

**Does Landscape-Scale Habitat Reclamation and the Umbrella Species Concept Work to Conserve Sagebrush Songbirds?**

by

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## **Author's Declaration**

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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## **Statement of Contributions**

The manuscripts presented in this thesis are the work of Natasha Barlow, in collaboration with her co-authors and advisors. The co-authors include Dr. Brad Fedy, Chris Kirol, and Dr. Kevin Doherty. Natasha Barlow is first author on both of the manuscripts, and was responsible for the data collection, data analysis, writing, and preparation of all the following manuscripts, including figures and tables. The contents of the manuscripts were edited by co-authors.

The first manuscript is being prepared for submittal to *Ecological Applications* and the second manuscript is in review for publication in the *Journal of Wildlife Management*.

## Abstract

Declines in the spatial extent of the sagebrush ecosystem have prompted the use of conservation strategies including habitat reclamation and the consideration of the greater sage-grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”) as an umbrella species. However, the response of wildlife to reclamation in sagebrush ecosystems remains largely undocumented, and recent literature has questioned the efficacy of using the sage-grouse as an umbrella species at finer spatial scales. In North America, grassland and shrubland songbird populations are declining faster than other avian groups. I measured avian species abundance ( $n = 8$  species) in sagebrush habitats across a gradient of development: 1) active oil and gas, 2) a landscape-scale reclamation area, and 3) within an undisturbed control-site containing no energy development. Additionally, I quantified nest-site selection for a sagebrush-obligate songbird, the Brewer’s sparrow (*Spizella breweri*), and then compared the fine-scale habitat variables that influenced Brewer’s sparrow nest-site selection with fine-scale nest-site selection for sage-grouse. I used a Bayesian hierarchical approach to determine the influence of treatment (reclaimed, active, and control), and habitat variables on songbird abundance (2016-2018). Nest-site selection was modelled using conditional logistic regression for Brewer’s sparrow (2016-2017), and logistic regression for sage-grouse (2004-2007). I found that sagebrush songbird species responses to energy development and reclamation is variable, and I did not observe the expected outcome of increasing abundance with decreasing human disturbance (active to reclaimed to control) in any species. Reclamation efforts seemed to produce a measurable influence on some species abundance, although the habitat variables that best represent where we can most easily target reclamation efforts had minimal influence on most species abundance. Most of the conservation objectives for protection of sage-grouse habitats appear to be beneficial or inconsequential for

Brewer's sparrow. Local habitat management for sage-grouse as a proxy for conservation of other species may be justified, if the microhabitat preferences of the species under the umbrella are well understood to avoid unintentional negative impacts.

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# 1 General Introduction

Sagebrush (*Artemisia* spp.) ecosystems historically covered around 63 million ha in western North America (Knick et al. 2003). Declines in their spatial extent by roughly 50% are largely a result of wildfire, agriculture, invasive species, urbanization, and energy development (Homer et al. 2015). As a result, this ecosystem has become one of the most imperiled in North America (Finch et al. 2016), which has led to federal and state agencies prioritizing conservation and protection of sagebrush ecosystems (Clement et al. 2014). Species that rely on sagebrush ecosystems are similarly in decline (Sawyer et al. 2006, Vander Haegen 2007, Garton et al. 2011, Gilbert and Chalfoun 2011), including grassland and shrubland songbirds, which have experienced the fastest population declines of any avian group in North America (Knick et al. 2003, Gilbert and Chalfoun 2011).

To inform strategies on how to best conserve and protect sagebrush songbirds, it is necessary to understand how current conservation practices influence their populations. A vast array of studies have been completed that focus on the impacts of oil and gas development on the high-profile, sagebrush-obligate gamebird species, the greater sage-grouse (*Centrocercus urophasianus*; Lyon and Anderson 2003, Doherty et al. 2008, Copeland et al. 2009, Garton et al. 2011, Fedy et al. 2015, Holloran et al. 2015). Resource managers consider the greater sage-grouse an umbrella species for most of the sagebrush ecosystem (Rowland et al. 2006), even though the effectiveness of this strategy in conserving the species under the umbrella, including songbirds, is uncertain (Roberge and Angelstam 2004, Hanser and Knick 2011, Carlisle et al. 2017a, b). In addition to managing the sagebrush ecosystem for umbrella species, specifically greater sage-grouse, federal agencies are increasingly emphasizing habitat reclamation as a way to mitigate the impacts of energy development on greater sage-grouse and sagebrush wildlife

(U.S Fish and Wildlife Service 2013, Clement et al. 2014). No studies have quantified the response of sagebrush songbirds to habitat reclamation, and few studies have assessed the effectiveness of using the greater sage-grouse as an umbrella species for sagebrush songbirds. This thesis aims to fill this knowledge gap, to improve the success of conservation and protection of sagebrush songbirds.

## **2 Literature Review**

### **2.1 Ecology and Conservation**

Two of the primary goals of traditional ecology are to determine the abundance of a target species in a certain area, and the habitat characteristics influencing their abundance (Binckley and Resetarits 2005, Buckland et al. 2015, Boyce et al. 2016). This can be simplified by asking, how many animals are there, and why are they there? These two questions underlying ecological research are also the primary focus of studies on wildlife management and ecosystem conservation, since answering these questions has been suggested as a way to solve many global conservation issues (Morris 2003, Jonzen 2008, Kellner and Swihart 2014, Kery and Royle 2016).

#### **2.1.1 Abundance**

Efficient conservation and management of a species is unsurprisingly impossible without determining the population size (Buckland et al. 2015). Therefore, the abundance of a species is a key parameter influencing conservation and management agency initiatives (Akçakaya and Sjögren-Gulve 2000, Schwartz 2008, Mooers et al. 2010, MacKinnon et al. 2011, Environment and Climate Change Canada 2017). Conducting a complete census of a population is the ideal method of gathering abundance data. However, in most situations, this is not possible due to logistics, cryptic behavior in some species, and imperfect detection of individuals, and so a variety of survey methods and analysis techniques are continually being developed to estimate abundance based on observed sample data (Royle 2004, Royle et al. 2004, White 2005, Buckland et al. 2015, 2016; Kery and Royle 2016, Barker et al. 2017, Zhao and Royle 2019).

Estimates of abundance based solely on count data is generally biased since it does not take into account detectability (Gu and Swihart 2004, Royle et al. 2004, 2007; White 2005). For

example, if two observers are completing botanical surveys at different locations, and observer A is more experienced than observer B, it is possible that observer A will record a higher number of target species at their location. However, this does not mean that there are in fact more species at observer A's location, rather, that observer A may have detected more plants simply because of their experience. Failure to account for imperfect detection can lead to inaccurate conclusions, including under or overestimation of abundance, and flawed inference of a species relationship with habitat characteristics, which is particularly concerning when abundance metrics are informing conservation and management strategies (Gu and Swihart 2004, Kéry and Schmidt 2008, Chen et al. 2013, Kellner and Swihart 2014, Durso and Seigel 2015).

Hierarchical models that include multiple sub-models which correct for the imperfect detectability of individuals during a survey have been developed to more accurately estimate abundance (Royle et al. 2007, Kery and Royle 2016). The sub-models are probability models that are conditionally related to each other to describe the measurement error during observation of field data, and the true state of the parameter of interest (e.g., abundance; Kery and Royle 2016). However, using these models without developing a study design for data collection that minimizes uncertainties in abundance estimates may also lead to bias and erroneous conclusions (Chen et al. 2013, Matsuoka et al. 2014, Durso and Seigel 2015). Classical statistics or frequentist approaches do not directly accommodate complex study designs that employ sampling techniques that collect count data to estimate abundance (Kery and Royle 2016). Therefore, count data collected using complex study designs are more easily analyzed using hierarchical models built within a Bayesian framework (Cressie et al. 2009, Kery and Royle 2016). Overall, careful study design and analysis is needed to ensure that ecological research does not misinform policy which can lead to a distrust of ecologists (Kellner and Swihart 2014).

### **2.1.2 Habitat Selection**

A habitat is the set of physical and environmental characteristics and conditions that allow for a species to survive and reproduce in the area that they occupy (Krausman 1999, Jones 2001). Habitat selection is the disproportionate use of a habitat as a result of a behavioral response that influences survival (Hutto 1985, Jones 2001). Applying habitat selection theory to ecological research often draws inference regarding species preferences by comparing a species usage of habitat with the availability of habitat (Johnson 1980). However, comparing usage with availability between different spatial scales could misrepresent true habitat preferences since animals select different habitat characteristics at different scales (Johnson 1980, Mayor et al. 2009). Therefore, I use the terminology of Johnson (1980) to define the hierarchical ordering of habitat selection. Selection at the landscape scale includes first and second order selection, relating to the geographical range and home range, respectively (Johnson 1980). Local scale refers to third and fourth order selection, which are the usage of habitat components within the home range and selection of local features to meet life requirements, respectively (Johnson 1980, Meyer and Thuiller 2006). Since some habitats within a landscape are used more than others, understanding local scale habitat selection is necessary to determine the probability that an animal will select a certain habitat characteristic (Johnson 2007, Lele et al. 2013).

Understanding why species occupy certain habitats and why they persist in specific areas is necessary to achieve conservation and management goals. In the past two decades, habitat selection studies have become increasingly popular since habitat selection information is being incorporated into conservation planning (Jones 2001). Describing spatially explicit resource use can be used to determine habitat quality, areas in need of protection, patterns in population trends, and the effectiveness of management strategies (Jones 2001, Jonzen 2008). In human

altered landscapes it is especially important to conduct studies on species abundance and habitat selection to inform conservation planning, due to current global landscape changes and the subsequent influence on wildlife populations (Morris 2003).

## **2.2 Global Human Disturbance**

The human population is expected to reach 9 billion by 2050 (Wagner et al. 2016), leading to a projected increase of 50% in the global energy demand between 2007 and 2030 (Copeland et al. 2009). In the USA alone, energy production is expected to increase 27% by 2040, with oil and natural gas production contributing to the majority of landscape impacts (Trainor et al. 2016). It was estimated that the infrastructure associated with oil and gas development built between 2000 to 2012 in the USA (e.g., well pads, roads, wells, etc.) covers approximately 3 million ha, which is about the size of three Yellowstone National Parks (Allred et al. 2015). Non-renewable oil and gas development may be considered a pulse disturbance if once the disturbance is removed the ecosystem regains its initial equilibrium (Bender et al. 1984, Morrison et al. 2006). However, oil and gas development areas create avoidance responses in wildlife, increase habitat fragmentation and conversion, and increase wildlife mortality as a result of easier access for humans to wild lands (Northrup and Wittemyer 2013). As habitat fragmentation, loss, and degradation are still the biggest threats to global biodiversity (Hanski 2011), an increase in energy production will have detrimental impacts on global ecosystems (Jones et al. 2015). Therefore, mitigation of these human-driven impacts is necessary to sustain healthy natural wildlife populations.

## **2.3 Mitigating Human Disturbance**

Mitigation strategies that focus on minimizing the negative impacts of development on wildlife generally attempt to alter development strategies and implement best management

practices (Northrup and Wittemyer 2013, Clement et al. 2014). Ecological restoration and surrogate species management are two of these methods used to mitigate human-driven impacts on global ecosystems (Wortley et al. 2013, Hunter et al. 2016).

### **2.3.1 Habitat Restoration**

Habitat restoration is used as an attempt to minimize or reverse the degradation, loss, or destruction of ecosystems (Society for Ecological Restoration International 2004, Rey Benayas et al. 2009). Globally, the number of habitat restoration projects and research focused on ecological restoration has increased dramatically in the past decade (Chazdon et al. 2015, Nilsson et al. 2016). Restoration of ecosystems is one of the most promising strategies for mitigating the negative impacts of human alteration of landscapes, as it inherently assumes that some damage to ecosystems is recoverable (Young 2000, Young et al. 2005, Devoto et al. 2012, Balaguer et al. 2014). Restored landscapes worldwide have shown increases in provision of biodiversity and ecosystem services in comparison to degraded ecosystems, although these values are often lower than that of undisturbed landscapes (Rey Benayas et al. 2009). The Society for Ecological Restoration's Primer (2004) outlines attributes to assess when determining if a restoration project was successful, which includes determining if species assemblages at a restored site resemble a reference ecosystem. However, poorly defined targets and lack of quality monitoring prevents a comprehensive understanding of the 'success' of restoration projects (Wortley et al. 2013). Most research in ecological restoration focusses on community, ecosystem, and population ecology of flora and invertebrates (Young 2000, Wortley et al. 2013). Since studies evaluating the monitoring aspect of restoration projects are lacking in literature, and spatial patterns of animal abundance are a primary focus of ecological research that underpins conservation (Royle et al. 2007), it is crucial to assess the response of wildlife

species abundance to restored habitats to accurately inform adaptive management strategies (Nilsson et al. 2016).

### **2.3.2 Umbrella Species Concept**

Practical conservation and management issues are increasingly becoming focused on the viability of species at risk or surrogate species (Akçakaya and Sjögren-Gulve 2000). Surrogate species management focusses conservation efforts on one aspect of a system (e.g., single-species, ecosystem process, etc.; Caro 2010, Hunter et al. 2016). This ‘conservation shortcut’ can be an efficient way of simultaneously protecting a suite of species or an ecosystem (Caro 2010). The umbrella species concept is one form of the surrogate species management approach, where the protection of one species is assumed to provide a benefit to other naturally co-occurring species (Roberge and Angelstam 2004, Hunter et al. 2016). However, many criticisms exist in determining which species should be the umbrella (Andelman and Fagan 2000, Caro 2003, 2010; Roberge and Angelstam 2004, Maslo et al. 2016). Management for a single-species as a proxy for protection of the ecosystem as a whole may have little conservation value if either the umbrella species or species under the umbrella have specialized habitat requirements that are irrelevant among species (Simberloff 1998, Andelman and Fagan 2000, Caro 2010). The umbrella species strategy is also not consistently effective at different spatial scales, offering different levels of protection to various species under the umbrella (Andelman and Fagan 2000, Caro 2003, Roberge and Angelstam 2004, Maslo et al. 2016). Additionally, umbrella species may not offer protection to species of unrelated taxonomic groups (Simberloff 1998, Roberge and Angelstam 2004).

## 2.4 Study System

### 2.4.1 Sagebrush Ecosystem

Sagebrush (*Artemisia* spp.) ecosystems are one of the most imperiled ecosystems in North America, as constant disturbance due to agriculture, wildlife, invasive species, urbanization, and energy development, have resulted in loss of spatial extent by over 50% (Knick et al. 2003, Homer et al. 2015, Finch et al. 2016). Since the amount of sagebrush habitat has an inverse relationship with natural gas development, continued energy development will lead to loss, degradation, and fragmentation of these ecosystems throughout the range (Walston et al. 2009). Declines in the spatial extent of the sagebrush ecosystem have prompted resource managers to prioritize the conservation and restoration of the sagebrush ecosystem through various means, including surrogate species management and habitat restoration (Knick et al. 2003, Bureau of Land Management 2004, Rowland et al. 2006, Pyke 2011, Pyke et al. 2015). A vast array of studies have been completed on the impacts of energy development on an upland gamebird, the greater sage-grouse (*Centrocercus urophasianus*), which is considered an umbrella species for most of the sagebrush ecosystem (Lyon and Anderson 2003, Rowland et al. 2006, Doherty et al. 2008, Copeland et al. 2009, Garton et al. 2011, Fedy et al. 2015, Holloran et al. 2015). However, the effectiveness of using this strategy in conserving the species under the umbrella is uncertain (Roberge and Angelstam 2004, Hanser and Knick 2011, Carlisle et al. 2017a, b).

Additionally, the agencies that manage a large portion of the remaining sagebrush habitats in North America have recently increased their focus on habitat restoration as a means to mitigate the impacts of oil and gas development on sagebrush species (U.S Fish and Wildlife Service 2013, Clement et al. 2014). Past research has explored soil and vegetation recovery in

restored fossil fuel areas (Gasch et al. 2014, Curran et al. 2015). However, the recovery of sagebrush wildlife in habitats restored after energy development is generally assumed and understudied. Therefore, to better conserve sagebrush ecosystems, empirical assessments are necessary to inform restoration practices (Wortley et al. 2013), and umbrella species should be chosen at appropriate spatial scales, after carefully completing quantitative studies (Maslo et al. 2016).

