Beyond Sage-Grouse: Effects of Conifer Expansion and Removal on Fauna in the Sagebrush Steppe

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Abstract

Ecosystems around the world, and the wildlife species that rely on them, have been impacted by changes in the structure and composition of vegetation. Multiple factors may contribute to habitat degradation, but two common factors are invasion by non-native plants and the expansion of native plants beyond their historical ranges. Habitat degradation, defined as a reduction in habitat quality, occurs when altered habitat lowers an individual's probability of occupying and reproducing in a habitat, either due to increased risk of predation or reduced resources such as food. Therefore, understanding how changes to habitat structure affect distributions of both predator and prey species is an important part of assessing the impact of structural changes on habitat quality.

The sagebrush ecosystem of the western United States is one such ecosystem that has been impacted by invasive and expanding plants. Invasions of non-native annual grasses, most notably cheatgrass (*Bromus tectorum*), and the expansion of pinyon (*Pinus spp.*) and juniper (*Juniperus spp.*) into habitat once dominated by sagebrush have impacted wildlife. Changes to plant structure and composition in sagebrush ecosystems may impact wildlife by altering the availably of resources such as food and cover, leading to changes in the composition of the wildlife community.

One species that has been impacted by habitat degradation in the sagebrush steppe is the greater sage-grouse (*Centrocercus uropahsianus*). Populations of this sagebrush obligate have declined across their range, and conservation efforts, including conifer removal, have been undertaken to support remaining populations. Other groups of species associated with sagebrush cover have received less study, but community dynamics for these species are likely to be affected by altered habitat structure as well. Because the conifer woodland and

sagebrush communities feature little overlap in composition, the final outcomes of a stable state transition from sagebrush to conifer woodland are well understood for many species. However, the potential effects of early-stage conifer establishment in sagebrush habitat are relatively unknown for sagebrush-associates other than sage-grouse.

Beginning in 2019, the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project initiated the removal of conifer within an area of up to 676,000-ha of multiuse land managed by the Bureau of Land Management (BLM) in southwest Idaho. Our study examined the first year of conifer removal in an area of ~ 15,000 ha. The goal of this management is to improve habitat for sage-grouse populations. However, the BOSH project also presents a unique opportunity to examine the ways in which the presence of conifer in a sagebrush landscape potentially affects population processes for a suite of functional groups. My study examined the dynamics of the songbird and avian predator communities both before and after the removal of ~15,000 ha of juniper. My study also investigated the relationship between small mammals and habitat characteristics, including conifer and shrub structure. Understanding the ways that habitat mediates species distributions and interactions, as well as the consequences of these interactions for the wildlife community, will allow managers to better predict the results of management actions for both sagebrush and juniper woodland-associated species.

Avian predators

In chapter two of this dissertation, I examine the relationship between habitat characteristics and occupancy of two generalist avian predators, common ravens (*Corvus corax*) and red-tailed hawks (*Buteo jamaicensis*). Conifer woodlands have been implicated as a factor that may facilitate habitat use for avian predators through the addition of nest and perch sites. However, empirical evidence for a causal relationship between conifer expansion in sagebrush habitats and increased abundances of avian predators is lacking. Anecdotal evidence suggests that conifer expansion may affect predator-prey dynamics because survival rates for sage-grouse that use habitat featuring conifers are lower than those for sage-grouse in areas with no conifers. However, structural resources such as trees are not the only factor that may influence habitat use for avian predators. Prey resources may also be an important aspect of habitat quality that influences habitat use. To investigate the importance of structural and prey resources on habitat use by avian predators, we used a Bayesian occupancy analysis to test the effects of habitat characteristics on habitat use by avian predators. Increased conifer cover, especially cover > 20%, was associated with increased occupancy probability for common ravens but not red-tailed hawks. For red-tailed hawks, distance to the nearest cliff was the most influential factor for occupancy probability. As the distance to the nearest cliff increased, occupancy probability for red-tailed hawks decreased. We did not find support for an effect of prey abundance on habitat use for either species.

Small mammals

In chapter three of this dissertation, I examined the effects of habitat structure along an invasion gradient for small mammals. Small nocturnal mammals, including mice and voles, are an important component of the ecosystem because they serve as both predator and prey and alter vegetation structure and composition through herbivory and caching behavior. Therefore, changes to species distributions and interactions among species within the small mammal community may have implications for a broad suite of ecosystem functions. We examined small mammal density, survival, and home-range size along a gradient of cheatgrass and conifer establishment for the deer mouse (*Peromyscus maniculatus*), a generalist omnivore, and the Great Basin pocket mouse (*Perognathus parvus*), a specialized herbivore. Neither density nor survival for either species was affected by cheatgrass cover. However, the home-range size of deer mice was 2.3 times smaller in areas with high cover of cheatgrass compared to areas with no or low cheatgrass cover. Conifer cover was an important predictor of density for deer mice, as well as survival for both deer mice and pocket mice. Deer mouse density was highest in habitat with 10% conifer cover, but deer mouse density decreased as conifer cover increased beyond 10%. Survival of deer mice decreased as conifer stem density increased, while survival of pocket mice increased as conifer stem density increased. We found evidence of intraspecific effects of density on home-range size for pocket mice. Home-range size for pocket mice was two times smaller in areas with the highest densities of deer mice compared to areas with low deer mice densities. These results suggest that the removal of conifers as part of wildlife management efforts will likely affect community dynamics for small mammals.

