74
Well density cat (0.5km) + Road density 1km	-5512.87	586.74
Road density 5km	-5511.53	588.07
Well density cat (0.5km) + Road density 0.5km^2	-5506.24	593.37
Road density 0.5km	-5505.17	594.43
Null	-5501.97	597.64
Road density 0.5km^2	-5498.74	600.86
Well density cat (0.5km) + Road density 5km	-5494.82	604.78
Well density cat (0.5km)	-5494.08	605.53
Landscape cover		
Sagebrush cover (5km) + Topographic roughness^2	-5726.29	0.00
Sagebrush cover (5km) + Topographic roughness	-5682.65	43.64
Sagebrush cover (5km)	-5666.35	59.94
Sagebrush cover (5km) + Topographic roughness	-5611.06	115.23
Sagebrush cover (0.5km) + Topographic roughness^2	-5607.06	119.23
Sagebrush cover (1km) + Topographic roughness^2	-5603.70	122.59
Sagebrush cover (0.5km) + Topographic roughness	-5571.67	154.62
Sagebrush cover (1km) + Topographic roughness	-5554.57	171.71
Topographic roughness	-5551.73	174.56
Sagebrush cover (0.5km)	-5522.19	204.10
Sagebrush cover (1km)	-5504.73	221.56
Null	-5501.97	224.32

Natural Disturbance		
Prairie dog colony cat 0.5km	-5517.34	0.00
Prairie dog colony cat 5km	-5514.42	2.92
Null	-5501.97	15.37
Prairie dog colony cat 1km	-5493.41	23.92
Distance to prairie dog colony^2	-5442.31	75.02
Distance to prairie dog colony	-5441.75	75.59

Appendix 1b. Results of model selection process for models predicting Brewer's sparrow within the Thunder Basin National Grassland, USA, 2015–2017.

Models	AICc	ΔAICc	K	weight
Step 2				
Long term prairie dog disturbance (0,1)+Wellcat(500m) + Road density(1km)^2+Sagebrush cover (250m) + Topographic roughness^2+Sagebrush+Litter+Herbaceous canopy + Cactus	9323.48	0.00	15	1.00
Long term prairie dog disturbance (0,1)+Sagebrush cover (250m) + Topographic roughness^2+Sagebrush+Litter+Herbaceous canopy + Cactus	9528.49	205.01	12	0.00
Sagebrush cover (250m) + Topographic roughness^2+Sagebrush+Litter+Herbaceous canopy + Cactus + Wellcat(500m) + Road density(1km)^2	9698.56	375.09	14	0.00
Long term prairie dog disturbance (0,1)+Wellcat(500m) + Road density(1km)^2+ Sagebrush + Litter + Herbaceous canopy + Cactus	9801.45	477.97	10	0.00
Year + Sagebrush cover (250m) + Topographic roughness^2+ Long term prairie dog disturbance (0,1)+Sagebrush cover (250m) + Topographic roughness^2	9905.30	581.83	8	0.00
Year + Sagebrush cover (250m) + Topographic roughness^2+ Sagebrush + Litter + Herbaceous canopy + Cactus	9932.43	608.95	11	0.00
Sagebrush + Litter + Herbaceous canopy + Cactus +Long term prairie dog disturbance (0,1)	10000.28	676.80	7	0.00
Sagebrush + Litter + Herbaceous canopy + Cactus +Wellcat 500m + Road density 1km^2	10243.17	919.70	9	0.00
Year + Sagebrush cover (250m) + Topographic roughness^2 +Wellcat 500m + Road density 1km^2	10375.42	1051.94	10	0.00
Year + Sagebrush cover (250m) + Topographic roughness^2 +Long term prairie dog disturbance (0,1) +Wellcat 500m + Road density 1km^2	10375.42	1051.94	10	0.00
Sagebrush + Litter + Herbaceous canopy + Cactus	10467.49	1144.01	6	0.00

Year + Sagebrush cover (250m) + Topographic roughness^2	10614.55	1291.07	7	0.00
Long term prairie dog disturbance (0,1)	10975.85	1652.37	3	0.00
Wellcat 500m + Road density 1km^2	11905.20	2581.72	5	0.00
Wellcat 500m + Road density 1km^2 +Long term prairie dog disturbance (0,1)	11905.20	2581.72	5	0.00
Null	12157.39	2833.91	2	0.00