#### **2.4.2 Sagebrush Songbirds**

Landbirds are often used as an indicator of environmental change (Askins 1995, Foster et al. 2017). Landbird monitoring programs have been suggested as one of the greatest tools in reaching conservation goals (Hutto 1998). Songbirds are one of the most visible groups of vertebrates, and they often actively vocalize, making data collection easier and less time consuming, while allowing for the observer to collect multiple data points at once (Hutto 1998). This could lead to more easily uncovered occurrence patterns, resulting in the development of strong habitat selection models (Hutto 1998). Birds also respond to environmental change over multiple spatial scales, and their occurrence, abundance, and survival is influenced by the surrounding habitat characteristics (Carignan and Villard 2002). Migratory birds may also provide an opportunity to quickly assess the impact of changing habitat quality, as they have known life histories and make habitat use decisions every year (Tankersley 2004).

The sagebrush ecosystem is home to grassland and shrubland songbirds, which have experienced the fastest population declines of any avian group in North America (Knick et al. 2003, Gilbert and Chalfoun 2011). Decreases in avian species richness, abundance, and nest survival has been observed with increased energy development in the sagebrush ecosystem (Gilbert and Chalfoun 2011). However, no studies exist that assess the influence of habitat

restoration on sagebrush songbird abundance. Additionally, recent literature has questioned the efficacy of using the greater sage-grouse as an umbrella species for a suite of other sagebrush songbirds (Carlisle et al. 2018a, b).

## **2.5 Research Questions and Thesis Outline**

The purpose of this thesis is to study the impact of two conservation strategies on the sagebrush ecosystem, and specifically on sagebrush songbirds. The two studies presented in this thesis aim to answer the following questions:

1. What habitat variables and habitat treatments influence the abundance of sagebrush songbirds?
2. What fine-scale habitat variables influence Brewer's sparrow nest-site selection?
3. Do fine-scale habitat variables influence nest-site selection of Brewer's sparrow and greater sage-grouse similarly?

Chapter 3 aims to answer question 1, namely whether habitat reclamation influences the abundance of sagebrush songbirds. This study determines how the abundance of certain sagebrush songbird species are influenced by undisturbed sagebrush habitat, active natural gas fields, and reclaimed natural gas fields. Additionally, it assesses how the abundance of certain sagebrush songbirds are influenced by key habitat variables.

Chapter 4 aims to answer questions 2 and 3, namely whether the greater sage-grouse umbrella species concept works at fine-spatial scales for a species under its umbrella, the Brewer's sparrow. This study quantifies habitat selection at the third and fourth order, to determine the habitat characteristics influencing nest-site selection of Brewer's sparrow. Then, it compares the influence of the habitat variables present in the top Brewer's sparrow nest-site selection model to the probability of nest-site selection of greater sage-grouse.

## 2.6 Study Area

The Powder River Basin (PRB) region of eastern Wyoming and Montana has a long history of energy development due to the presence of shallow coal beds (Naugle 2011). This region has seen an exponential increase of natural gas extraction since the 1990's, with a current estimate of over 35,000 producing wells (Naugle 2011). Specifically, it is one of the fastest growing coal bed natural gas (CBNG) development areas in the USA (Bergquist et al. 2007). Currently, it is home to seven out of the ten largest coal mines (U.S Energy Information Administration 2017), and sixteen of the largest natural gas fields in the USA (U.S Energy Information Administration 2015). These developments are estimated to have impacted over 24,000 km<sup>2</sup> of wildlife habitat, and more wells have been authorized (Walker et al. 2007). However, even though Wyoming has undergone intensive energy development, it continues to be a stronghold for some of the last remaining intact sagebrush habitats (Knick et al. 2003).

Our study site is located within sagebrush-steppe habitat in the PRB region in northeastern Wyoming, primarily in Johnson County (44.2603°N, -106.3095W°). Study sites were selected across a gradient of energy development and fell into 3 categories: 1) restored oil and gas fields, 2) active oil and gas development, and 3) undisturbed sagebrush habitat. We selected 4 plots (~0.4 km<sup>2</sup>) within each of these categories for a total of 12 plots to collect songbird abundance data, further described in Chapter 3. Within these 12 plots, 6 plots (~0.25 km<sup>2</sup>) were selected in which to collect Brewer's Sparrow nest-site information, further described in Chapter 4.

### **3 Do Sagebrush Songbirds Benefit from Landscape-Scale Habitat Reclamation?**

#### **3.1 Introduction**

Energy development can impact ecosystems through habitat loss and fragmentation, increased water consumption, noise pollution, invasions by non-native species, and impacts to air and water quality (McDonald et al. 2009, Jones et al. 2015). Total global energy consumption is projected to increase 48% between 2012 – 2040, with natural gas being the primary source of energy consumption (U.S. Energy Information Administration 2016). Similar trends are reflected in the USA, where energy production is expected to increase 27% by 2040, with oil and natural gas production being the most substantial drivers of landscape change (Trainor et al. 2016). Oil and gas development can negatively impact multiple wildlife species through avoidance, increased habitat fragmentation and conversion, and increased wildlife mortality as a result of easier access for humans to wild lands (Naugle 2011, Northrup and Wittemyer 2013). Additionally, invasive species introduced by vehicles, soil, reseeding activities, and resource subsidies (e.g., water) during the lifespan of the energy development project, can alter fire and disturbance regimes, leading to habitat degradation, and subsequent loss of native species richness and abundance (Evangelista et al. 2011, Jones et al. 2015). Although oil and gas extraction periods have finite timelines, and are therefore being considered ‘pulse’ disturbances, mitigation of these human-driven impacts is necessary to sustain healthy natural wildlife populations. Mitigation generally attempts to minimize wildlife impacts through altering development strategies, implementing best management practices, and restoring habitats (Northrup and Wittemyer 2013, Clement et al. 2014).

Ecological restoration is the practice of assisting in the recovery of a degraded ecosystem (Rey Benayas et al. 2009), and is an increasingly popular mitigation strategy incorporated into natural resource policies (Menz et al. 2013, Wortley et al. 2013, Chazdon et al. 2015). Restored landscapes worldwide demonstrate increased biodiversity and provision of ecosystem services in comparison to degraded ecosystems, although these values are often lower than undisturbed landscapes (Rey Benayas et al. 2009). Restoration projects which encompass more than several square kilometers (hereafter “landscape-scale” restoration) are needed to effectively reverse the negative impacts of human development on ecosystems and wildlife (Holl et al. 2006, Montoya et al. 2012, Menz et al. 2013). Wortley et al. (2013) found that the majority of studies focusing on ecological restoration, assess species richness and abundance of flora and invertebrates. However, few studies have assessed the response of wildlife species to landscape-scale restoration activities (Gardali et al. 2006, Golet et al. 2008, Pejchar et al. 2018), with most efforts being targeted at smaller-scale restoration projects (Holl et al. 2006). Given that wildlife abundance underpins conservation efforts, there is a substantial gap in our understanding of how wildlife will respond to landscape-scale restoration.

Sagebrush (*Artemisia* spp.) ecosystems historically covered around 63 million ha in western North America, but have declined in their spatial extent by roughly 50% due to wildfire, agriculture, invasive species, urbanization, and energy development (Knick et al. 2003, Homer et al. 2015). These impacts have resulted in sagebrush ecosystems becoming one of the most imperiled ecosystems in North America with oil and natural gas development as one of the main agents of ecosystem change (Knick et al. 2003). Wyoming is one of the top producers of oil and gas in the USA (Wyoming Game and Fish Department 2017). Many studies have documented the negative impacts (e.g., avoidance, reduced abundance, increased mortality) of energy

development and infrastructure (e.g., roads, well pads) on sagebrush species in Wyoming (Sawyer et al. 2006, Walker et al. 2007, Doherty et al. 2008, 2011b; Gilbert and Chalfoun 2011, Naugle 2011, Fedy et al. 2014, Smith et al. 2014, Hethcoat and Chalfoun 2015a, b; Wyoming Game and Fish Department 2017). To reduce the loss and degradation of sagebrush ecosystems, federal and state organizations are increasingly emphasizing the use of ecological reclamation in policy planning and mitigation strategies (Pyke 2011, U.S Fish and Wildlife Service 2013, Clement et al. 2014, Finch et al. 2016). In this context, “reclamation” is a type of restoration, that focusses on returning the land to a self-sustaining, re-naturalized environment that may or may not reflect pre-industrial conditions (Society for Ecological Restoration International 2004). Wyoming has mandated site reclamation following the abandonment of oil and gas developments since 1983 (Rottler et al. 2018). As in other ecosystems, the first studies on reclamation in sagebrush ecosystems have focused on the recovery of soil and vegetation (Lysne 2005, Pyke 2011, Davies et al. 2013, Gasch et al. 2014, Curran et al. 2015, Minnick and Alward 2015, Rottler et al. 2018). The response of wildlife to landscape-scale reclamation remains largely undocumented.

Landbird abundance is often used as an indicator of habitat quality (Foster et al. 2017). Migratory species, in particular, may provide an opportunity to quickly assess the impact of changing habitats on abundance on the breeding grounds, as individuals must make habitat use decisions every year on arrival from winter habitats (Tankersley 2004). Though, in some species this may be constrained by site fidelity (Wiens and Rotenberry 1985). Several migratory songbird species that rely on sagebrush for survival (hereafter “sagebrush-obligate”) have lower nest survival and decreased abundance in response to oil and gas development (Ingelfinger and Anderson 2004, Gilbert and Chalfoun 2011, Hethcoat and Chalfoun 2015b, Mutter et al. 2015).

Thus, we can detect a difference in species abundance between areas of active oil and gas development and relatively undisturbed areas. A critical remaining question is how do species respond to habitat reclamation? We addressed this general question by measuring avian species abundance ( $n = 8$  species) in sagebrush-steppe habitats across a gradient of development from: 1) active oil and gas, 2) a landscape-scale reclamation area, and 3) within an undisturbed control-site containing no energy development. We designed our study to best isolate the influence of reclamation efforts and compare species abundance among sites. Additionally, it is possible that habitat composition may have differential influences on species abundance. Therefore, we also examined variation in the influence of key habitat variables on species abundance.

## **3.2 Methods**

### **3.2.1 Study Site**

Study sites were located in sagebrush-steppe habitat in northeastern Wyoming, USA, within the Powder River Basin (PRB) region (44.2603°N, -106.3095W°). Land use was primarily coal bed natural gas (CBNG) extraction and cattle ranching. Elevation ranged between 1268 m – 1442 m. Wyoming big sagebrush (*A. tridentata wyomingensis*) was the dominant shrub, with plains silver sagebrush (*A. cana cana*) and black greasewood (*Sarcobatus vermiculatus*) present at much lower abundances. The plant community understory was dominated by green and gray rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), native grasses including blue grama (*Bouteloua gracilis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and non-native Japanese brome (*Bromus japonicas*) and cheatgrass (*B. tectorum*). More details on the study region can be found in previous publications (Walker et al. 2007, Doherty et al. 2011a, Fedy et al. 2014, 2015; Kirol et al. 2015).

### 3.2.2 Site Selection

Study sites were selected across a gradient of energy development and fell into 3 categories: 1) reclaimed oil and gas fields, 2) active oil and gas development, and 3) undisturbed sagebrush habitat. We refer to these study sites as ‘treatments’, with categories of reclaimed, active, and control, respectively throughout. The treatments were proximal to each other with the reclaimed treatment in the central portion of our study region, the active treatment in the southern portion, and the control treatment to the north (Figure 1).

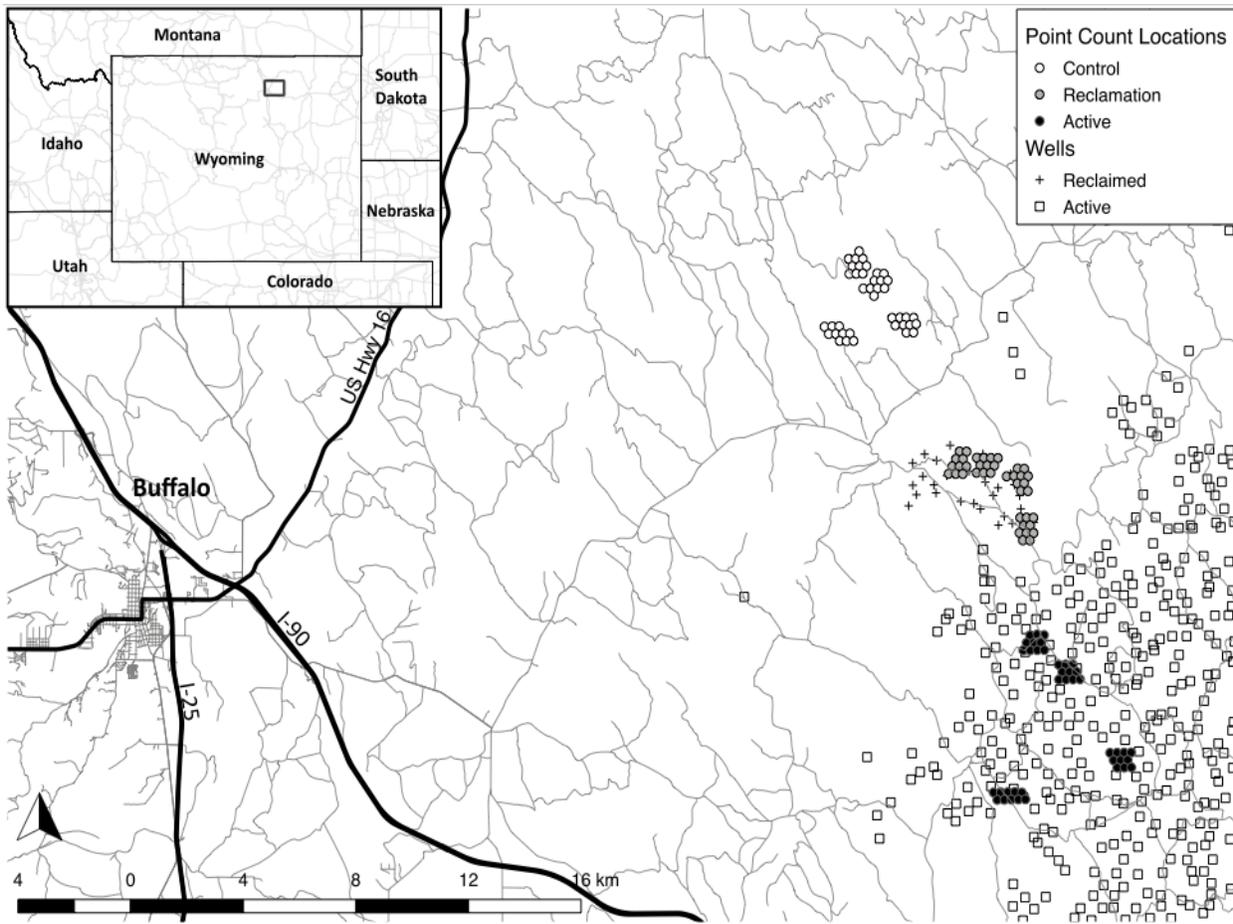


Figure 1. Map of study area, point count locations by habitat treatments, and well locations, in northeastern Wyoming, USA, 2016-2018.

### **3.2.3 Reclamation Treatment**

The reclaimed treatment was a former active gas development in which 30 CBNG wells were plugged and abandoned (mostly in 2013). The landscape area influenced directly by reclamation activities was ~8.6 km<sup>2</sup>. Following the cessation of gas extraction, reclamation activities included the removal of all infrastructure, stripping and re-spreading topsoil, re-contouring roads to create topography similar to pre-disturbance conditions, and may also have included other accepted reclamation practices (e.g., ripping, tilling, disking on contour, dozer track-imprinting; Anadarko Petroleum Corporation 2014). Once the area was prepared, re-seeding was completed with a no-till drill (Anadarko Petroleum Corporation 2014).