Songbirds

In chapter four of this dissertation, I examined the effect of conifer and shrub structure in sagebrush habitat on the density of shrub-nesting songbirds, as well as the short-term response of shrub-nesting and conifer-nesting songbirds to conifer removal. Shrub structure is a critical feature of habitat for shrub-nesting songbirds, so conifer removal alone may not increase the density of shrub-nesting songbirds if existing shrub structure is not adequate. Different species of shrub-nesting songbirds responded to conifer cover at different spatial scales. Brewer’s sparrow (*Spizella breweri*) density was negatively associated with conifer cover within 500 m, while sage thrasher (*Oreoscoptes montanus*) density was strongly negatively associated with conifer cover > 5% within 100 m. Conversely, green-

tailed towhee (*Pipilo chlorurus*) density increased as conifer cover within 1000 m increased. Brewer’s sparrow and green-tailed towhee, but not sage thrasher, were positively associated with greater density, volume, and mean height of sagebrush. Following conifer removal, mean density of shrub-nesting species increased compared to the three years prior to conifer removal. Locations where the highest amount of conifer was removed exhibited smaller increases in shrub-nesting songbird density compared to locations where less conifer was removed, suggesting removal of dense conifer may not immediately lead to increased abundance of sagebrush songbirds. The density of conifer-nesting songbirds, which was strongly associated with conifer cover > 20%, increased or was unchanged in areas of remaining conifer woodlands.

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Dedication

I dedicate this dissertation to my parents Becky and Chris, who have always been so supportive and helped me get here, there, and everywhere.

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Statement of Contribution

Aaron C. Young was the primary in conducting statistical analyses and writing the following chapters, and Tracey N. Johnson assisted with editing content

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Chapter 1: Introduction

The sagebrush-steppe ecosystem is dominated by the eponymous foundation species *Artemisia tridentata* (Prevey et al. 2009) which controls water availability, grass and forb composition, and provides resources such as food and shelter for a variety of species (Davies et al. 2011). Increases in the interval of high-elevation fires combined with climatic changes and livestock grazing have facilitated the establishment of conifer trees within the sagebrush steppe across the intermountain west (Miller and Rose 1995). Trees in a typically treeless ecosystem can inordinately affect ecosystem processes which may alter community dynamics (Tews et al. 2004, Manning et al. 2006). Over time, conifer expansion may advance such that sagebrush shrubs are eliminated and replaced with conifer which dominates ecosystem processes as a new foundation species (Miller et al. 2005). These alternative stable states, sagebrush steppe and juniper woodland, are utilized by unique and often non-overlapping faunal communities (Knick et al. 2017). The transition between these two stable states, characterized by scattered conifer trees that alter community dynamics but don’t yet dominate ecosystem function, is likely to feature a mixture of sagebrush shrubs, conifer woodland, and faunal species associated ecotones. This modified environment may lead to increases in abundance for some species and decreases for others based on changes in the availability suitable habitat. However, for sagebrush obligates, this transition is unlikely to be beneficial because of life-history traits evolved to exploit sagebrush ecosystem processes.

The sagebrush steppe ecosystem has received much recent conservation focus due to concern over the population status of the Greater Sage-Grouse (*Centrocercus uropahasianus*, hereafter referred to as “sage-grouse”; Connelly et al. 2004, Carlisle et al. 2018). Populations of this sagebrush obligate have declined across its large, multi-state range (Braun 1998, Schroeder et al. 2004), and have been attributed in part to the expansion of conifer. Areas of conifer cover < 4% lower the probability of occupancy and are associated with a reduction in survival rates for sage-grouse (Baruch-Mordo et al. 2013, Coates et al. 2017).

Beginning in 2019, the Bruneau-Owyhee Sage-grouse Habitat (BOSH) project removed conifer from ~15,000 ha of multiuse land managed by the Bureau of Land Management (BLM) in southwest Idaho. The primary goal of this conifer removal is to improve habitat for sage-grouse populations. However, the BOSH project also presents a unique opportunity to examine the ways that a keystone structure in the landscape potentially affects population processes for a suite of faunal groups. My study examined the dynamics of avian predators and songbirds both before and after the removal of conifer. This before-after control-impact design (BACI) allows us to better account for spatial and temporal variations in ecological processes, thereby increasing the power to detect any effects of conifer expansion (Stewart-Oaten et al. 1986). My study also examined the relationship between small mammals and habitat characteristics along a gradient of invasive grass and expanded conifer. Understanding the ways that habitat mediates species interactions, as well as the consequences of these interactions for species distributions, will allow managers to better predict the results of management actions for species associated with both both sagebrush and conifer woodlands.

Avian predators

The effects of predation on prey species can impact population persistence, especially for vulnerable or declining species. For prey species that have evolved with low predation pressure or a specific predator interactionns, changes in the composition of the predator community or changes in habitat that influence predator-prey interactions may be especially impactful (*sensu* Sinclair et al. 1998, Didham et al. 2007). Habitat alterations can lead to mismatches in evolved predator avoidance techniques or life history strategies (Robertson et al. 2013), which may ultimately lower demographic rates in areas where individuals are unable to accurately assess or mitigate predation risk (Robertson and Hutto 2006).