Step 1

Local Vegetation

Sagebrush + Litter + Herbaceous canopy + Cactus	10462.83	0.00	6	0.85
Sagebrush + Litter + Herbaceous canopy	10466.32	3.48	5	0.15
Sagebrush + Bare + Herbaceous canopy + Cactus	10519.18	56.35	6	0.00
Sagebrush + Bare + Herbaceous canopy	10523.28	60.44	5	0.00
Shrub + Litter + Herbaceous canopy + Cactus	10526.65	63.82	6	0.00
Shrub + Litter + Cactus	10532.30	69.46	5	0.00
Sagebrush + Cactus + Herbaceous canopy	10547.83	84.99	5	0.00
Sagebrush + Herbaceous canopy	10548.43	85.59	4	0.00
Shrub +Bare + Canopy + Cactus	10588.69	125.86	6	0.00
Shrub+ Bare + Cactus	10594.45	131.61	5	0.00
Shrub + Cactus + Canopy	10615.92	153.08	5	0.00
Shrub + Canopy	10617.62	154.78	4	0.00
Visual obstruction + Litter + Herbaceous canopy	10763.15	300.32	5	0.00
Visual obstruction + Litter + Herbaceous canopy + Cactus	10763.51	300.68	6	0.00
Visual obstruction + Bare ground +Herbacous canopy	10818.16	355.33	5	0.00
Visual obstruction + Bare + Cactus + Herbaceous canopy	10818.86	356.02	6	0.00
Visual obstruction + Herbaceous canopy	10826.95	364.12	4	0.00
Visual obstruction + Cactus + Herbaceous canopy	10828.57	365.74	5	0.00
Shrub + Bare	10992.63	529.79	4	0.00
Sagebrush + Cactus	10998.80	535.97	4	0.00
Cactus	10998.80	535.97	4	0.00
Sagebrush + Litter	11009.12	546.28	4	0.00
Sagebrush	11011.30	548.46	3	0.00
Shrub+ Bare	11050.07	587.24	4	0.00
Shrub +Cactus	11053.72	590.88	4	0.00
Visual obstruction + Litter	11059.54	596.71	4	0.00
Shrub + Litter	11066.21	603.38	4	0.00
Bare ground	11068.38	605.54	4	0.00
Visual obstruction + Cactus	11068.78	605.94	4	0.00
Shrub	11069.35	606.52	3	0.00

Visual obstruction	11074.57	611.74	3	0.00
Herbaceous canopy	11442.83	980.00	3	0.00
Bare	12016.11	1553.27	3	0.00
Litter	12111.08	1648.24	3	0.00
Null	12157.39	1694.55	2	0.00
Landscape				
Year + Sagebrush cover (250m) + Topographic roughness^2	10614.55	0.00	7	1.00
Year +Sagebrush cover (250m) + Topographic roughness	10638.64	24.09	6	0.00
Year +Sagebrush cover (250m)	10639.91	25.36	5	0.00
Year +Sagebrush cover (500m) + Topographic roughness^2	11493.00	878.45	7	0.00
Year +Sagebrush cover (500m)	11512.54	897.99	5	0.00
Sagebrush cover (500m) + Topographic roughness	11513.37	898.82	6	0.00
Year +Sagebrush cover (1km) + Topographic roughness ^2	11695.60	1081.05	7	0.00
Year +Topographic roughness ^2	11696.39	1081.84	6	0.00
Year +Sagebrush cover (1km) + Topographic roughness	11722.08	1107.53	6	0.00
Year +Topographic roughness	11725.29	1110.74	5	0.00
Year +Sagebrush cover (1km)	11730.59	1116.04	5	0.00
Year	11734.52	1119.97	4	0.00
Null	12157.39	1542.84	2	0.00
Natural Disturbance				
Long term prairie dog disturbance (0,1)	10975.85	0.00	3	1.00
Current prairie dog disturbance (0,1)	11477.28	501.44	3	0.00
Null	12157.39	1181.54	2	0.00
Anthropogenic disturbance				
Wellcat 500m + Road density 1km^2	11905.20	0.00	5	0.99
Wellcat 500m + Road density 1km	11915.27	10.07	4	0.01
Wellcat 500m + Road density 500m^2	11933.09	27.90	5	0.00
Wellcat 500m + Road density 500m	11958.22	53.03	4	0.00
Wellcat 500m + Road density 250m	12017.28	112.08	4	0.00
Wellcat 500m + Road density 250m^2	12019.12	113.92	5	0.00
Wellcat 1km + Road density 1km^2	12022.43	117.23	5	0.00
Wellcat 250m + Road density 1km^2	12023.42	118.22	5	0.00
Wellcat 500m	12023.55	118.35	3	0.00
Road density 1km^2	12025.99	120.79	4	0.00
Wellcat 1km + Road density 1km	12030.26	125.06	4	0.00