### **3.2.4 Plot Selection**

We selected 4 plots (~0.4 km<sup>2</sup>) within each treatment for a total of 12 plots for point count surveys. We first selected a sample ( $n = 30$ ) of 25 hectare, “candidate” plots overlying CBNG well locations across the three treatments, including producing wells (active treatment), reclaimed wells (reclaimed treatment), or those that were permitted but never developed (control treatment). These plots had to satisfy the following 4 criteria: 1) sagebrush was the dominant shrub cover, 2) contained 1-2 CBNG well locations, 3)  $\geq 300$  m from gravel access roads and overhead power lines, and 4) located predominantly on Wyoming State or BLM Land. In order to isolate the effect of the reclamation activities, we first selected plots within the reclaimed treatment, which resulted in the plots having an average sagebrush cover between 10-14% with a standard deviation of 2-5%, and terrain roughness values between 50-550. Once four plots were selected in the reclaimed treatment, we used satellite imagery, elevation, and vegetation cover layers in GIS to identify candidate plots in the active and control treatments to ensure that the environmental and habitat characteristics were similar across all plots. The selected active and

control plots maintained the same average sagebrush cover and standard deviation, terrain roughness values, and average elevations, as the reclaimed plots (Appendix A). The treatments were separated from each other by >400 m, to ensure that reclaimed plots were not being influenced by adjacent active wells. Sagebrush layers were processed from Wyoming sagebrush products (Homer et al. 2012). Roughness values were based upon a terrain roughness index (Evans et al. 2014), derived from a Digital Elevation Map (DEM). Average elevations within plots were also calculated from a DEM (Evans et al. 2014). All layers were processed at a 30 m resolution using ArcGIS 10.2 (ESRI 2016).

### **3.2.5 Bird Surveys**

Point count surveys followed a distance sampling protocol (Buckland et al. 2015), similar to the those developed by the Rocky Mountain Bird Observatory (Hanni et al. 2016). Each plot contained 10 point count locations that were ~250 m apart (Ralph et al. 1995, Hanni et al. 2016). This resulted in 40 point count locations in each treatment, for a total of 120 point count locations across the entire study area. At each point, an observer conducted an unlimited-distance survey by recording the species of each individual bird and distance from the point, using visual and auditory cues, for 6 minutes (Ralph et al. 1995, Matsuoka et al. 2014, Hanni et al. 2016). We truncated points to 125 m post-surveys since this buffer represents areas that should reduce the probability of double counting individuals since point count locations were spaced ~250 m apart (Matsuoka et al. 2014, Carlisle et al. 2018a). Distances to the birds were recorded using Bushnell Sport 850 rangefinders (Bushnell Corporation, Overland Park, KS). Surveys were conducted within a 4-hour window starting at approximately sunrise, to maximize efforts during times of peak bird activity (Ralph et al. 1993). Surveys were completed on days without high wind or rain. Observers surveyed 10 point count locations per day, unless inclement weather postponed

some surveys. We visited all 120 point count locations twice each year (2016-2018) between late May and late June. Observers were randomly assigned point count locations, and the same observer did not survey the same point count locations on the second visit within a year. The order in which the point count locations were surveyed was not repeated between visits within a year.

To standardize across observers, all observers underwent intensive training in visual and auditory bird identification and we conducted multiple training sessions in the field with each crew to ensure that all observers were recording the same species and approximately the same distances prior to data collection. We further addressed the observation process in our modelling approach (described below).

### **3.2.6 Spatial Layers and Habitat Variables**

We reviewed the literature for our focal species and identified potentially important habitat variables influencing abundance. Additionally, we included variables relevant to habitat reclamation in sagebrush ecosystems. Vegetation structure in sagebrush ecosystems, including shrub cover, and understory ground cover, may influence songbird diversity and abundance (Williams et al. 2011a, Earnst and Holmes 2012). Therefore, we obtained spatial layers for sagebrush cover, shrub cover, and litter cover from the U.S Geological Survey (2017), as well as annual and perennial herbaceous cover, and bare soil cover from Jones et al. (2018). Songbird abundance can have a positive relationship with the Normalized Difference Vegetation Index (NDVI) as a measure of primary productivity (McFarland and van Riper 2013, Harrower et al. 2017). NDVI layers were obtained for ~May 9<sup>th</sup> each year (2016 – 2018) from Robinson et al. (2017), since our focal species arrived on the breeding grounds and established territories in

early May. Sagebrush-obligate songbird abundance can also be influenced by terrain roughness (Aldridge et al. 2011).

Mean values for each habitat variable were calculated using zonal statistics that averaged all pixel values located within a 125 m radius of each point count location. All continuous habitat variables were standardized prior to modeling. When variables were correlated ( $r \geq |0.60|$ ; Akoglu 2018), we chose the most biologically relevant variable to include in our analysis. GIS imagery was processed at a 30 m resolution using ArcGIS 10.2 – 10.4 (ESRI 2016).

### 3.2.7 Abundance Analysis

We used a Bayesian hierarchical approach to determine the influence of treatment (reclaimed, active, and control), and habitat variables on songbird abundance, while accounting for survey-specific detection probabilities. Our modeling approach was based off of a hierarchical open-population binomial mixture model (Kellner et al. 2016, Pejchar et al. 2018). Under the assumption of population closure between surveys within the same year, observed counts of an individual species were modeled as:

$$y_{jkt} \sim \text{Binomial}(N_{jt}, p_{jkt}),$$

where  $j$  = point count location,  $k$  = survey, and  $t$  = year.  $N_{jt}$  was the true total abundance of birds per species at each point count location per year, and  $p_{jkt}$  was the probability of detection for each point count location, survey, and year. Abundance was modelled as:

$$N_{jt} \sim \text{Poisson}(\lambda_{jt}),$$

where  $\log(\lambda_{jt})$  was modeled as a function of the combination of the habitat variables and treatments. Observer skill and habitat specific covariates can influence detection (Kellner and Swihart 2014, Carlisle et al. 2018a). Therefore,  $p_{jkt}$  was modeled as a function of the combination

of observer effect and sagebrush cover. We included observer identification as a random effect and sagebrush cover using the logit link:

$$\text{logit}(p_{jkt}) \sim \alpha * \text{Observer}_{jkt} + \text{SagebrushCover}_{jt},$$

where a unique random intercept is estimated for each observer  $i$ :

$$\alpha_i \sim (\mu, \tau)$$

where  $\mu$  and  $\tau$  are estimated using the normal and gamma distributions, respectively. We specified gaussian priors for all habitat variables and treatments. We used estimated posterior means, and the 95% credible intervals (CI) for interpretation of the effect of variables on abundance. Only species with  $\geq 50$  observations were analyzed in each modeling step (Kellner et al. 2016, 2018). We fit all models in JAGS using R version 3.5.2 (R Core Team 2018).

### 3.3 Results

We considered 719 point count surveys in our analysis (reclaimed;  $n = 239$ , active;  $n = 240$ , control;  $n = 240$ ). One point count survey from the reclaimed treatment was excluded due to missing data. Eight species were recorded with  $\geq 50$  observations (Table 1).

Table 1. Common and Latin names, species code, and the total number of observations recorded in each treatment for species included in our analysis from point counts conducted in northeastern Wyoming, USA (2016-2018).

Common Name	Latin Name	Code	Reclamation	Active	Control
Brewer's sparrow	<i>Spizella breweri</i>	BRSP	288	355	208
Vesper sparrow	<i>Pooecetes gramineus</i>	VESP	74	67	87
Lark sparrow	<i>Chondestes grammacus</i>	LASP	47	68	27
Spotted towhee	<i>Pipilo maculatus</i>	SPTO	84	12	33
Loggerhead shrike	<i>Lanius ludovicianus</i>	LOSH	39	15	17
Western meadowlark	<i>Sturnella neglecta</i>	WEME	456	456	508
Brown-headed cowbird	<i>Molothrus ater</i>	BHCO	43	36	30
Brewer's blackbird	<i>Euphagus cyanocephalus</i>	BRBL	69	64	47

### 3.3.1 Treatment Effect

We determined the influence of treatment on predicted species abundance through examination of the posterior distributions for each treatment condition (i.e., reclaimed, active, control; Figure 2). The patterns of overlap in the posterior distributions for each treatment varied across species (Figure 2). Western meadowlark had distribution estimates for treatment that were highly overlapping, indicating no detectable differences in abundance. Loggerhead shrike posterior distributions indicated no difference between the active and control treatments, but with slightly higher abundance in the reclaimed treatment, although the distribution estimates were highly overlapping. Three species demonstrated a pattern of increasing abundance with increasing disturbance from control to reclaimed to active. These species were, brown-headed cowbird, lark sparrow, and Brewer's blackbird. Spotted towhee demonstrated differentiation across all three treatments with a pattern of increasing abundance from active, to control, to reclaimed. Brewer's sparrow posterior distributions indicated no difference between the active and reclaimed treatments, but with lower abundance in the control treatment. Vesper sparrow showed no difference between control and reclaimed and suggested lower abundance in the active treatment, though with considerable overlap.

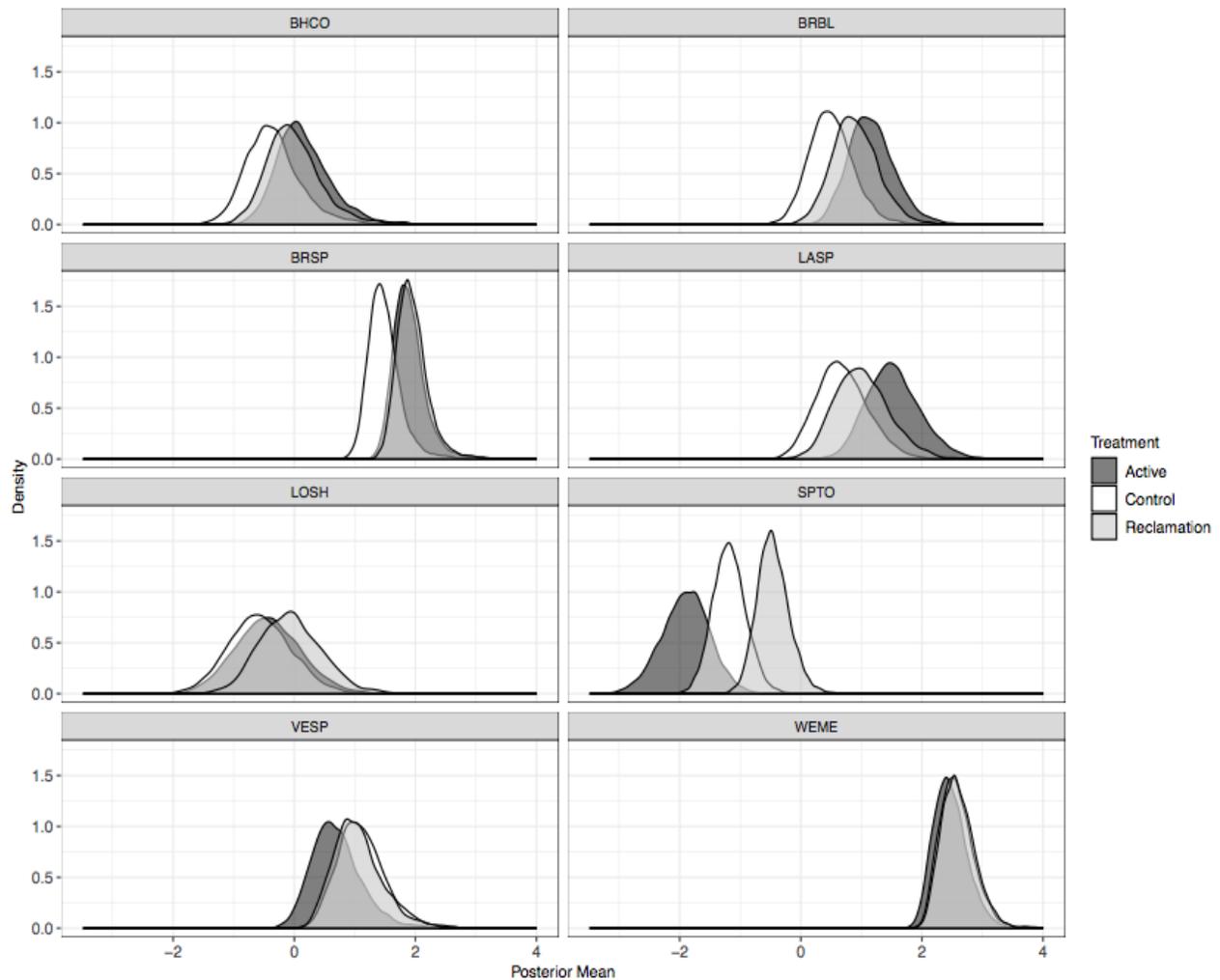


Figure 2. Posterior distributions of sagebrush songbird abundance across a gradient of energy development (i.e., active energy development sites, undisturbed ‘control’ sites, and reclaimed sites) in northeastern Wyoming, USA (2016-2018).

### 3.3.2 Habitat Variables

In addition to treatment effect, we considered four habitat variables in the process model (sagebrush cover, perennial herbaceous cover (hereafter “herbaceous cover”), terrain roughness (hereafter “roughness”), and NDVI; Figure 3). Given our efforts to ensure sites were as similar as possible across treatments it is unsurprising that the distribution of the habitat variables had similar distributions across treatments (Appendix A). The only exception to equivalent distributions was roughness which varied slightly across treatments following a pattern of

increasing roughness from active to control to reclaimed (Appendix A). The conclusion of a positive or negative influence of a habitat variable on species abundance was based on the posterior mean estimates and whether the 95% CI overlapped zero (Figure 3). Sagebrush cover had a positive influence on the abundance of Brewer's sparrow, Brewer's blackbird, and spotted towhee, and a negative influence on lark sparrow abundance. Herbaceous cover and NDVI did not appear to influence the abundance of any species, with the exception of vesper sparrow abundance, which was negatively influenced by herbaceous cover. Roughness impacted the abundance for every species with the exception of lark sparrow. Brewer's blackbird, loggerhead shrike, spotted towhee, and brown-headed cowbird were positively influenced by roughness. Brewer's sparrow, vesper sparrow, and western meadowlark abundances were negatively influenced by roughness.