Fragmentation of sagebrush steppe caused by juniper expansion has been implicated as a factor leading to changes in the avian predator community including increased densities of common ravens (*Corvus corax*) and red-tailed hawks (*Buteo jamaicensis*; Coates et al. 2016). One potential cause for increased densities of avian predators may be anthropogenic or natural vertical structures used as nest sites (Coates et al. 2014, Howe et al. 2014). Buteos and other avian predators may nest on the edges of dense juniper woodlands and forage in the open sagebrush (Coates et al. 2014). Given the demographic consequences observed for sage-grouse that use habitat featuring conifer, altered composition of the predator communtity caused by conifer expansion may also play an important role in regulating demography for groups such as songbirds and small mammals.

Vertical structure may play a role in altering predator-prey dynamics beyond the direct demographic effects of increases in predator abundance or occupancy. Avian predators are largely visual hunters, and the availability of vertical perch structures may increase search efficiency by improving the ability to detect prey (Leyhe and Ritchison 2004, Andersson et al. 2009). This increased search efficiency would then create an edge effect where prey individuals with home ranges closer to perches are more likely to have lower survival or reproductive success (Creswell et al. 2010). Taken together, increases in both occupancy and predation efficiency by avian predators may have large impacts on the small mammal and songbird communities.

Small mammals

Changes in habitat structure may drive changes in species composition for small mammals based on their functional traits and species interactions (McGill et al. 2006, Ceradini and Chalfoun 2017). Understory grass and forb composition is an important driver of small mammal community composition because these plant groups make up a large part of the diet for many herbivorous and graniverous rodent species and also affect predation risk (Parmenter and MacMahon 1983, Ostoja and Schupp 2009, Thompson and Gese 2012). Reductions in forb and grass cover caused by conifer expansion should therefore favor more generalist omnivore species leading to community homogenization, though this prediction is untested for the sagebrush community. However, total small mammal community abundance can increase in areas following removal of dense juniper and pinyon (Turkowski and Reynolds 1970, Baker and Frischknecht 1973, O'Meara et al. 1981, Severson 1986).

Because small mammals can simultaneously act as both prey and predator within a system, changes in small mammal density may play a role in regulating populations of other species. Generalist omnivores like deer mice and ground squirrels can be important predators of songbird nests, and high densities of these species can lead to lowered reproductive success for songbirds (Hethcoat and Chalfoun 2011). Small mammals are also important prey for raptors and corvids, and small mammal density is often an important predictor of habitat use for avian predators (Korpimaki 1984; Janes 1985; Marzluff et al. 1997a,b; Crandall et al. 2015). Small mammal communities are often highly dynamic, with abundance and composition fluctuating spatiotemporally via both density-dependent and density-independent processes (Koprimaki and Krebs 1996, Yarnel et al. 2007). Avian predators may switch prey when small mammal density is low, resulting in increased predation on songbird nests and adults (Ims et al. 2013). These trophic interactions may have important implications for other sagebrush-associated populations.

Songbirds

Sagebrush-associated songbirds have received less conservation focus than sage-grouse, although species within this group are known to be sensitive to habitat alterations. Populations of all three sagebrush obligates, Brewer’s sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee (*Pipilo chlorurus*), are declining (Knick et al. 2003, Sauer et al. 2017). Most of the distribution of breeding populations for Brewer’s sparrow (55%) and sage thrasher (63%) is found on public, multi-use lands managed by the BLM (Fink et al. 2013). As a result, management decisions that alter habitat on BLM lands will affect tthe majority of the breeding population for these species.

Management actions undertaken to improve habitat for sage-grouse may also benefit sagebrush songbirds (Crow and van Riper 2010, Holmes et al. 2017). However, evidence for these benefits has often been inconclusive (Knick et al. 2014, Bombaci and Pejchar 2016). Areas with 10-20% juniper cover had lower densities of sagebrush species than similar areas where juniper had been removed (Holmes et al. 2017). However, where post-removal sites retained 6-24% juniper cover, no increases in sagebrush songbird abundance occurred (Knick et al. 2014). This result suggests that the relationship between sagebrush songbird abundance and juniper may be non-linear. Sagebrush songbird occupancy and abundance are known to be dependent on sagebrush structure (Sedgwick 1987, Chalfoun and Martin 2007, Harrison and Green 2010), likely resulting in an interactive relationship between juniper cover and sagebrush structure. The level of juniper cover that may be tolerated in otherwise suitable habitat has not been examined.

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Chapter 2: Structural resources and generalist avian predators: implications for tree expansion in shrubland ecosystems.