Wellcat 250m + Road density 1km	12031.75	126.55	4	0.00
Wellcat 1km + Road density 500m^2	12033.02	127.82	5	0.00
Road density 1km	12034.03	128.83	3	0.00
Road density 500km^2	12043.71	138.51	4	0.00
Wellcat 250m + Road density 500m^2	12044.92	139.72	5	0.00
Wellcat 1km + Road density 500m	12059.60	154.41	4	0.00
Road density 500km	12069.38	164.18	3	0.00
Wellcat 250m + Road density 500m^2	12070.25	165.05	4	0.00
Wellcat 1km + Road density 250m	12129.63	224.43	4	0.00
Wellcat 1km + Road density 250m^2	12129.71	224.52	5	0.00
Wellcat 250m + Road density 250m	12136.98	231.79	4	0.00
Wellcat 250m + Road density 250m^2	12138.09	232.89	5	0.00
Road density 250km	12139.11	233.92	3	0.00
Road density 250km^2	12139.93	234.73	4	0.00
Wellcat 1km	12149.34	244.15	3	0.00
Wellcat 250m	12154.40	249.20	3	0.00
Null	12157.39	252.19	2	0.00

Appendix 1c. Results of model selection process for models predicting sage thrasher presence within the Thunder Basin National Grassland, USA, 2015–2017.

Model	AICc	ΔAICc	K	weight
Step 2				
Sagebrush cover (1km) + Topographic roughness + Year +Sagebrush + Litter	510.91	0.00	8	0.67
Long term prairie dog disturbance (0,1)+Sagebrush cover (1km) + Topographic roughness + Year + Sagebrush + Litter+	512.37	1.47	9	0.32
Sagebrush + Litter	520.37	9.46	4	0.01
Sagebrush + Litter + Long term prairie dog disturbance (0,1)	521.37	10.46	5	0.00
Long term prairie dog disturbance (0,1)+Sagebrush cover (1km) + Topographic roughness + Year	542.11	31.21	7	0.00
Year	548.11	37.21	6	0.00
Long term prairie dog disturbance (0,1)	550.34	39.43	3	0.00
Null	558.19	47.29	2	0.00
Step1				
Local				
Shrub+ Bare	523.80	3.43	4	0.05
Shrub+ Bare + Cactus	525.67	5.30	5	0.02
Shrub +Bare + Canopy + Cactus	527.49	7.12	6	0.01
Shrub +Cactus	527.40	7.03	4	0.01
Shrub + Cactus + Canopy	528.14	7.77	5	0.01
Shrub + Canopy	526.14	5.77	4	0.01
Shrub + Litter	522.60	2.23	4	0.09
Shrub + Litter + Cactus	524.42	4.05	5	0.03
Shrub + Litter + Herbaceous canopy + Cactus	526.32	5.95	6	0.01
Shrub + Bare	521.85	1.48	4	0.12
Sagebrush+Bare+Herbaceous canopy	523.63	3.26	5	0.05