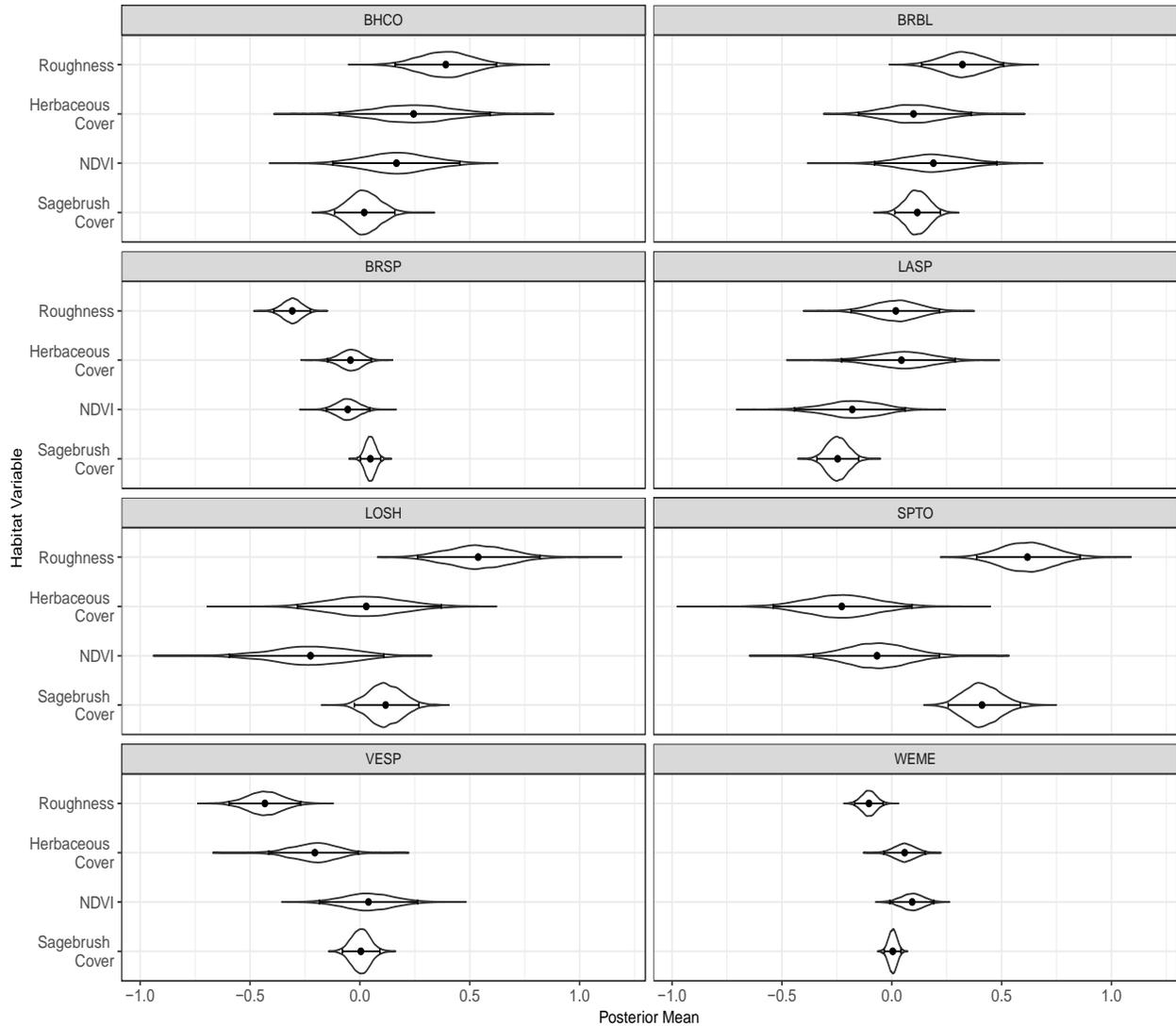


Figure 3. Posterior distributions and 95% credible intervals depicting the influence of four habitat variables on sagebrush songbird abundance in northeastern Wyoming, USA (2016-2018).

### 3.4 Discussion

Our study was designed to assess the response of species abundance across a gradient of energy development. Based on previous research that documented declines in abundance at energy fields for some of our species, we expected to observe the same trend for the same species (Gilbert and Chalfoun 2011). For species adapted to human-disturbance, we expected an increase in abundance with increasing disturbance. Additionally, for many of our species, there is

insufficient information to make a prediction, although we expected to observe an increase in abundance with decreased disturbance based on previous research on other sagebrush songbirds. Reclamation efforts seemed to produce a measurable influence on some species abundance. However, our results were not consistently in the predicted direction. Indeed, for some species, the pattern of predicted abundance across treatments was opposite of what we would expect based on previous research, and no species demonstrated our expected outcome of increasing abundance with decreasing disturbance. Somewhat unexpectedly, half of the species increased in abundance with active development.

We also determined the influence of key habitat variables on species abundance, including those that are often used in reclamation projects, to better inform reclamation. Our assessment was largely consistent with species ecology. However, most species were influenced by roughness and sagebrush cover. The habitat covariates that best represent where we can most easily target reclamation efforts (i.e., NDVI and herbaceous cover; Davies et al. 2013, Anadarko Petroleum Corporation 2014, Avirmed et al. 2015, Pyke et al. 2015), had minimal influence on most species abundance.

### **3.4.1 Abundance Response to Treatment**

As expected, of all 8 species, western meadowlark abundance had the highest posterior distribution overlap among treatments. This is consistent with previous research that has demonstrated that western meadowlark abundance remains unaffected in relation to oil and gas development (Ludlow et al. 2015, Thompson et al. 2015), presence of roads (Sutter et al. 2000), and grassland reclamation (Fletcher and Koford 2003). Western meadowlarks are generalist species that occupy a wide range of grassland habitat and show considerable variation in habitat preferences (Dechant et al. 1999, Davis and Lanyon 2008, Harrison et al. 2010), suggesting that

the change in habitat due to energy development and subsequent reclamation still created habitat conditions that fell within the acceptable range.

An increase in brown-headed cowbird and Brewer's blackbird abundance was detected with increasing disturbance from control to reclaimed to active, which was expected. This finding is consistent with literature demonstrating that brown-headed cowbird (Ludlow et al. 2015, Bernath-Plaisted et al. 2017, Farwell et al. 2019), and Brewer's blackbird (Stepney and Power 1973, Blair 1996, Martin 2002) abundance is positively associated with increased human development. Specifically, brown-headed cowbird abundance increased 3 – 4x in areas with oil and gas well infrastructure (Ludlow et al. 2015, Bernath-Plaisted et al. 2017). Brown-headed cowbirds also do not avoid roads (Thompson et al. 2015), and increased in abundance in edge habitat (Howell et al. 2007). This may be due to their use of linear corridors (e.g., roads, power lines) for breeding and roosting core ranges (Gates and Evans 1998). Brewer's blackbird also prefer open, human-modified habitats, including corridors like roads, fence lines, and railways, although there is considerable plasticity in their habitat preferences (Blair 1996, Martin 2002).

Of all 8 species, we expected to observe a decrease in Brewer's sparrow abundance with increasing disturbance. However, Brewer's sparrow abundance was the lowest in the control treatment, with no observable difference between reclaimed and active treatments. Brewer's sparrow abundance decreased in abundance with increasing well density within 1 km<sup>2</sup> of point count locations in a highly productive well field (Jonah Field) in Wyoming (Gilbert and Chalfoun 2011). At the same location, Brewer's sparrow abundance significantly decreased within 100 m of a road (Ingelfinger and Anderson 2004). At this site, the average traffic volume was over 600 vehicles per day (Ingelfinger and Anderson 2004, Gilbert and Chalfoun 2011). However, Gilbert and Chalfoun (2011) also observed no significant difference in Brewer's

sparrow abundance at an energy field (LaBarge) with lower traffic volume (e.g., 5 vehicles per day). They attributed the lower abundance to increased infrastructure that can influence edge effects, nest success, and species interactions (Gilbert and Chalfoun 2011). Similarly, Brewer's sparrow occupancy decreased with increasing intensity of development (Mutter et al. 2015). However, there was no influence of proximity to roads or wells on Brewer's sparrow occupancy at the local or landscape scale (Mutter et al. 2015). Additionally, Brewer's sparrow density slightly increased within 100 m of pipelines (Ingelfinger and Anderson 2004), and increased with well density at the landscape scale, although the parameter estimate's confidence interval included zero (Mutter et al. 2015). At our study site, traffic volume in the active treatment is considerably lower than that at Jonah Field in the study conducted by Gilbert and Chalfoun (2011). The traffic volume at our active sites most resembles that at LaBarge (Gilbert and Chalfoun 2011), with infrequent vehicles traveling the roads or visiting wells. Therefore, traffic volume may not have influenced Brewer's sparrow abundance at our site. Additionally, Brewer's sparrow density increased with increasing number of basal and canopy gaps in Wyoming, suggesting that homogenous, dense sagebrush stands with no horizontal and vertical heterogeneity would decrease Brewer's sparrow abundance (Williams et al. 2011b). Therefore, creation of horizontal and vertical heterogeneity in the stand structure by removal of some sagebrush in the active and reclaimed treatments may positively influence the abundance of Brewer's sparrow.

Previous research on the influence of energy development and reclamation on the remaining 4 species is entirely lacking or abundance trends are inconsistent throughout the species range. Since a decrease in the abundance of some sagebrush songbirds with closer proximity to energy development fields has previously been recorded (Ingelfinger and Anderson

2004, Aldridge et al. 2011, Gilbert and Chalfoun 2011), we expected to observe an increase in abundance with decreasing disturbance (active to reclaimed to control). However, we did not observe this trend for any species. Lark sparrow abundance increased with increasing disturbance (control to reclaimed to active). There is only one study that has been completed on the influence of energy development on lark sparrow abundance, which documented a decline in abundance with proximity to well pad sites in Wyoming, however, the association was weak (Aldridge et al. 2011). In other studies on human-caused disturbance, lark sparrow density and occurrence increased with increasing percentage of disturbance by vehicle tracks (Tazik 1991). Spotted towhee abundance increased from active to control to reclaimed in our study. There is little information on the influence of energy development on spotted towhee abundance. However, consistent with our results that documented decreased abundance in active areas, LaGory et al. (2001) reported significantly lower numbers of spotted towhee near compressor stations and wells due to their sensitivity to noise. Vesper sparrows were the least abundant in the active treatment, with no observable difference in abundance between the reclaimed and control treatments in our study. Vesper sparrow abundance similarly declined in response to increased well density in Wyoming, possibly due to intensified edge effects, decreased nest success, or altered species interactions (Gilbert and Chalfoun 2011). Vesper sparrow also avoid urbanized landscapes (Bock et al. 1999), pipelines (Aldridge et al. 2011), and mining operations (Schaid et al. 1983). However, this trend is not consistent throughout the range, as vesper sparrow abundance also increased in proximity to oil and gas roads (Linnen 2008), wells (Rodgers and Koper 2017), and was found in higher abundances closer to roads in comparison to trails (Sutter et al. 2000). The influence of energy development or reclamation on loggerhead shrike has not been previously assessed.

### 3.4.2 Perch Sites

Perch sites are an important component of songbird habitats as they provide elevated areas to sing for territory defense and mate attraction (Collins 1981, Castrale 1983). Loggerhead shrike abundance was slightly greater in the reclaimed treatment, with no detectable difference between active and control, although with considerable overlap in posterior distributions. Spotted towhee abundance was also the greatest in the reclaimed treatment, followed by the control and active treatments. Both species abundance also increased at our study site with increasing roughness, and this trend has been previously observed for loggerhead shrike (Duchardt et al. 2018). Duchardt et al. (2018) suggested that loggerhead shrike likely use sparse trees as perch sites, which are present in drainages associated with rougher terrain (Becker et al. 2009). Spotted towhee also actively use high perches for singing (Smith and Greenlaw 2015). Therefore, although not directly tested for in our analysis, both species abundance may have been influenced by the tall trees present in drainages associated with rough terrain, increasing their abundance in the reclaimed treatment.

Fencing, and oil and gas wells in human disturbed areas provide perch sites for many species in our analysis which may have influenced their abundance (Rodgers and Koper 2017). Rodgers and Koper (2017) speculated that an increase in western meadowlark abundance with closer proximity to wells was likely due to increased availability of perch sites (e.g., fencing around wells and well infrastructure) for vocalizations. Similarly, the abundance of the two human-commensal species in our analysis, Brewer's blackbird and brown-headed cowbird, as well as lark sparrow and Brewer's sparrow, may have increased with development as perch sites became more readily available. Perches allow brown-headed cowbird to more effectively locate potential host nests (Thompson and Gottfried 1976, Ludlow et al. 2015, Thompson et al. 2016),

and Brewer's blackbird to use as guard perches for predator detection and mate defense (Laidlaw 1952, Horn 1968, 1970; Martin 2002). Additionally, lark sparrow (Tullsen 1911, Renwald 1977, Martin and Parrish 2000), and Brewer's sparrow (Castrale 1983, Rotenberry et al. 1999), use perches for vocalizations during the breeding season. Perching opportunities for songbirds may increase with increased infrastructure (e.g., fences, oil and gas wells), and may lead to higher abundances in human-disturbed areas (Sutter et al. 2000, Rodgers and Koper 2017).

Brown-headed cowbird and Brewer's blackbird abundances also increased with rougher terrain. Rough terrain may increase the availability of vantage points and may act in a similar way as fences and wells for perching. Additionally, similarly to loggerhead shrike, the sparse trees present in drainages of rough terrain may act as perch sites (Duchardt et al. 2018). Brewer's sparrow showed the opposite trend of decreasing abundance with increasing roughness. Brewer's sparrow do not often use highly elevated perches (Castrale 1983), suggesting that they would not make use of tall trees found in drainages associated with rough terrain, and would not be expected to increase in abundance with increasing roughness.

### **3.4.3 Abundance Response to Habitat Variables**

Roughness and sagebrush cover were influential on more species abundance than herbaceous cover and NDVI, based on posterior means and 95% CIs (Table 2). However, despite some 95% CIs crossing zero, clear trends on the influence of habitat variables on songbird abundance emerged.

Table 2. The influence of terrain roughness, sagebrush cover, herbaceous cover, and NDVI on sagebrush songbird abundance in northeastern Wyoming, USA, 2016-2018. Effect direction is based on estimated posterior means, and 95% credible intervals (CI) <sup>a</sup>.

Species	Roughness	Sagebrush Cover	Herbaceous Cover	NDVI
Brown-headed cowbird	+	0	0	0
Brewer's blackbird	+	+	0	0
Brewer's sparrow	-	+	0	0
Lark sparrow	0	-	0	0
Loggerhead shrike	+	0	0	0
Spotted towhee	+	+	0	0
Vesper sparrow	-	0	-	0
Western meadowlark	-	0	0	0
Total	7	4	1	0

<sup>a</sup>Effect directions are denoted as follows: Positive (+), negative (-), and neutral (0).

As mentioned previously, western meadowlark are generalist species that often use areas of high forb and grass cover (Davis and Lanyon 2008). NDVI and herbaceous cover posterior distributions were positively associated with western meadowlark abundance, although the CIs crossed zero. These habitat variables may not have influenced this generalist species abundance at our study site, possibly because they fell within the range of acceptable habitat conditions across the landscape. Vesper sparrow are also considered generalist grassland species that inhabit a variety of open habitats, and they occur in areas with patchy herbaceous vegetation, increased bare ground cover, less litter, and short shrubs (Jones and Cornely 2002, Ludlow et al. 2015, Rodgers and Koper 2017). This is consistent with our results that show an increase in vesper sparrow abundance with decreasing herbaceous cover. Lark sparrow abundance was not influenced by NDVI or herbaceous cover at our study site. Lark sparrows are associated with structurally open habitats with grass ground cover and scattered sparse trees and shrubs for breeding, and are often found in ecotone boundaries (Martin and Parrish 2000, Aldridge et al. 2011). Additionally, lark sparrow have shown a preference for grazed and burned areas that have lower shrub cover and open grassy areas (Bock and Webb 1984, Bock et al. 1984, Martin and Parrish 2000, Lusk et al. 2012, Gallo et al. 2017). Lark sparrow abundance may not be related to

total herbaceous cover at our study area, rather, it may be influenced by large areas of open grassland, which active and reclaimed well pads and roads provide.

An increase in sagebrush cover was associated with an increase in loggerhead shrike, spotted towhee, Brewer's blackbird, and Brewer's sparrow abundance, although the CIs crossed zero for loggerhead shrike. All of these species use sagebrush for nesting and foraging in sagebrush ecosystems, so it is unsurprising that sagebrush cover positively influenced abundance (Horn 1968, Orians and Horn 1969, Baker et al. 1976, Woods and Cade 1996, Van Vuren 2013, Smith and Greenlaw 2015). Specifically, Brewer's sparrow are considered sagebrush-obligate species as they primarily use sagebrush for breeding (Baker et al. 1976). Lark sparrow abundance had the opposite response to sagebrush cover, as decreasing sagebrush cover increased lark sparrow abundance. This is consistent with previous literature that documented a decrease in lark sparrow abundance with increasing shrub density (e.g., sagebrush, rabbitbrush, and black greasewood; McAdoo et al. 1989).

#### **3.4.4 Nests, Predation, and Ecological Traps**

The concept of energy development areas becoming equal preference ecological traps for species in the sagebrush ecosystem has been previously proposed (Hethcoat and Chalfoun 2015a). Our study provides a crucial piece of this puzzle, since bird counts likely act as an appropriate indicator of breeding habitat quality and nest success, although this relationship is more variable in human-disturbed environments (Bock and Jones 2004). Therefore, we thought that discussing the known influence of energy development on nest success and density in comparison with our study provides a more comprehensive understanding of the influence of energy development on species abundance.