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Abstract

Shrublands globally have undergone structural changes due to plant invasions, including the expansion of native trees. Removal of native conifer trees is occurring across the Great Basin of the western U.S. to support declining sagebrush (*Artemisia* spp.) habitats and associated dependent wildlife species, including greater sage-grouse (*Centrocercus urophasianus*). One assumption used to justify conifer removal is that it will improve survival of sagebrush wildlife by reducing the abundance of predator species. However, there is uncertainty about the connection between conifer expansion predator distributions. Further, although structural characteristics of habitat are important for generalist predators, overall prey abundance may also affect their distributions. We examined the response of common ravens (*Corvus corax*) and red-tailed hawks (*Buteo jamaicensis*), two generalist predators whose populations are increasing in western North America, to variation in habitat structural characteristics and prey abundance in a study area where juniper removal occurred across ~ 14,000 ha for three years before and one year after removal. Structural characteristics of habitat were important predictors of occupancy probability for both ravens and red-tailed hawks, whereas indices of prey abundance were unimportant for both species. Before conifer removal, ravens, but not red-tailed hawks, responded positively to increasing cover of western juniper (*Juniperus occidentalis*) and occupancy probability was highest (> 0.95) where juniper cover within 100 m was > 20%. Occupancy probability of red-tailed hawks, but not ravens, was greater closer to cliffs but was not associated with juniper cover. Over four years, the mean occupancy probability for ravens (*n* = 37 transects) was lowest (0.34) in the year following removal of juniper. Our study suggests that removal of conifer in similar environments may lower occupancy probability for ravens, a predator with significant impacts to sage-grouse, which may improve sage-grouse reproductive success and survival depending on responses to juniper removal from other predators of sage-grouse. For both ravens and red-tailed hawks, the structural characteristics of habitat were more important than any prey group or combination of prey groups, likely because generalist predators can use a wide variety of food resources. Our results have implications for other rangeland ecosystems around the world undergoing expansion of conifer and other woody vegetation. Though species differ, similar processes may occur for generalist avian predators.

Introduction

Changing habitat structure from altered vegetation composition due to anthropogenic influence is a global phenomenon. Many arid, semi-arid, and Mediterranean-type ecosystems are affected by recent expansion of woody plants largely attributed to land use (especially livestock grazing), fire suppression, and climate change (Archer et al. 2017, Nackley et al. 2017). Since Euro-American settlement of the western United States, portions of the sagebrush (*Artemisia* spp.) biome have experienced an expansion of conifer trees, mostly pinyon pine (*Pinus* spp.) and juniper (*Juniperus* spp.), particularly in the Great Basin (Miller et al. 2005, Davies et al. 2011). The effects of conifer expansion on wildlife species associated with shrubland likely varies regionally, and changes to vegetation structure can mediate shifts in faunal composition and interactions among species (Marvier et al. 2004, Stefanescu et al. 2012, Thompson et al. 2012, Klaus and Noss 2016). Furthermore, as species interactions are altered, direct and indirect effects of habitat on demography can interact to compound the effects of habitat change on wildlife populations (Calizza et al. 2017). For example, expansion of woody plants can directly reduce resources such as food or shelter for a species while indirectly increasing predation risk by subsidizing predator populations (Vickery et al. 2001, Evans 2004, Whittingham et al. 2004, Rand and Louda 2006). Given the impacts that altered vegetation structure can have on wildlife populations, understanding the effects of conifer expansion on the predator community is vital for conserving imperiled prey populations.

Habitat structure and the abundance and composition of food resources are important features that influence species distributions (Manning et al. 2006, Rullman and Marzluff 2014, Coates et al. 2014a, 2014b). For avian predators, structural resources such as trees, cliffs, and utility poles may provide nesting substrates or protection from predation (Janssen et al. 2007, Howe et al. 2014). Structural resources may also facilitate hunting strategies, either as concealment for ambush hunters or as perches for visual hunters (Andersson et al. 2009, Valeix et al. 2009, Zagorski et al. 2020). However, structural resources are also important for prey species as nesting substrates and protection from predation (Arthur et al. 2004, Litt et al. 2013, Klecka and Boukal 2014). The spatial distribution of both structural and food resources influences prey distributions because prey must balance predation risk with the need to gather food resources (O'Brien et al. 2018). Therefore, changes to the structure and/or composition of vegetation can alter the composition and behavior of the prey-species assemblage, potentially impacting food abundance or hunting success for predators.

Although prey abundance is an integral part of habitat selection theory, it has rarely been incorporated into studies of habitat use by avian predators (but see Rullman and Marzluff 2014). As a proxy for prey abundance, studies of habitat use by avian predators often test for effects of physical landscape features under the assumption that these structures influence the distribution of prey as well as hunting efficiency for aerial predators (e.g., Howe et al. 2014, O'Neil et al. 2018). However, studies that have directly tested the effect of prey abundance on habitat use by avian predators have found either that an interaction between habitat structure and prey abundance affects habitat use by avian predators (Southern and Lowe 1968, Baker and Brooks 1981, Preston 1990), or that habitat use is influenced by habitat structure and not prey abundance (e.g., Beier and Drennan 1997, Rullman and Marzluff 2014). For specialist predators, changes to habitat structure that reduce access to a primary prey resource may lead to population declines for predators (Rand and Tscharntke 2007). For generalist predators, changes to composition of the prey community may be less important than changes in the availability of structural resources because generalist predators are better able to adapt to changing conditions by switching prey (Tylianakis et al. 2008, Baudrot et al. 2013). Understanding the associations of both prey and predators with altered habitat structure may shed light on the conservation of wildlife populations in ecosystems experiencing broadscale expansion of woody plants.