Sagebrush+Bare+Herbaceous canopy + Cactus	525.35	4.99	6	0.02
Sagebrush + Cactus	525.43	5.06	4	0.02
Sagebrush + Cactus + Herbaceous canopy	525.93	5.57	5	0.02
Sagebrush + Herbaceous canopy	523.98	3.61	4	0.04
Sagebrush + Litter	520.37	0.00	4	0.26
Sagebrush+Litter+Herbaceous canopy	522.12	1.75	5	0.11
Sagebrush+Litter+Herbaceous canopy + Cactus	523.94	3.57	6	0.04
Bare ground	539.13	18.76	4	0.00
Visual obstruction + Bare ground +Herbacous canopy	541.12	20.75	5	0.00
Visual obstruction + Bare + Cactus + Herbaceous canopy	542.34	21.98	6	0.00
Visual obstruction + Litter	537.33	16.96	4	0.00
Visual obstruction + Litter + Herbaceous canopy	539.34	18.97	5	0.00
Visual obstruction + Litter + Herbaceous canopy + Cactus	540.77	20.40	6	0.00
Visual obstruction + Cactus	542.97	22.60	4	0.00
Visual obstruction + Cactus + Herbaceous canopy	544.63	24.26	5	0.00
Visual obstruction + Herbaceous canopy	542.88	22.51	4	0.00
Bare	550.08	29.71	3	0.00
Cactus	560.20	39.83	3	0.00
Herbaceous canopy	556.16	35.79	3	0.00
Litter	546.34	25.97	3	0.00
Null	558.19	37.82	2	0.00
Shrub	525.38	5.02	3	0.02
Sagebrush	523.44	3.07	3	0.06
Visual obstruction	541.15	20.79	3	0.00

Landscape cover

Year + Sagebrush cover 1km + Topography	548.11	0.00	6	0.26
Year + Sagebrush cover 500m + Topography	549.04	0.93	6	0.16
Year + Sagebrush cover 250m + Topography	549.34	1.23	6	0.14
Year + Sagebrush cover 1km + Topography^2	550.09	1.98	7	0.10
Year + Sagebrush cover 1km	550.27	2.16	3	0.09
Year + Sagebrush cover 500m	550.90	2.79	3	0.06
Year + Sagebrush cover 500m + Topography^2	551.04	2.93	7	0.06
Year + Sagebrush cover 250m	551.17	3.06	3	0.06
Year + Sagebrush cover 250m + Topography^2	551.27	3.16	7	0.05
Year	554.44	6.33	4	0.01
Year + Topography	555.67	7.56	5	0.01
Year + Sage cover (1km) + Topography	557.52	9.41	6	0.00
Null	558.19	10.08	2	0.00
Natural Disturbance				
Long-term colony cover	550.34	0.00	3	0.95
Colony cover	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 250km	558.71	0.51	3	0.10
Wellcat 500m	559.48	1.29	3	0.07
Road density 500km	559.64	1.45	3	0.06
Road density 1km	559.73	1.54	3	0.06
Wellcat 500m + Road density 250m	559.80	1.60	4	0.06
Wellcat 250m	560.18	1.99	3	0.05
Wellcat 1km	560.20	2.01	3	0.05
Road density 250km^2	560.68	2.49	4	0.04
Wellcat 250m + Road density 250m	560.68	2.49	4	0.04
Wellcat 1km + Road density 250m	560.72	2.53	4	0.04
Wellcat 500m + Road density 500m	560.86	2.66	4	0.03
Wellcat 500m + Road density 1km	561.05	2.86	4	0.03

Wellcat 250m + Road density 500m^2	561.60	3.41	4	0.02
Road density 500km^2	561.61	3.42	4	0.02
Wellcat 1km + Road density 500m	561.66	3.47	4	0.02
Wellcat 500m + Road density 250m^2	561.71	3.52	5	0.02
Road density 1km^2	561.72	3.53	4	0.02
Wellcat 250m + Road density 1km	561.72	3.53	4	0.02
Wellcat 1km + Road density 1km	561.74	3.55	4	0.02
Wellcat 250m + Road density 250m^2	562.65	4.46	5	0.01
Wellcat 1km + Road density 250m^2	562.69	4.50	5	0.01
Wellcat 500m + Road density 500m^2	562.80	4.61	5	0.01
Wellcat 500m + Road density 1km^2	563.05	4.86	5	0.01
Wellcat 250m + Road density 500m^2	563.56	5.37	5	0.01
Wellcat 1km + Road density 500m^2	563.63	5.44	5	0.01
Wellcat 250m + Road density 1km^2	563.72	5.53	5	0.01
Wellcat 1km + Road density 1km^2	563.73	5.54	5	0.01