Increased densities of Brewer's sparrow, vesper sparrow, and western meadowlark nest predators (e.g., rodents, corvids, badgers, etc.) are associated with energy development areas (Grant et al. 2006, Davis and Lanyon 2008, Coates et al. 2014, Hethcoat and Chalfoun 2015b, Ludlow et al. 2015, Bernath-Plaisted et al. 2017, Sanders and Chalfoun 2018). Specifically for vesper sparrow, Bernath-Plaisted and Koper (2016) determined that vesper sparrow nest density increased with proximity to infrastructure, leading to decreased nest success, likely due to an increase in nest predators near development areas. In our study, of these three species, vesper sparrow was the only species to decrease in abundance in the active treatment. Brewer's sparrow abundance was the greatest in the active and reclaimed sites, and western meadowlark abundance remained unaffected. With an increase in nest predator densities with increasing disturbance, it is surprising that Brewer's sparrow and western meadowlark did not avoid the active development treatments. An increase in nest predator density and perching opportunity in the active areas may increase the risk of active sites becoming equal preference ecological traps for songbirds, and this relationship requires further study.

### **3.4.5 Conclusions**

Our study focusses on the influence of a gradient of disturbance and key habitat variables on sagebrush songbird abundance. We determined that species responses to energy development and reclamation are variable, and we did not observe our expected outcome of increasing abundance with decreasing human disturbance (active to reclaimed to control) in any species. This may be due to the intensity of development, which was low at our study area. However, there are documented negative impacts of energy development on some species, that in our analysis, were more abundant in human-disturbed areas. Specifically, for our only sagebrush-obligate species, loss of sagebrush habitat from increased energy development can lead to a

decrease in Brewer's sparrow nest survival (Hethcoat and Chalfoun 2015a), and decreases in abundance (Gilbert and Chalfoun 2011). Increased predation pressure at active energy development sites may also lead to these areas becoming equal preference ecological traps (Hethcoat and Chalfoun 2015b, Sanders and Chalfoun 2019). We focussed on the influence of development on abundance, and the logical next step is to look at songbird survival and fitness parameters across this gradient of development at our study site.

We highlight the possible influence of increased perching availability on the abundance of songbirds at human-disturbed sites. Research on the influence of mitigation strategies in the PRB have primarily focussed on the high-profile gamebird, the greater sage-grouse (*Centrocercus urophasianus*; Fedy et al. 2015). These mitigation strategies include reducing the intensity of road and well construction (Lyon and Anderson 2003, Wisdom et al. 2011), which may limit the availability of perching sites, while also benefitting songbird nest survival (Gilbert and Chalfoun 2011). Therefore, explicitly testing the hypothesis that increasing perching availability with increasing development influences sagebrush songbird abundance, is necessary to uncouple these complex mechanisms.

A clear trend of increasing abundance with increasing disturbance was observed for the two species in our analysis that are more adapted to human development (i.e., Brewer's blackbird and brown-headed cowbird). Additionally, the differences in roughness and sagebrush cover across our gradient of development were small between sites, but those slight differences in landscape topography and context may limit short-term reclamation potential when looking at sagebrush-obligates such as Brewer's sparrow. Therefore, using human-commensal species as indicators may provide to be more useful in determining if reclaimed areas better reflect the conditions at undisturbed or active development sites.

We documented the influence of terrain roughness on songbird abundance. To our knowledge, this has not been observed previously for various species in our analysis, and the mechanisms influencing abundance due to roughness are currently unknown. Roughness had the greatest influence on abundance of our habitat variables, which suggests that this habitat variable should be included in future studies on modeling abundance. Sagebrush cover also influenced the abundance of our species, and NDVI and herbaceous cover did not influence the abundance of most of our species. This suggests that the habitat variables that are the most difficult to manipulate in reclamation projects (e.g., terrain roughness and sagebrush cover; Davies et al. 2013), are the most influential on songbird abundance, which should be taken into account when determining the ‘success’ of reclamation projects.

Our study is the first to assess the influence of landscape-scale reclamation on songbird abundance in the sagebrush ecosystem. The use of ecological reclamation for the sagebrush ecosystem is becoming more prevalent in policy planning and mitigation strategies (Pyke 2011, U.S Fish and Wildlife Service 2013, Clement et al. 2014, Finch et al. 2016). However, it is possible that the reclamation practices that were completed were not ambitious enough in terms of scope and spatial scale, since some reclamation practices are determined by landowner preference (Anadarko Petroleum Corporation 2014). Habitat selection in animals is a hierarchical process, and species select breeding areas based on different spatial scales (Johnson 1980). As reclamation projects become more popular in the sagebrush ecosystem, studies on the response of wildlife abundance to reclaimed landscapes at different spatial scales are needed to fully understand the consequences of development and subsequent reclamation. Additionally, sagebrush has a recovery period of up to 120 years post-disturbance (Baker 2006, Avirmed et al. 2015). Since data collection for this study began 3 years after reclamation was completed, this

may not be enough time for us to detect substantial differences in species abundance between our three treatments. Therefore, continued monitoring will be required to determine the long-term impact on wildlife abundance.

## 4 Testing the Umbrella Species Concept at Fine Spatial Scales

### 4.1 Introduction

Habitat loss is still the biggest threat to global biodiversity (Hanski 2011), and understanding habitat selection is crucial to inform conservation planning that prioritizes habitat protection. Habitat selection in animals is a hierarchical process, including landscape (i.e., first and second order) and local scale (i.e., third and fourth order) selection (Johnson 1980, Meyer and Thuiller 2006). Since habitat treatments and management must occur at the local scale, studies that quantify species local habitat preferences are needed to effectively guide species management.

Habitat fragmentation, degradation, and loss of sagebrush (*Artemisia* spp.) ecosystems in North America have been driven by wildfire, agriculture, invasive species, urbanization, and energy development (Knick et al. 2003, Homer et al. 2015). These and other factors have contributed to sagebrush ecosystems becoming increasingly imperiled (Finch et al. 2016). Over 350 species rely on sagebrush ecosystems for survival (Finch et al. 2016), including grassland and shrubland songbirds which have experienced the fastest population declines of any avian group in North America (Knick et al. 2003). Brewer's sparrow (*Spizella breweri*) is a migratory songbird species that has experienced population declines of ~35% between 1970-2014 (Dumroese et al. 2015, Rosenberg et al. 2016). It primarily uses sagebrush for breeding and is thus considered a sagebrush-obligate species (Baker et al. 1976). Although globally secure, it is a species of conservation concern in the USA as the current population trend is decreasing and there is long term concern over the species persistence (U.S. Fish and Wildlife Service 2008, BirdLife International 2018). Management of sagebrush ecosystems, including Brewer's sparrow habitat, has historically focused on few umbrella species, which assumes that the conservation of

one species (i.e., the umbrella species) will benefit the conservation of other naturally co-occurring species (Roberge and Angelstam 2004, Hunter et al. 2016). The greater sage-grouse (*Centrocercus urophasianus*; hereafter “sage-grouse”) has been proposed as an umbrella species for much of the sagebrush ecosystem, specifically for conservation of sagebrush-obligate and associated wildlife (Rowland et al. 2006, Connelly et al. 2011, Hanser and Knick 2011, Copeland et al. 2014, Finch et al. 2016).

The sage-grouse is a sagebrush-obligate gamebird (Doherty et al. 2010a, 2011a, Hanser and Knick 2011, Kirol et al. 2012, Fedy et al. 2014), that occupies approximately half of its historic range, and has received much conservation attention in recent years (Connelly et al. 2011, Knick and Connelly 2011, Conover and Roberts 2016). Declines in sage-grouse populations across the range have been mainly attributed to habitat loss and degradation (Conover and Roberts 2016). This has resulted in targeted habitat management efforts at the state and federal level intended to benefit sage-grouse populations (U.S Fish and Wildlife Service 2013, Finch et al. 2016). These include, but are not limited to, invasive species management, habitat reclamation, and management of plant communities (Finch et al. 2016). Sage-grouse meet the criteria of an umbrella species in that they have a broad geographic range, resource requirements that overlap with many species (namely sagebrush-obligates), has experienced range-wide population declines, and sage-grouse responses to human induced habitat changes are well-documented (Rowland et al. 2006, Doherty et al. 2008, 2011b; Connelly et al. 2011, Fedy et al. 2015, Holloran et al. 2015, Kirol et al. 2015).

At the landscape scale, sage-grouse may be a useful umbrella species for Brewer’s sparrow, but their effectiveness as a conservation proxy may be limited at finer spatial scales (Rich et al. 2005, Rowland et al. 2006, Hanser and Knick 2011, Copeland et al. 2014, Finch et al.

2016). Few studies have assessed the effectiveness of sage-grouse as an umbrella species at the local scale for the conservation of sagebrush habitats (Hanser and Knick 2011, Holmes et al. 2017, Carlisle et al. 2018a, b). Recently, Carlisle et al. (2018a) suggested that caution must be used when implementing habitat management for sage-grouse conservation. Complete loss of breeding habitat for sagebrush-obligate passerines, including Brewer's sparrow, was observed at mowed sites intended to increase herbaceous plant growth for sage-grouse brood-rearing habitat (Carlisle et al. 2018a). However, it is important to note that the benefit of mowing as a habitat treatment for sage-grouse is questionable (Hess and Beck 2012, Smith and Beck 2018). Previous avian research in sagebrush habitats have independently examined local habitat influences on passerine abundances and density (Gilbert and Chalfoun 2011, Hanser and Knick 2011, Holmes et al. 2017, Carlisle et al. 2018a), and sage-grouse (Doherty et al. 2008, 2010a, 2011a, Kirol et al. 2012, Holloran et al. 2015, Lockyer et al. 2015, Dinkins et al. 2016); however, direct comparison of these studies is difficult because rigorous comparison of the habitat needs of different species require data quantified in a similar region using similar approaches. Carlisle et al. (2018b) determined that some species of different taxonomy, restricted distributions, and affinity to sagebrush, were not well protected by sage-grouse reserves because they did not explicitly try to incorporate distributions of these other species. According to Carlisle et al. (2018b), the amount of Brewer's sparrow habitat protected by an established sage-grouse Core Area in Wyoming, USA, was ~37%. Additionally, 85% of pinyon-juniper removal experiments conducted across the majority of the sage-grouse range that were intended to benefit sage-grouse populations, overlapped landscape areas of moderate to high Brewer's sparrow abundance (Donnelly et al. 2017). However, it is difficult to apply the results from these studies directly to on-the-ground treatments, since these studies were focused on landscape scale habitat selection.

The availability of nesting habitat is critical to avian productivity (Martin 1998). We evaluated habitat characteristics influencing nest-site selection of Brewer's sparrow and sage-grouse at a study site in northeastern Wyoming, USA (~1,350 km<sup>2</sup>). Wyoming contains large intact sagebrush ecosystems, where sage-grouse occupy ~70% of the state, and contains ~37% of the total male sage-grouse population (Connelly et al. 2004, Doherty et al. 2010b, Fedy et al. 2014, United States Department of the Interior 2015). By using established protocols for sage-grouse microhabitat data collection (Connelly et al. 2003) at the third order (hereafter "nest patch") and fourth order (hereafter "nest shrub") selection processes (Johnson 1980, Krausman 1999), we collected Brewer's sparrow nest and non-nest (random) microhabitat data to examine the habitat characteristics influencing nest-site selection of Brewer's sparrow, and compare the influence of the habitat variables present in the top Brewer's sparrow nest-site selection model on the probability of nest-site selection of sage-grouse at our study site (Doherty et al. 2010b, 2011a).

#### **4.2 Study Area**

Our study site was located in sagebrush-steppe habitat in northeastern Wyoming, USA, within the Powder River Basin region (44.2603°N, -106.3095W°; Figure 4). The plant communities in this area were dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*), black greasewood (*Sarcobatus vermiculatus*), green and gray rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), native grasses including blue grama (*Bouteloua gracilis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and non-native Japanese brome (*Bromus japonicas*) and cheatgrass (*B. tectorum*). Land use in the region was predominantly industrial oil and gas extraction and cattle ranching. Elevation ranged between 1268 m – 1442 m. Previous research in this region focused primarily on sage-grouse and detailed descriptions of the region

can be found in those studies (Walker et al. 2007, Doherty et al. 2011a, Fedy et al. 2014, 2015; Kirol et al. 2015).

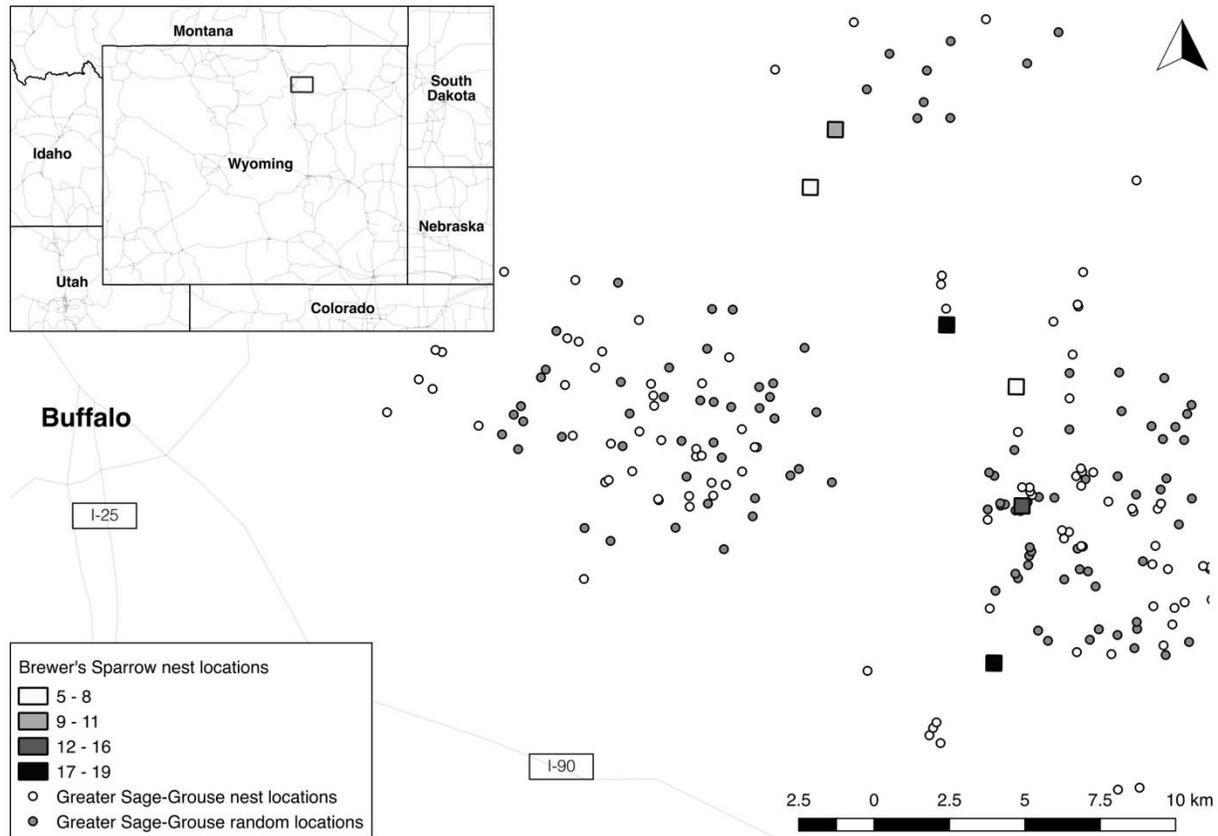


Figure 4. Map of study area and nest-searching plots for Brewer's sparrow in northeastern Wyoming, USA, 2016-2017. Greater sage-grouse nest and random locations are denoted by white and gray circles, respectively, 2004-2007. Nest-searching plots are denoted by squares.

### 4.3 Methods

#### 4.3.1 Nest Searching

We searched intensively for Brewer's sparrow nests in six, 500 m × 500 m plots distributed across the study site in 2016 and 2017 (Figure 4). Nest searching took place ~4.5 days/week throughout the breeding season between 9 May and 15 July. We used auditory and visual clues to locate the nests and recorded the locations of all active nests. All research was approved by the University of Waterloo's Animal Care Committee (Animal Utilization Project

Protocol #16-06), and the State of Wyoming which allowed research on Wyoming State trust lands.