The sagebrush steppe ecosystem in the western United States has received much recent conservation focus due to concern over status of the greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse"). Sage-grouse populations are distributed throughout the vast sagebrush biome but have declined range-wide (Schroeder et al. 2004, Garton et al. 2011). Conifer expansion is a regional threat to sage-grouse because population and declines for sage-grouse have been attributed in part to the expansion of conifers into sagebrush habitat that was previously treeless (Severson et al. 2017). Sage-grouse rely on sagebrush as a food source and as cover for nests, and they generally avoid areas where conifers exceeds

10% cover (Coates et al. 2017, Rabon et al. 2021). Increasing conifer cover has been shown to commensurately reduce both cover and richness of shrub and herbaceous species required by sage-grouse (Severson et al. 2017). Therefore, conifer expansion can represent a direct loss of habitat for sage-grouse as shrub cover is reduced or eliminated and conifer cover increases. However, conifer expansion may also change interactions between sage-grouse and their predators, thereby indirectly lowering survival rates. In recent years, increased abundance in sagebrush habitat of common ravens (*Corvus corax*) and red-tailed hawk (*Buteo jamaicensis*), two generalist predators of sage-grouse and other sagebrush-associated wildlife, have been attributed to human development (O'Neil et al. 2018, Coates et al. 2020). Ravens are a common predator of sage-grouse nests, and the removal of ravens has increased recruitment of sage-grouse (Coates et al. 2012, Peebles et al. 2017, Olsen et al. 2021). Anecdotal evidence suggests that conifer expansion may affect predator-prey dynamics because survival rates for sage-grouse that use habitat featuring conifers are lower than those for sage-grouse in areas with no conifers (Coates et al. 2017). However, few studies have directly tested the effect of conifer expansion on predator habitat use (but see Ewanyk 2020, Kendall 2020). To our knowledge, no empirical data exist demonstrating a relationship between use of habitat by avian predators and conifer expansion in sagebrush habitat.

Given the negative effects of conifer expansion on sage-grouse populations, large-scale conifer removal projects have been initiated in sagebrush habitats across the Great Basin (Bombaci and Pejchar 2016). One such project, the Bruneau-Owyhee Sage Habitat (BOSH) project, will remove western juniper across 250,000 ha (BLM 2018). Policies that have been recently enacted by the federal government will facilitate additional conifer removal in the Great Basin by minimizing environmental review requirements for projects (BLM 2020). However, critical information gaps exist concerning wildlife responses to conifer removal in sagebrush habitat, especially those of predators. If prey distributions are the primary influence of predator habitat use, then potential increases in prey abundance following conifer removal may increase occupancy of avian predators in sagebrush habitat. For example, the overall density of small mammal is lower in conifer woodlands than sagebrush habitat (Peterson et al. 2016, Hamilton et al. 2019). If generalist avian predators are insensitive to changes in habitat structure because they shift diet composition in response to prey abundances, costly efforts to remove conifer may be ineffective. Conversely, if structural resources are the primary influence of avian predator habitat use, then conifer removal may reduce the presence of avian predators and associated predation risk for prey. Information about relationships between habitat-use by avian predators and structural resources provided by tree expansion and tree removal may therefore help guide habitat restoration efforts for sagebrush-dependent wildlife before larger investments are made in tree removal. Toward that aim, we leveraged the landscape-level BOSH project as a quasi-experiment in which we tested the effects of conifer removal on generalist avian predators. We had two main objectives: 1) evaluate the relationship between habitat structures and avian predator occupancy in sagebrush-juniper habitat; and 2) test for an effect of potential prey resources on avian predator occupancy. We tested three hypotheses: 1.) habitat structural resources would be the primary influence on avian predator occupancy, 2.) prey distributions would be the primary influence on avian predator occupancy, and 3.) an interaction between habitat structural resources and prey distribution would be the primary influence on avian predator occupancy. We predicted that areas with greater conifer cover would exhibit increased probability of habitat use by avian predators, but that prey abundance would further influence predator habitat use. Consequently, we also expected conifer removal to decrease avian-predator occupancy relative to pre-removal habitat conditions.

Methods

Study site

Removal of juniper occurred in southwest Idaho, USA in the northern Great Basin (Figure 2.1) and began in August 2019. The study area is composed primarily of big sagebrush (*Artemisia tridentata*) and low sagebrush (*Artemisia arbuscula*) interspersed with one conifer species, western juniper (*Juniperus occidentalis;* hereafter, juniper). In areas classified as < 10% conifer cover at our study site, juniper has an average height of 2.7 m ± SD 2.1 and an average stem density of 19 trees/ha ± SD 25. In areas classified as >20% conifer cover at our study site, junipers have an average height of 3.6 m ± SD 2.3 and an average stem density of 198 trees/ha ± SD 193, but individual trees could reach heights of 12 m, and areal coverage of juniper can approach 60% (Young et al. unpublished data).

Cheatgrass (*Bromus tectorum*) has invaded much of the study area, especially at lower elevations.

The climate of the project area is typified by hot summers and cold, snowy winters with an average of ~ 35 cm of precipitation annually (BLM 2018). Elevation ranges 1,250 − 1,920 m and topography is varied with low-lying riparian areas interspersed with open sagebrush tablelands and rocky ridgelines. Before European settlement, juniper was limited to rocky outcrops in small portions of the study area, presumably limited by historical fire regimes (Miller and Rose 1999). Since European settlement, juniper has expanded into sagebrush communities forming a gradient of tree cover across the landscape, and areas of dense juniper are currently found along ridgetops and in drainages (Davies et al. 2011) Lesser, more scattered juniper cover typifies open sagebrush flats. Cattle grazing is ubiquitous across the study site, occurring at lower elevations during April-May and moving to higher elevations as summer progresses.

The BOSH project will eventually remove juniper cover classified as < 20% (at a 2-ha scale) from habitat formerly dominated by sagebrush across a 250,000-ha landscape to support sage-grouse and other sagebrush-obligate species. Our sampling encompassed ~30,000 ha, and in the fall of 2019 14,000 ha of juniper was hand-cut within our study site. Juniper was cut using chainsaws and scattered so that no debris was higher than one meter.

Raven and raptor counts

We conducted repeated-visit surveys for three years before and one year after juniper removal began. We surveyed along 800-m transects (*n* = 37) to assess the effects of habitat structure on the occurrence probability of avian predators within our study site. We selected locations for survey transects using random points in a GIS stratified by juniper phase category and location with respect to treatment plans for juniper removal (Figure 1). Eighteen of 37 transects were within areas where juniper would be removed, hereafter referred to as "treatment transects". Surveys consisted of walking transects with three stationary, ten-minute observation periods placed at the beginning, middle, and end of each transect. Observers recorded any avian predators seen or heard while walking between or while at stationary observation points. Each survey lasted ~ 45 minutes total. We limited our data to observations of birds within 500 m of the observer to allow for more precise estimates of the effect of habitat on occupancy probability and because this allowed us to assume that birds were influenced by the habitat surrounding the survey transect. We used laser range finders to estimate distances for birds detected visually and by sound. Each survey was conducted by a single observer and three observers conducted 98% of surveys over four years. We conducted surveys before 10 am local time and never during steady rain or when estimated wind speeds exceeded 10 km/h.

Prey abundance

To test the effect of prey abundance on occupancy of avian predators, we estimated abundance, density, and presence for important prey groups. We considered the following prey group indices: densities of the most common species of small mammals including deer mouse (*Peromyscus maniculatus*) and Great Basin pocket mouse (*Perognathus parvus*); ground squirrel presence/absence; distance to sage-grouse lek site; and relative abundance of songbirds.

To estimate density of small mammals, we deployed 740 traps at five of the avian-predator transects in 2017 and 896 traps at the same five avian-predator transects in 2018 and 2019. We selected trapping locations for small mammals that represented a gradient of juniper cover, cheatgrass cover, and shrub structure (see Young 2022). In 2017, we used one trap array that consisted of 148 traps at the center of the avian predator transect. In 2018 and 2019, we used three trap arrays of 64 traps each at the center and ends of avian predator transects. We trapped small mammals over nine days broken up into four- and five-day sessions one month apart.

To estimate songbird abundance, we conducted 1,269 point-count surveys over four years along our avian-predator transects. Each survey transect for avian predators had three point counts stations placed 400 m apart along the transect. We surveyed songbirds concurrent with avian-predator surveys. We conducted 10-minute point counts three times per year at each avian-predator transect. We limited songbird observations to within 100 m of the point count station. We conducted songbird surveys from sunrise to 10 am and never during steady rain or winds stronger than 10 kph.

We noted the presence or absence of ground squirrels within 100 m of a survey transect because ground squirrels are an important food resource for red-tailed hawks. Ground squirrel presence is therefore treated as a categorical predictor variable. Belding's ground squirrels (*Urocitellus beldingi*), which occur in large semicolonial populations, are the most common ground squirrel at our study site.

Prey indices

We used individual indices of prey groups as predictor variables to assess the importance of prey for predator occupancy. We estimated density of small mammals in response to habitat characteristics at transect locations using a spatially explicit capture-recapture design (see Young 2022). We then predicted small mammal density in relation to habitat characteristics for transects where we did not trap small mammals. We measured the following habitat characteristics which may influence small mammal density; mean height, and mean volume of sagebrush, and juniper cover.

To calculate an index of songbird abundance, we pooled observations of all individuals and species and estimated the mean relative abundance of songbirds the three points per transect. We did not adjust songbird observations for detection probability because differences in detectability among species would bias our abundance estimates, and previous studies examing the influence of songbird abundance on avian predator habitat use have also used unadjusted relative mean counts (Rullman and Marzluff 2014).

To evaluate if sage-grouse activity influenced predator occupancy, we calculated the distance to the nearest sage-grouse lek for each avian-predator transect. Sage-grouse are a known food resource for both ravens and red-tailed hawks, and our site contained at least six active sage-grouse leks (J. Rabon 2020). The majority of sage-grouse hens nest within 3 – 5-km of leks (Holloran and Anderson 2005), so we assumed that distance to lek is an index of relative sage-grouse nest and chick availability. The relative frequency of sage-grouse eggs and chicks in avian predator diets is not known, but avian predator abundance can be higher around breeding sage-grouse (Bui et al. 2010).