#### **4.3.2 Habitat Sampling**

Habitat sampling was completed at the nest site and two paired random locations for all Brewer's sparrow nests. We sampled nest and paired random locations immediately after the Brewer's sparrow nesting season concluded each year. To minimize detrimental effects on nest initiation and egg and chick survival, we did not sample immediately after individual nests fledged. Brewer's sparrows nest together in loose colonies and may double and triple-clutch (Rotenberry et al. 1999, Mahony et al. 2001). Further, we were trying to avoid biasing nest initiation and survival associated with investigator disturbance because in a companion study we are investigating how these demographics are influenced by the proximity to human development features.

Habitat measurements at random locations were completed the same day or within a few days of the nest site sampling because of concerns of phenological biases (Gibson et al. 2016, Smith et al. 2018). Brewer's sparrows have breeding territories between 0.25 - 0.50 hectares (Hansley and Beauvais 2004), and maintain spacing between nests which are generally in the center of their territories (Rotenberry et al. 1999). We selected random locations by following a random compass bearing 25 m from the nest shrub. This distance was based on the breeding ecology of the species and assumes an average breeding territory of 0.25 hectares with the nest at the center of this territory (Reynolds 1981). Thus, the random sites should, on average, have been available to the individual for selection. We thoroughly searched random sites for any evidence of current or past Brewer's sparrow nesting, and sites were not included if evidence of nesting was found. Since the average nest shrub height for Brewer's sparrow can vary

considerably (*i.e.*, 43 cm  $\pm$  18 SD to 71.36 cm  $\pm$  1.23 SE) between locations (Rich 1980, Petersen and Best 1985, Rotenberry et al. 1999), and is likely influenced by availability, the random sites were centered on the closest sagebrush plant taller than 30 cm, which was the minimum height of a shrub containing a nest at our site in 2016 when sampling began. We measured habitat characteristics along two perpendicular 10 m transects in cardinal directions, centered at each nest or random shrub. Brewer's sparrow habitat sampling was designed to be directly comparable to habitat sampling techniques developed for sage-grouse research (Doherty et al. 2010a, Kirol et al. 2012, Dinkins et al. 2016).

Sage-grouse and Brewer's sparrow are both considered sagebrush-obligates due to their reliance on sagebrush for breeding (Rotenberry et al. 1999, Chalfoun and Martin 2007, Kirol et al. 2012, Fedy et al. 2014, Doherty et al. 2016). Therefore, we recorded multiple shrub characteristics at all sites including species, height, width, vigor, and branching density (Table 3). Along each transect we measured shrub canopy cover, height, and variation in shrub height using the line intercept method (Canfield 1941, Connelly et al. 2003, Wambolt et al. 2006).

Nest predation influences reproductive success and birds select habitats to impede detection by potential predators (Ricklefs 1969, Chalfoun and Martin 2010, Coates and Delehanty 2010). We estimated visual obstruction at the nest or random shrub using a 3 cm diameter  $\times$  1.5 m long modified Robel pole (Robel et al. 1970, Ralph et al. 1993). The pole was placed in the middle of the nest or random shrub. We situated an observer at the end of the transects at each cardinal direction at a 1 m height above the ground and recorded the first half or full decimeter that was visible along the pole. These four measurements were averaged to give one visual obstruction estimate for the plot.

During the breeding season, sage-grouse prefer areas with higher herbaceous ground cover but may avoid invasive grasses (Kirol et al. 2012), and the influence on Brewer's sparrow isn't well understood (Petersen and Best 1985, Paczek and Krannitz 2005, Hagen et al. 2007, Harrison and Green 2010). We estimated percent cover of annual invasive (non-native) grass, cool grass, warm grass, forbs, subshrubs, litter, gravel and rock, and bare soil, in addition to grass droop height and forb richness (Table 3), within 6 cover classes in 9, 20 cm × 50 cm (0.1 m<sup>2</sup>) Daubenmire quadrats (Daubenmire 1959), placed along each transect. We designated cover classes as: 0 = 0%, 1 = 0.1–1%, 2 = 1.1–5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, and 6 = 75.1–100%. We used midpoints of 0.0, 0.55, 3.05, 15.05, 37.55, 62.55, and 87.55%, respectively, to estimate percent cover.

Table 3. Microhabitat variables used to assess Brewer’s sparrow nest-site selection. Data were collected at 73 nests and 146 random locations in 2016-2017 in northeastern, Wyoming, USA.

Variable Name	Description
<b>Nest Shrub</b>	
Shrub Height	Height of the center shrub at the nest or random location, excluding inflorescences
Max Width	Maximum canopy width
Perp Width	Perpendicular canopy width
Vigor	Percentage of alive foliage (nearest 10%)
Branching Density	Branching density categories: 1 = very sparse, 2 = sparse, 3 = moderate, 4 = dense, 5 = very dense
Nest Height	Height to the bottom of the nest cup from the ground
Visual Obstruction	Average of Robel pole measurements
<b>Nest Patch: Shrub Cover and Density</b>	
Variation	Standard deviation of shrub heights along line intercept per plot
Percent ARTR	Percent alive sagebrush cover
Percent Total	Percent total shrub cover
<b>Nest Patch: Herbaceous Cover</b>	
Invasive Grass	% invasive grass cover
Cool Grass	% cool grass cover
Warm Grass	% warm grass cover
Forbs	% forb cover
Subshrub	% subshrub cover
Litter	% litter cover
Grass and Rock	% gravel and rock cover
Bare Soil	% bare soil cover
Grass Height	Tallest droop grass height
Forb Richness	Forb richness; number of forb species

### 4.3.3 Sage-grouse Data

To compare the habitat characteristics that influence nest-site selection of Brewer’s sparrow and sage-grouse, we used nesting habitat data for sage-grouse that were collected in the same region using similar methods (Doherty et al. 2010a, 2011a). The same center shrub, shrub cover, and shrub density variables were collected for both the sage-grouse and Brewer’s sparrow. Visual obstruction measurements for the sage-grouse dataset were taken from 1 m closer to the center shrub in comparison to the Brewer’s sparrow data. The same herbaceous cover variables were not collected for both species and are therefore not included in the comparison analysis. We

used sage-grouse habitat data from 217 nest sites and 195 random locations collected between 2004 and 2007 (Figure 4). Sage-grouse consistently display similar habitat preferences across broad spatial scales throughout their range and through time, despite some variability in the shape of response curves throughout the range (Hagen et al. 2007, Doherty et al. 2008, Knick and Connelly 2011, Kirol et al. 2012, Fedy et al. 2015). Therefore, the time lag between collection of the sage-grouse data and the Brewer's sparrow data did not likely influence the results. Habitat sampling plots for the sage-grouse data were larger than the Brewer's sparrow plots, 30 m × 30 m versus 10 m × 10 m, due to Brewer's sparrows smaller territories and home range size. Non-categorical habitat variables were standardized for both the sage-grouse and Brewer's sparrow vegetation measurements to provide for direct comparison. Therefore, the only differences were that measurements for shrub cover that were taken for the sage-grouse nests were averaged over a larger area (30 m x 30 m).

#### **4.3.4 Statistical Analysis**

##### **4.3.4.1 Brewer's sparrow nest-site selection**

We modeled nest-site selection for Brewer's sparrow using conditional logistic regression (Compton et al. 2002). We standardized all non-categorical habitat variables prior to modelling. When variables were correlated ( $r \geq |0.60|$ ; Akoglu 2018), we chose the variable that made the most biological sense to move forward to the next modeling step. To determine the most informative habitat variables, we ran univariate models and filtered uninformative variables by degree of 85% confidence intervals (CI) overlap of zero (Hosmer and Lemeshow 2000, Smith et al. 2014, Dinkins et al. 2016). We compared all candidate models based on the difference in  $AIC_c$  values ( $\Delta AIC_c$ ), and competing models within  $\Delta AIC_c \leq 4$  from the top were considered the 'best' models (Burnham and Anderson 2002). Since we were also interested in the importance of

individual habitat variables influencing Brewer's sparrow nest-site selection, variable weights ( $w_i$ ) were computed, which were determined using the weights of the competitive model set within  $\Delta AIC_c \leq 2$  (Burnham and Anderson 2002, Arnold 2010). We used 85% CIs for variable interpretation because they are more appropriate than 95% CIs under an AIC model selection framework (Arnold 2010).

#### **4.3.4.2 Comparison to sage-grouse data**

In the comparison analysis, we were not interested in producing top models representing the habitat variables that best describe nest-site selection by sage-grouse. This information was previously presented by Doherty et al. (2010a, 2011a). Our purpose was to understand how much overlap there is between microhabitat selection by Brewer's sparrow during nesting with that of the sage-grouse.

Logistic regression was previously used on the sage-grouse dataset to evaluate nest-site selection (Doherty et al. 2010a, 2011a). To provide for direct comparison, we modelled sage-grouse nest-site selection using logistic regression and included only the variables present in the top conditional logistic model for Brewer's sparrow nest-site selection. When variables in the top model for Brewer's sparrow nest-site selection were not collected for sage-grouse, they were removed and estimated coefficients between the models with and without removal were compared to test coefficient stability. This allowed us to compare the magnitude and overlap of the coefficient estimates between the species. For clarity, we refer to the set of habitat variables used in models to compare the coefficients between species as the 'comparison variables'.

Marginal effects can be plotted from a fitted logistic regression model and are an excellent way to visualize the shape of model-predicted discrete change for individual covariates. However, population-level marginal effects cannot be computed within a conditional logistic

modelling approach (as we applied to the Brewer’s sparrow data). Therefore, to produce marginal effects plots comparing the shape of the influence of the comparison variables on the probability of nest-site selection for Brewer’s sparrow and sage-grouse, we used the comparison variables to produce a logistic regression model for Brewer’s sparrow. We checked for coefficient stability between a conditional logistic model and logistic model using the comparison variables. All statistical analyses were performed using R version 3.4.2 (R Core Team 2017).

#### 4.4 Results

##### 4.4.1 Nest Shrub and Nest Patch Characteristics

We sampled 73 Brewer’s sparrow nests ( $n = 31$  in 2016,  $n = 42$  in 2017) and 146 paired random locations between 2016-2017. One random location was excluded from analysis due to missing data. Nests were located in sagebrush ( $n = 72$ ) and black greasewood ( $n = 1$ ). Brewer’s sparrow nest heights averaged  $21.8 \pm 10.4$  cm. On average, sage-grouse used larger and taller shrubs, and nest patches with less sagebrush cover than Brewer’s sparrow (Table 4).

Table 4. Comparison of habitat characteristics at the nest shrub and nest patch scale between Brewer’s sparrow ( $n = 73$ ; 2016-2017) and Greater sage-grouse ( $n = 217$ ; 2004-2007) in northeastern Wyoming, USA.

Scale	Variable	Brewer’s sparrow		Greater sage-grouse	
		Mean $\pm$ SD	Range	Mean $\pm$ SD	Range
Nest	Nest Height (cm)	21.8 $\pm$ 10.4	5.0 – 80.0	0.0	0.0
Nest Shrub	Max Width (cm)	84.1 $\pm$ 28.4	43.0 – 176.0	145.9 $\pm$ 43.6	55.0 – 305.0
	Perp Width (cm)	63.6 $\pm$ 24.0	26.0 – 137.0	102.7 $\pm$ 30.4	40.0 – 205.0
	Shrub Height (cm)	60.6 $\pm$ 16.0	30.0 – 108.0	69.2 $\pm$ 15.4	39.0 – 145.0
	Vigor (%)	64.5 $\pm$ 16.5	20.0 – 90.0	70.8 $\pm$ 17.8	0.0 - 100.0
	Visual Obstruction (dm)	3.4 $\pm$ 1.3	1.4 – 6.8	2.7 $\pm$ 1.4	0.1 – 6.8
	Branching Density	3.1 $\pm$ 0.9	2.0 – 5.0	3.0 $\pm$ 0.9	1.0 – 5.0
	Percent ARTR (%)	26.1 $\pm$ 10.7	1.4 – 56.3	19.0 $\pm$ 8.6	1.4 – 48.1
Nest Patch	Forbs (%)	7.8 $\pm$ 4.3	0.4 – 22.6	N/A	N/A
	Variation (cm)	20.2 $\pm$ 6.0	6.8 – 34.5	N/A	N/A

#### **4.4.2 Brewer's sparrow Nest-site Selection**

The habitat variables that were highly correlated were maximum width and perpendicular width, forb richness and forb cover, and percent sagebrush cover and percent total shrub cover. Of these pairings, maximum width, percent sagebrush cover, and forb cover were moved forward in the modelling steps. Maximum and perpendicular width both likely explain the same influence on nest-site selection, therefore perpendicular width was removed. The dominant shrub in our ecosystem was sagebrush, and management of these ecosystems explicitly target sagebrush cover. Therefore, the percent of sagebrush cover was kept as a habitat variable instead of the percent of total shrub cover. Previous literature has suggested that the percentage of forb ground cover may influence sage-grouse (Kirol et al. 2012), therefore, forb cover was moved forward with modeling. Habitat variables considered in the Brewer's sparrow nest-site selection analysis were percent sagebrush cover, variation, shrub height, vigor, visual obstruction, branching density, and forb cover. Among the 256 total conditional logistic regression models, four were within 2  $\Delta AIC_c$  (Table 5). The global model was not competitive ( $K = 7$ ,  $\Delta AIC_c = 5.03$ ).

Table 5. Top and competing conditional logistic models ( $\Delta AIC_c \leq 4$ ) best explaining Brewer's sparrow nest-site selection in northeastern Wyoming, USA, 2016-2017. K is the number of model parameters,  $\Delta AIC_c$  is the difference between  $AIC_c$  values from the competitive and top model, and  $w_i$  is the model weight. The break in the table denotes models within 2  $\Delta AIC_c$  of the top.

Model	K	Log(likelihood)	$\Delta AIC_c$	$w_i$
Forbs + Shrub Height + Vigor + Visual Obstruction	4	-62.93	0.00 <sup>b</sup>	0.17
Branching Density + Forbs + Shrub Height + Vigor + Visual Obstruction	5	-62.35	0.94	0.11
Forbs + Vigor + Visual Obstruction	3	-64.65	1.36	0.09
Forbs + Shrub Height + Vigor	3	-64.82	1.69	0.07
Forbs + Shrub Height + Variation + Vigor + Visual Obstruction	5	-62.92	2.06	0.06
Forbs + Shrub Height + Percent ARTR+ Vigor + Visual Obstruction	5	-62.93	2.09	0.06
Branching Density + Forbs + Vigor + Visual Obstruction	4	-64.01	2.15	0.06
Branching Density + Forbs + Shrub Height + Vigor	4	-64.15	2.44	0.05
Forbs + Variation + Vigor + Visual Obstruction	4	-64.17	2.47	0.05
Branching Density + Forbs + Shrub Height + Variation + Vigor + Visual Obstruction	6	-62.28	2.90	0.04
Branching Density + Forbs + Variation + Vigor + Visual Obstruction	5	-63.34	2.91	0.04
Branching Density + Forbs + Percent ARTR + Shrub Height + Vigor + Visual Obstruction	6	-62.35	3.04	0.04
Forbs + Percent ARTR + Vigor + Visual Obstruction	4	-64.48	3.09	0.04
Forbs + Percent ARTR + Shrub Height + Vigor	4	-64.63	3.40	0.03
Shrub Height + Vigor + Visual Obstruction	3	-65.72	3.50	0.03
Forbs + Shrub Height + Variation + Vigor	4	-64.80	3.73	0.03
Branching Density + Forbs + Percent ARTR + Vigor + Visual Obstruction	5	-63.81	3.86	0.03
Vigor + Visual Obstruction	2	-66.97	3.94	0.02

<sup>b</sup> $AIC_c$  of top model = 134.1

We primarily focused our interpretations based on predictions from the model including branching density, forb cover, shrub height, vigor, and visual obstruction. In this model, the branching density coefficient estimate was the only variable with 85% CIs overlapping zero (Figure 5; Table 6). Branching density had the lowest variable weight when assessing relative variable importance, and vigor and forb cover have the highest variable weight (Table 6).