Finally, we combined all the above prey metrics into a prey abundance score and tested for interactions with other habitat features (*sensu lato* Beier and Drennan 1997, Rullman and Marzluff 2014). To do this, we added small mammal densities (range 0.1 – 10 individuals/ ha, x̄ = 4.74, SD = 2.78) and relative abundance of songbirds per transect (range 2 – 16.6 individuals, x̄ = 8, SD = 2.06) to values for distance to lek and ground squirrel presence. Transects less than 1 km from a lek received a score of 10, and the score declined by one for every 1-km increase in distance until transects > 10 km from leks received a score of zero. Transects featuring ground squirrel colonies within 100 m of the transect received five extra points. We chose this value because ground squirrels are an important food resource for red-tailed hawks, and we wanted the contribution of ground squirrels in our food index to be proportional to other values for food resource such as songbirds.

Habitat characteristics

We focused our sampling and analysis on natural and topographic features that may influence avian predator occupancy. We also included anthropogenic landscape features in our data collection (e.g., cabins, roads) because the effects of human subsidies such as artificial vertical structures, roads, and food are well-established as characteristics that influence the distribution of raptors and ravens. However, our study site was relatively free of human infrastructure compared to similar studies of avian predator occupancy (e.g Howe et al. 2014, O'Neil et al. 2018).

We classified juniper cover across our study site with imagery collected at a 1-m scale (National Agriculture Imagery Program, 2016). To identify juniper in the image, we conducted a supervised image classification in ArcGis (ESRI 2018). Next, we manually corrected any misclassifications for each of our transects using visual inspection and ground truthing. We then calculated the area of juniper cover within 100, 250, 500, 750, 1000, 1500, 2000, 2500, and 3000 m of our survey transects. These distances span a range of reported movements during the breeding season for ravens (mean movement 570 m from nest, 6.6 km^2 nest territory) and 40 km^2 core use area for non-breeding individuals (Smith and Murphy 1973, Howe et al. 2014, O'Neil et al. 2018) and breeding red-tailed hawks (x̄ = 3.88 km^2 nest territory [Bosakowski et al. 1996]). Three of our survey transects featured juniper mixed with mountain mahogany. We included mountain mahogany in our juniper-cover layer because individual tree species are not discernible in our classification and we are interested in the effect of vertical structure on avian predator occupancy. Thus, we assumed that avian predators respond to both tree species similarly, and that any association with trees in sagebrush-dominated habitats is a function of structure and not species composition. We calculated distance to cliff from each transect by defining cliffs as areas with greater than a 60° slope. We used a 10-m resolution digital elevation model (DEM; U.S. Geological Survey), and our definition of cliff areas as > 60° slope captures a 90° cliff that is 17 m high, a 100° cliff that is 25 m high, and a 110° cliff that is 54 m high. We also included a measure of distance to water using a GIS stream layer in combination with ponds created for livestock. We calculated distance to improved road and distance to nearest human dwelling for each transect.

Occupancy models

To assess the effect of habitat characteristics and juniper removal on occupancy of avian predators, we used Bayesian multi-season occupancy models (Royle and Dorrazio 2008). Multi-season occupancy models (MacKenzie et al. 2003, Royle and Kery 2007) are an extension of single-season occupancy models but allow for the estimation of changes in occurrence probability between seasons (in this case, years) through the estimation of parameters of extinction and colonization probability. Multi-season occupancy models assume that occupancy of a survey location is closed during each year but may change between years. We used the auto-logistic formulation of the multi-season occupancy model (Royle and Dorazio 2008) to allow for inference on the effects of habitat covariates on overall occupancy probability as opposed to a decomposition of occupancy into colonization and extinction parameters. Use of the auto-logistic formulation is suitable for a limited sample size of unique sites and puts the inference focus on occupancy probability for each site for each year, as opposed to colonization and extinction probability (Royle and Kery 2007).

To account for imperfect detection of avian predators, we tested covariates that can affect probability of detection using leave-one out cross validation (Vehtari et al. 2017). We allowed detection to vary by year for all models and tested the effect of a terrain roughness index (TRI) and time of year on detection. We did not include an observer effect because a single observer (ACY) conducted 344 of 409 avian predator surveys (85%). Because we were interested in testing the effect of juniper cover on occupancy, we did not include juniper cover as a covariate on detection in our occupancy models. We assumed that juniper cover would not lower our ability to detect large, loud species such as ravens. However, to validate this assumption we tested an exploratory model that included juniper cover within 100 m of the transect as a covariate on detection and with no covariates on occupancy. This exploratory model was not included in our set of candidate models. We standardized all predictor values and used normally distributed non-informative priors for all covariate parameters (mean = 0, precision = 0.01).