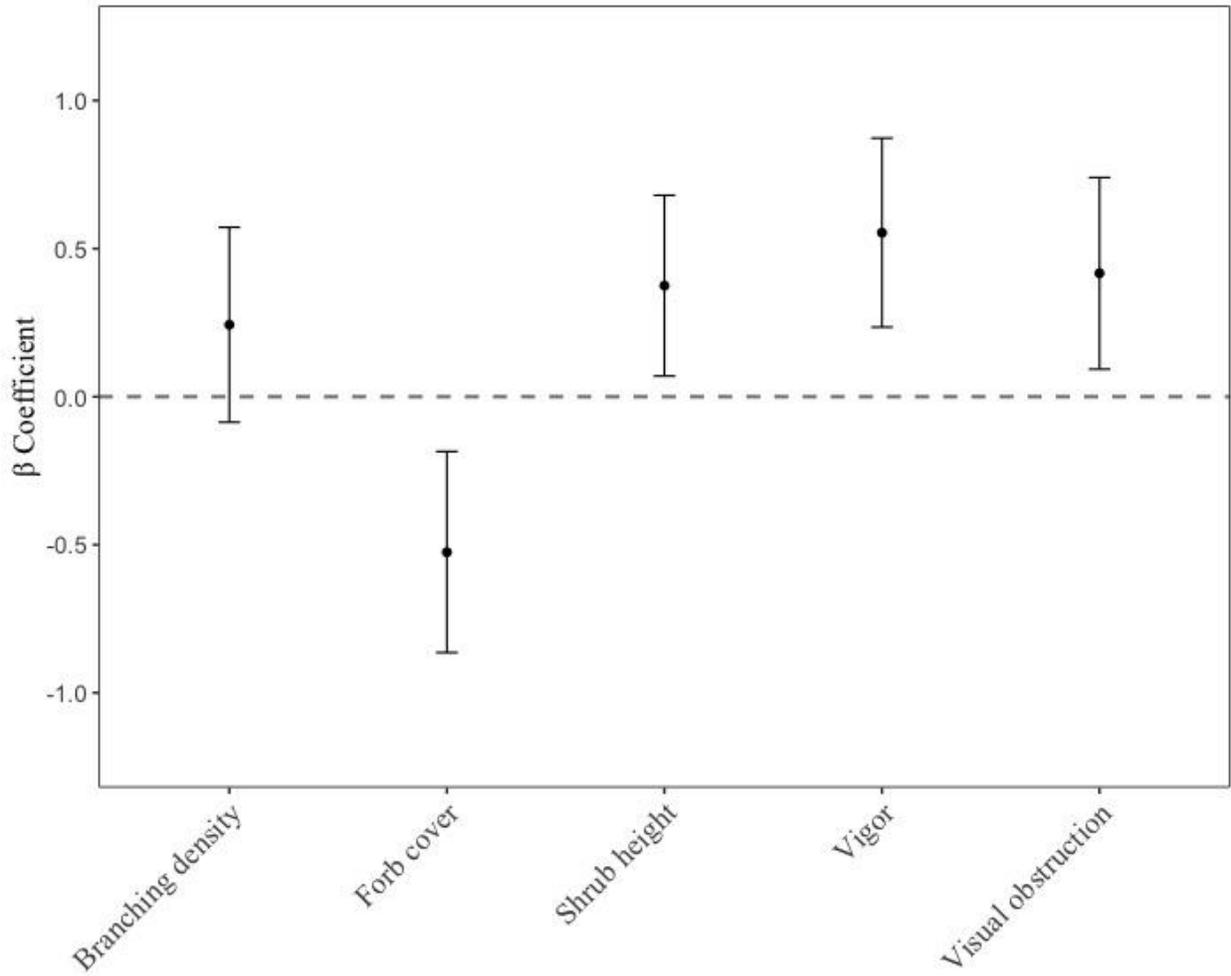


Figure 5. Beta-coefficient estimates and associated 85% confidence intervals for all variables included in the top conditional logistic model set for Brewer's sparrow nest-site selection in northeastern Wyoming, USA, 2016-2017. Estimates are based on the global model: Branching Density + Forbs + Shrub Height + Vigor + Visual Obstruction. Results are from standardized variables, with the exception of Branching Density, which is categorical.

Table 6. Summary of variable coefficients ( $\beta$ ), and variable weights determined by using conditional logistic models within  $\Delta AIC_c \leq 2$  of the top model for Brewer’s sparrow nest-site selection in northeastern Wyoming, USA, 2016-2017. The 85% confidence intervals (CI) and coefficients are from the global model: Branching Density + Forbs + Shrub Height + Vigor and Visual Obstruction. Results are from standardized variables, with the exception of Branching Density, which is categorical.

Scale	Habitat Variable	Variable Weight	Models present (no.)	$\beta$	Lower CI	Upper CI
Nest Shrub	Vigor	0.32	4	0.55	0.23	0.87
	Shrub Height	0.25	3	0.38	0.07	0.68
	Branching Density	0.07	1	0.24	-0.09	0.57
Nest Patch	Forb Cover	0.32	4	-0.53	-0.87	-0.19
	Visual Obstruction	0.26	3	0.42	0.09	0.74

#### 4.4.3 Species Comparison

Percent forb cover data were not collected for sage-grouse nests or random locations, and therefore the variable Forbs was removed from the Brewer’s sparrow top model to allow for comparison. Estimated coefficients between the models with and without removal were compared for stability. All coefficients remained stable, as the largest difference between coefficients was 0.056 (shrub height) with a similar standard error of  $\pm 0.01$  (vigor; Appendix B). Therefore, the set of comparison variables used for comparing the Brewer’s sparrow conditional logistic regression model to the sage-grouse logistic regression model are branching density, shrub height, vigor, and visual obstruction.

The coefficient estimates for Brewer’s sparrow and sage-grouse were similar for branching density and visual obstruction, although the 85% CIs for branching density as predicted by the Brewer’s sparrow model slightly overlapped zero. However, the effect direction suggested a positive relationship with these habitat variables for both species (Figure 6). Shrub height coefficient estimates were both positive, but the estimates diverged and did not overlap each other. Shrub height appears to be more strongly influential in nest-site selection for sage-

grouse than Brewer's sparrow compared to random locations. Vigor coefficient estimates diverged and suggested opposite effect directions, where sage-grouse select for less vigorous shrubs and Brewer's sparrow select for more vigorous shrubs for nesting (Figure 6).

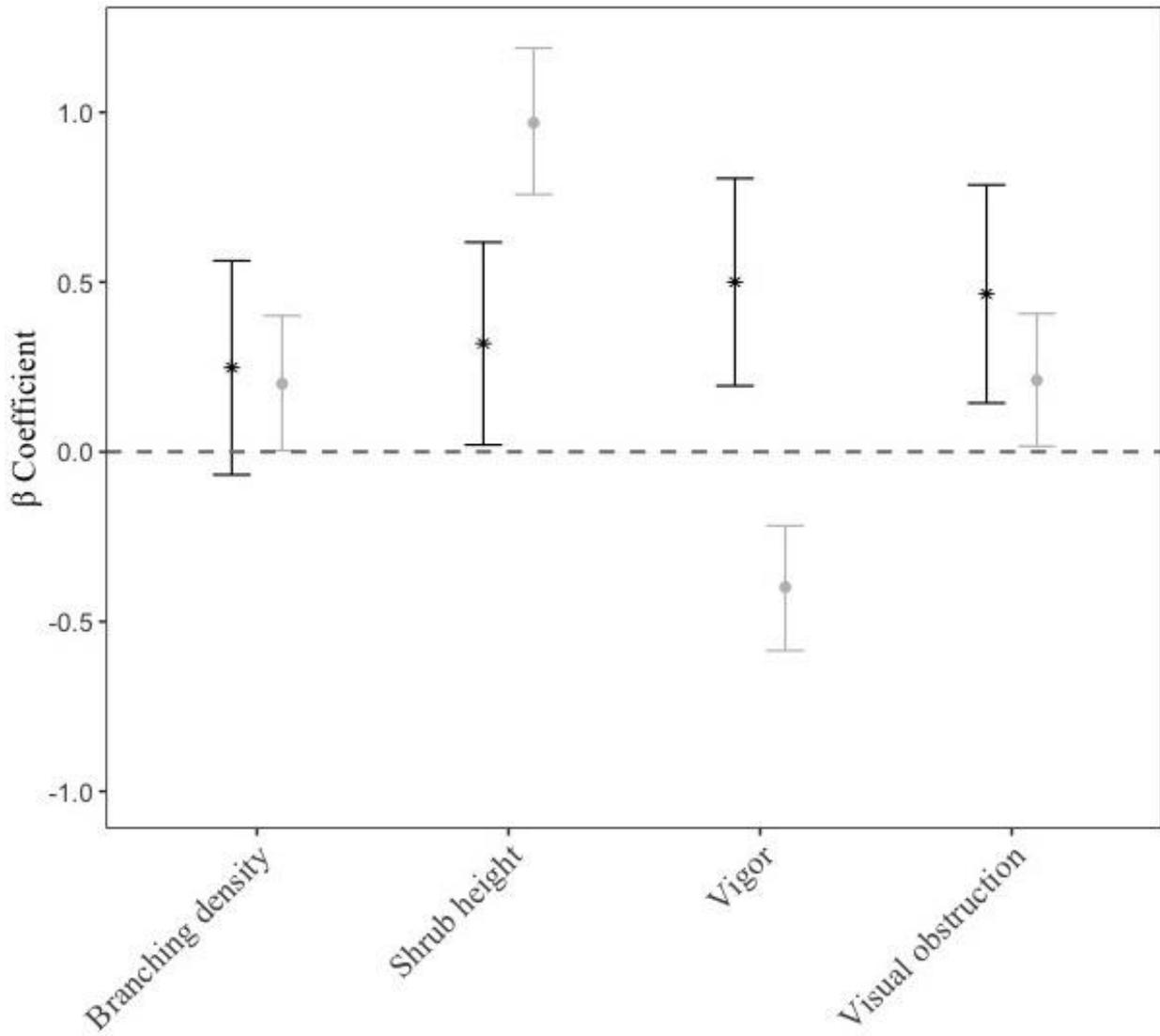


Figure 6. Beta-coefficient estimates and associated 85% confidence intervals for all variables included in the model: Branching Density + Shrub Height + Vigor + Visual Obstruction. Results are from standardized variables, with the exception of Branching Density, which is categorical. The gray lines represent coefficient estimates from the Greater sage-grouse logistic regression model using data collected between 2004-2007, and the black lines represent coefficient estimates from the Brewer's sparrow conditional logistic model using data collected between 2016-2017, in northeastern Wyoming, USA.

The estimated coefficients showed slight variation when comparing the conditional logistic regression model to the logistic regression model for Brewer's sparrow using the comparison variables (i.e. branching density, shrub height, vigor, and visual obstruction). The largest difference between coefficients was  $\pm 0.26$  (visual obstruction) with a mostly equivalent standard error of  $\pm 0.03$  (branching density).

Inspection of the marginal effects plots revealed a generally positive association with branching density, shrub height, and visual obstruction for both species (Figure 7). The response curve for shrub height was straighter and more consistent for Brewer's sparrow than sage-grouse, and both branching density and visual obstruction produced linear relationships for both species. The association with vigor was positive for Brewer's sparrow and negative for sage-grouse (Figure 7).

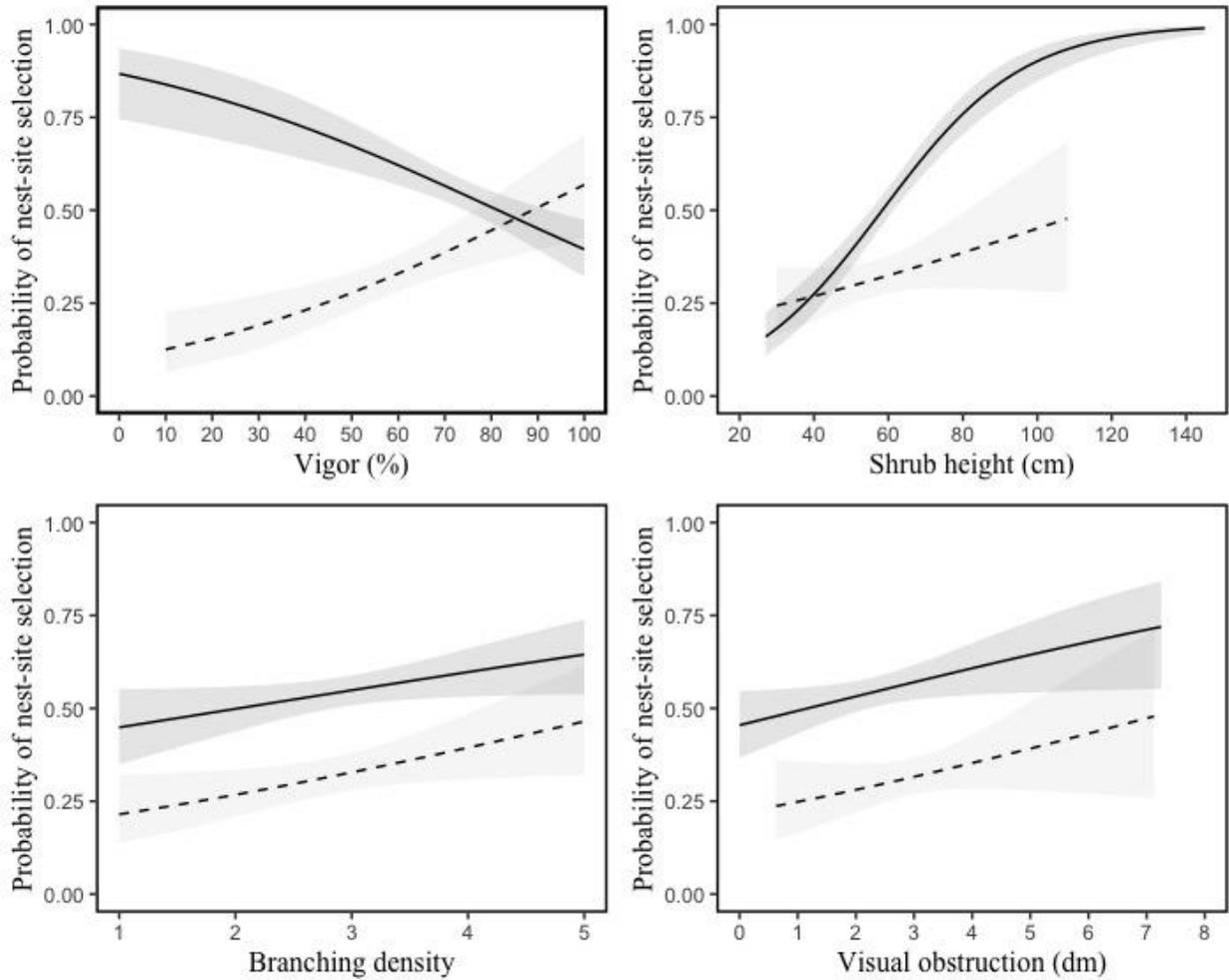


Figure 7. Marginal effects plots depicting the impact of four habitat variables on the probability of nest-site selection. Model predictions are based on the logistic regression model: Vigor + Shrub Height + Branching Density + Visual Obstruction. Dotted lines with light gray 85% confidence intervals represent Brewer’s sparrow model predictions (2016-2017), and solid lines with dark gray 85% confidence intervals represent Greater sage-grouse model predictions (2004-2007) for nest-site selection in northeastern Wyoming, USA.

#### 4.5 Discussion

The overlap in species preferences suggests that applying the umbrella species concept to local habitat management for the sage-grouse may be justified as a way to also conserve Brewer’s sparrow breeding habitat in our region.

#### 4.5.1 Brewer's sparrow

At the nest shrub scale (4<sup>th</sup> order selection), we found that taller, more vigorous shrubs with greater branching density increased the probability of nest-site selection of Brewer's sparrow (Figure 5). Additionally, at the nest patch scale (3<sup>rd</sup> order selection), Brewer's sparrows nested in areas with greater visual obstruction (Figure 5). These results are consistent with previous research that documented Brewer's sparrows nesting in shrubs with a dense branching structure that were mostly alive and taller than the surrounding shrubs (Best 1972, Rich 1980, Petersen and Best 1985, Knopf et al. 1990, Rotenberry et al. 1999). Brewer's sparrows also select breeding patches with greater sagebrush cover, total foliage, potential nest-site density, and habitat heterogeneity (horizontal and vertical; Rotenberry and Wiens 1980, Knick and Rotenberry 1995, Rotenberry et al. 1999, Chalfoun and Martin 2007, 2009; Vander Haegen 2007, Harrison and Green 2010). The percent of sagebrush cover and shrub height variation in the nest patch were also positively associated with the probability of Brewer's sparrow nest-site selection as expected (Table 5), but were not present in the top model. This suggests that although sagebrush cover and vertical heterogeneity in shrubs were important for Brewer's sparrow nest-site selection, there was a greater influence of other habitat characteristics, specifically vigor and forb cover (Table 6), at fine spatial scales for these birds. Brewer's sparrows avoided areas with higher forb cover when selecting nest locations (Figure 5). Additionally, grass cover and height did not influence Brewer's sparrow nest-site selection. Our results differ from those of previous researchers, who have reported higher Brewer's sparrow abundances in areas with specific forb and grass species (Paczek and Krannitz 2005) and higher nest success with greater cover of an exotic perennial grass (Ruehmann et al. 2011). Higher forb and grass productivity may increase seed production and insect population size leading to greater

food production for Brewer's sparrow nestlings and adults (Hansley and Beauvais 2004, Paczek and Krannitz 2005). However, Harrison and Green (2010) found that the influence of grass and forb cover on Brewer's sparrow occupancy at breeding sites were inconsistent between years. Consistent with our findings, Petersen and Best (1985) found that Brewer's sparrows selected nest-sites with less percent herbaceous cover, with no preference for invasive or native herbaceous cover. The equivocal role of forb and herbaceous cover may be influenced by the preference for higher shrub densities and suggests additional research is required to further untangle potential mechanisms.

Nest-site selection is driven, in part, by predation pressure, and it is one of the primary influences on nest survival in sagebrush passerines, including Brewer's sparrow (Rotenberry and Wiens 1989, Rotenberry et al. 1999, Vander Haegen 2007, Chalfoun and Martin 2009). Small rodents, primarily *Peromyscus* mice, were the main nest predators of Brewer's sparrows at sites impacted by energy development in Wyoming (Hethcoat and Chalfoun 2015a, b). The diet of *Peromyscus* mice in Wyoming also mainly consists of seeds, largely collected from forbs (Williams 1959). It is possible that Brewer's sparrows are selecting nest-sites with less forb cover to reduce their exposure to areas with greater predator abundance. In summary, our results are consistent with the knowledge that Brewer's sparrows select specific habitats to impede detection by potential predators (Welstead et al. 2005, Knight et al. 2016).

#### **4.5.2 Brewer's sparrow and greater sage-grouse**

Brewer's sparrow and sage-grouse demonstrated largely similar responses to the important habitat covariates with a few exceptions. Similar to Brewer's sparrow, branching density, shrub height, and visual obstruction all had positive associations with the probability of nest-site selection for sage-grouse (Figure 6; Figure 7). These results are consistent with several

studies that have documented greater concealment cover at nest-sites for sage-grouse, likely to avoid detection by predators (Schroeder et al. 1999, Holloran et al. 2005, Doherty et al. 2010a, 2011a, Hagen 2011, Kirol et al. 2012, Dinkins et al. 2016). Since sage-grouse are large ground nesting species, and Brewer's sparrows nest in the shrub, it is unsurprising that sage-grouse select taller shrubs than Brewer's sparrow for nesting, in comparison to random locations (Figure 6; Figure 7; Table 4). Although we did not observe selection for intermediate shrub height, Brewer's sparrows may also avoid nesting in very tall and large shrubs, because these shrubs often have open branching structure which decreases concealment for nests placed within the shrub (Petersen and Best 1985).

Research has shown that both grass cover and height are positively associated with the probability of sage-grouse nest-site selection, which may increase concealment from predators (Holloran et al. 2005, Hagen 2011, Kirol et al. 2012). Female sage-grouse need at least two openings in the cover of the nest shrub as an escape route in case of attempted predation (Schroeder et al. 1999). We hypothesize that in an already dense grass understory, if shrub vigor increases, the ability of a sage-grouse to quickly detect predators declines, which would decrease the attractiveness of a highly vigorous shrub as a potential nest site. Therefore, Brewer's sparrows may prefer a more vigorous shrub for nesting in order to obtain a comparable level of concealment as the sage-grouse, because sage-grouse are able to utilize areas with greater grass cover to aid in concealment of their ground nests.

Management of sagebrush ecosystems is increasingly becoming synonymous with management of sage-grouse habitat. The management initiatives targeted at improving sage-grouse habitat that may impact Brewer's sparrow include grazing management, fire suppression, maintenance and reclamation of native plant communities, and sagebrush removal. Connelly et

al. (2000) and Hagen et al. (2007) outline the general guidelines for management of sage-grouse breeding habitat as having between 15-25% sagebrush canopy cover,  $\geq 10\%$  forb cover,  $\geq 15\%$  grass canopy cover, and a height of  $\geq 18$  cm for perennial annual herbaceous cover. However, it is important to recognize these optimum values vary across the range (Doherty et al. 2016). Our results suggest that grass height and cover (both native and invasive) did not strongly influence the probability of nest-site selection of Brewer's sparrow. Additionally, in Montana, there was no difference in Brewer's sparrow abundance between sites that had been grazed continually throughout the year in comparison to those that were only grazed for 2 – 3 months (Golding and Dreitz 2017). Therefore, the influence of current grazing strategies on grass cover and height, which are intended to benefit sage-grouse nesting habitat, may be inconsequential to Brewer's sparrow.

Sage-grouse populations range-wide have been negatively influenced by exotic invasive annual grasses that thrive in fire disturbed habitats (Connelly et al. 2011, Miller et al. 2011, Lockyer et al. 2015, Coates et al. 2016), and fire suppression is intended to reduce fire frequency as a way to control the spread of these plants (U.S Fish and Wildlife Service 2013). Additionally, Hess and Beck (2012) demonstrated that prescribed burning reduces sagebrush canopy cover and height, and infrequently results in higher grass cover. Fire suppression is likely also beneficial to Brewer's sparrow, due to the protection of sagebrush stands, but its primary purpose of reducing invasive exotic species and increasing native grass cover may have no influence on Brewer's sparrow at the local scale we studied. However, if habitat management practices focus exclusively on increasing forb cover at the expense of sagebrush, it may reduce the amount of suitable breeding habitat available for Brewer's sparrow. Sagebrush removal has been suggested as a way to increase herbaceous understory growth, although the benefit of this habitat treatment

for sage-grouse is not supported, and at best uncertain (Beck et al. 2012, Hess and Beck 2012, Smith and Beck 2018). Our study further emphasizes that caution must be used when manipulating habitat with the intention of conserving sage-grouse. As mentioned previously, Brewer's sparrows selected nest-sites with higher sagebrush cover, visual obstruction, shrub height, and vertical variation at our study site (Figure 5; Table 4). Additionally, sage-grouse selected taller and less vigorous nest shrubs than Brewer's sparrow in comparison to random locations. Therefore, maintenance of heterogeneous sagebrush stands, specifically in regard to shrub height and vigor, may not only benefit sage-grouse (U.S Fish and Wildlife Service 2013), but may also aid in the protection of Brewer's sparrow.

#### **4.5.3 Management Implications**

The majority of the conservation objectives for protection of sage-grouse habitat outlined here, appear to also be beneficial, or at least inconsequential for Brewer's sparrow. At the nest shrub and nest patch scale, our research supports local habitat management for sage-grouse as a proxy for conservation of Brewer's sparrow breeding habitat in our region. For application of the sage-grouse umbrella species concept to other species, the microhabitat preferences of the species under the umbrella should be understood well enough to avoid unintentional negative impacts.

## 5 Conclusions

Over one-half of the Earth's land surface has been transformed by humans (Hooke et al. 2012), which has led to direct effects on global ecological processes and patterns (Ellis 2011). An expected increase in the human population will subsequently lead to greater energy demand and energy development (Copeland et al. 2009, Wagner et al. 2016). Conservation strategies and mitigation efforts need to focus on minimizing the influence of human development on wildlife populations, and studies that quantitatively assess their efficiency and use will be needed to effectively inform policy and management.

We determined the influence of landscape-scale reclamation on sagebrush songbirds and we assessed what habitat variables influenced their abundance. None of our target species displayed the expected trend of increasing abundance with decreasing levels of human disturbance (active to reclaimed to control). In fact, our only sagebrush-obligate species was the most abundant in the active treatment. Many species of songbird use perches during the breeding season for territorial displays and mate defense, which may have increased the abundance of these species in the active treatment where perches are more readily available (e.g., fences, and oil and gas wells). However, past research has observed a decrease in fitness and survival parameters for songbirds in closer proximity to energy development areas (Gilbert and Chalfoun 2011). Therefore, future studies should focus on assessing the hypothesis that energy development areas are acting as equal preference ecological traps. Additionally, the two human-commensal species in our analysis were the most abundant in the active treatment, followed by reclaimed, and then control. Therefore, we suggest using human-commensal species as target species to assess the 'success' of a reclamation project, since clear abundance trends were observed in our study for these species. Additionally, we show that the habitat variables that

represent what we can most easily target (e.g., NDVI and herbaceous cover) during reclamation efforts were the least influential on species abundance.

We also determined if the umbrella species concept works at fine spatial scales by comparing the microhabitat variables influencing nest-site selection of an umbrella species, the greater sage-grouse, and a species under the umbrella, the Brewer's sparrow. The habitat variables best explaining Brewer's sparrow nest-site selection were largely consistent with the species ecology, with the exception of forb cover. The effect direction of most habitat variables on the probability of nest-site selection were similar for greater sage-grouse and Brewer's sparrow. This translates to the majority of management strategies for greater sage-grouse nesting habitat having a positive or neutral impact on Brewer's sparrow nesting habitat. However, forb cover negatively influenced the probability of nest-site selection for Brewer's sparrow, and greater sage-grouse conservation strategies aim to maintain or increase the percentage of forb cover for availability during grouse brood rearing (Connelly et al. 2000, Hagen et al. 2007). Therefore, although the use of greater sage-grouse as an umbrella species for Brewer's sparrow is mostly justified at fine spatial scales, care should be taken to avoid unintentionally harming species under the umbrella. Umbrella species are the most useful as a conservation proxy for other species at landscape-scales (Rowland et al. 2006, Hanser and Knick 2011a). However, since on the ground habitat management occurs at fine spatial scales, it is crucial to study the influence of using this concept at fine spatial scales on a suite of species that fall under the umbrella, to ensure that alteration of habitat for the benefit of the umbrella species does not lead to negative consequences on species under the umbrella, essentially defeating the purpose of the umbrella species concept.

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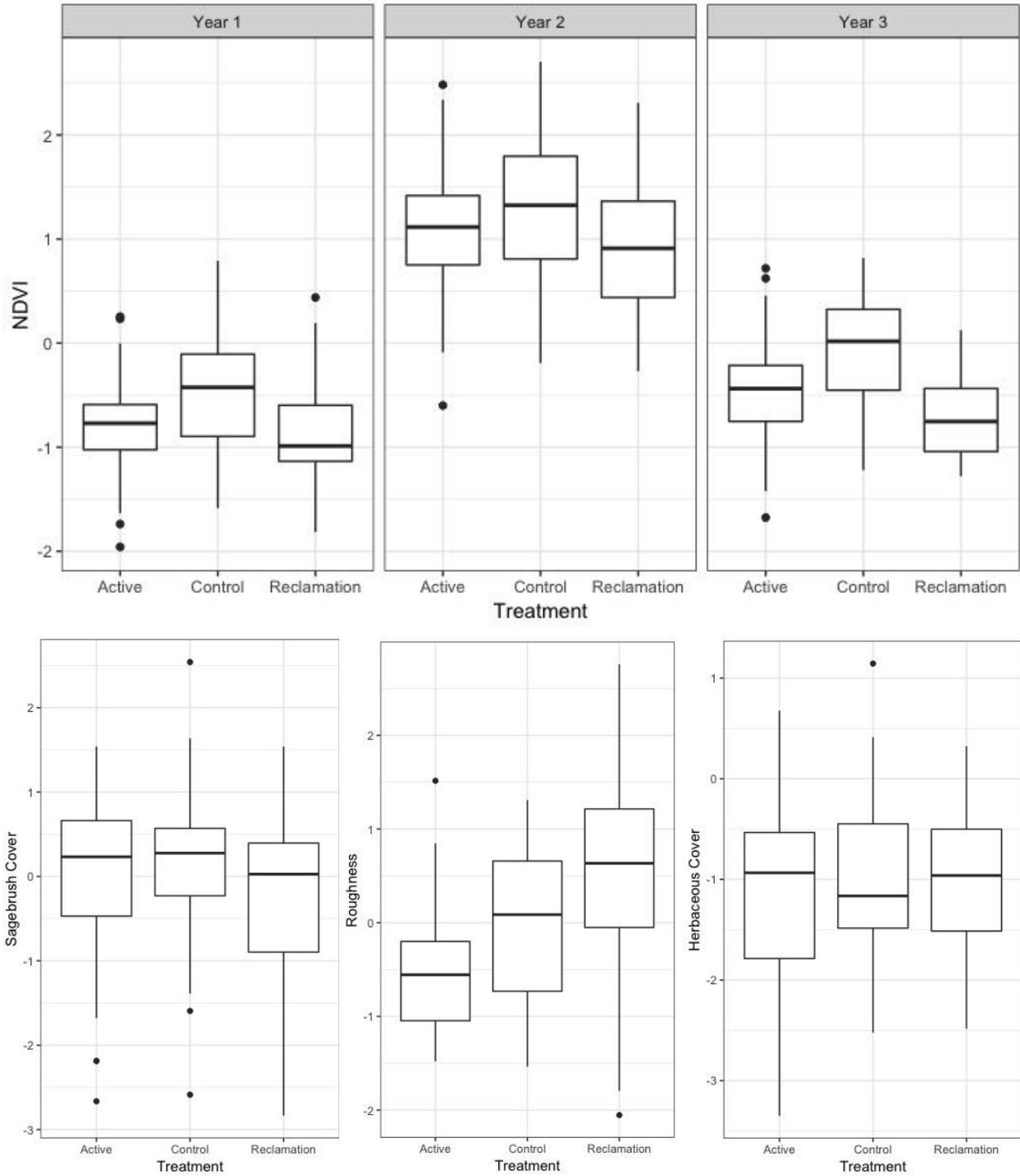
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## 7 Appendix: Supplementary Material

Appendix A. Comparison of the distribution of key habitat variables between treatments. Yearly NDVI values are included due to the variation between years.



Appendix B. Summary of the coefficients ( $\beta$ ) and 85% confidence intervals (CI) from the conditional logistic model including forbs ( $\beta^a$ ): Branching Density + Forbs + Shrub Height + Vigor and Visual Obstruction and excluding forbs ( $\beta^b$ ): Branching Density + Shrub Height + Vigor and Visual Obstruction, for nest-site selection of Brewer's sparrow in northeastern Wyoming, USA, 2016-2017. Results are from standardized variables, with the exception of Branching Density, which is categorical.

Scale	Habitat Variable	$\beta^a$	Lower CI	Upper CI	$\beta^b$	Lower CI	Upper CI
Nest Shrub	Vigor	0.55	0.23	0.87	0.50	0.19	0.81
	Shrub Height	0.38	0.07	0.68	0.32	0.02	0.62
	Branching Density	0.24	-0.09	0.57	0.25	-0.07	0.56
Nest Patch	Visual Obstruction	0.42	0.09	0.74	0.47	0.14	0.79