Variable and model selection

Uncertainty about the spatial scale at which habitat features may influence ecosystem processes is common for ecological studies. As a result, researchers are often interested in testing the effect of a habitat covariate at several spatial scales. However, the inclusion of all habitat covariates at all potentially relevant scales can lead to models that are difficult to interpret (Stevens and Conway 2019). We reduced the number of spatial scales for variables included in our models following the screening procedure recommended by Stevens and Conway (2019). We fit univariate multi-season occupancy models for each scale (100 m – 3,000 m) of juniper cover that we quantified. We also tested other juniper metrics at these scales, including clustering and proportion of landcover comprised of three cover categories (<10% cover, 10-20% cover, and >20% cover). We estimated clustering using a K-means nearest neighbor analysis in ArcGIS. We estimated proportion of juniper cover categories by categorizing 30 m^2 pixels based on our juniper cover classification. We then compared the predictive power of each model in the set with leave-one-out cross validation. Preliminary results from our model set testing the effect of different spatial scales of juniper measurement on occupancy suggest that ravens respond most strongly to the proportion of >20% juniper cover category habitat within 100 m of a transect. (median $\beta = 2.83$, 90% Crl 0.41, 6.16; 99% posterior direction; Appendix A1). However, because we were also interested in the relationship between all categories of juniper expansion and occupancy of ravens, we used continuous percent cover within 100 m of a survey transect, which was the next most competitive model, as a covariate in our occupancy model set (median $\beta = 1.32$, 90% Crl 0.13, 3.02; 99% posterior direction; Appendix A1).

Once we determined the spatial scale and measurement of juniper that best predicted occupancy of ravens and red-tailed hawks, we constructed a model set that included combinations of habitat features in addition to juniper that may influence avian predator occupancy (Table 2.1). We then ran each model for at least 300,000 iterations using JAGS called from R (Version 3.5.1, R core team 2018). We assessed model convergence using $\hat{r}$ values generated by JAGS (Plummer 2003) and model convergence using visual inspections of traceplots (Gelman 2013). We compared the predictive power of each model in the set using leave-one-out cross validation (Stolen et al. 2019, Muir and Tsai 2020) and assessed model fit using the Freeman-Tukey test statistic to generate a Bayesian *p*-value (Kery and Royle 2015). Models with *p*-values close to 0.5 adequately fit the data, while extreme values close to 0 or 1 indicate a lack of model fit due to over- or under dispersion. Finally, for each covariate in a model, we calculated the posterior direction, which is the percentage of the posterior distribution that has either a negative or positive value, depending on the sign of the covariate point estimate (Makowski et al. 2019). We calculated average occupancy and average detection probabilities for each year. In the final stage of modeling, we carried forward our top habitat structure model and tested for additive or interactive effects of prey abundance and habitat structure on avian predator occupancy (Table 2.1).

Results

Effect of habitat on occupancy

We completed 409 avian predator surveys on the 29 transects sampled from 2017 to 2020 and eight additional transects sampled from 2018 to 2020. In 2017, we completed three surveys at 21 transects, two surveys at 10 transects, and one survey at two transects (*n* = 76 surveys). In 2018-2020, we completed three surveys at each of 37 transects (*n* = 111 surveys/year). Mean juniper cover within 100 m of all treated and untreated survey transects (*n* = 37) was 7.5% (8.1% SD) before juniper removal and 5.2% (8.4% SD) after removal, representing an average reduction in juniper cover of 30.6% per 10 ha. At transects where juniper was removed in fall 2019, average juniper cover within 100 m of treated transects decreased from 4% (4% SD) to 0.009% (0.02% SD), representing an average reduction in juniper cover of 99% per 10 ha (Table 2.2).

We observed interannual variability in the number and spatial distribution of detections for both avian predator species (Table 2.2). We included TRI as a covariate for detection in our raven MSO models because TRI had the most predictive power for raven detection (β = 0.22, 90% Crl 0.008, 0.44; 90% posterior direction). Juniper cover had a positive effect on the probability of detection of ravens (median β = 0.43, 90% Crl 0.23, 0.59, 99% posterior direction, 0.12 Bayesian *p*-value). The probability of detection of ravens ranged from 0.43 - 0.58 (90% Crl range 0.27, 0.69) over four years. Raven occupancy was positively influenced by percent cover of juniper and proximity to water (Table 2.3, Figure 2.2). As juniper cover increased within 100 m of a transect, the probability of raven occupancy increased (median β = 1.74, 90% Crl 0.32, 3.76; 99.5% posterior direction), and the highest probability of raven occupancy was areas with > 20% juniper cover. Credible intervals for the effect of distance to water on raven occupancy overlapped zero (median β = -0.65, 90% Crl -1.40, 0.03), but most of the posterior distribution for distance to water indicated that occupancy probability of ravens declined as distance to water increased (95% posterior direction). The average occupancy probability for ravens declined by 55% in the year following juniper removal (2019 = 0.77, SE 0.05, 2020 = 0.34, SE 0.06, Table 2.4). Posterior predictive checks and visual inspections did not indicate a lack of fit or lack of convergence for the most predictive model (Freeman-Tukey *p* value = 0.35, $\hat{r}$ values = 1).

We did not identify important predictors for detection probability for red-tailed hawks. Percent juniper cover did not have a strong effect on detection probability for red-tailed hawks (β = -0.15, 90% Crl -0.39, 0.09), which ranged from 0.18 − 0.24 over four years (90% Crl 0.10, 0.32). Occupancy of red-tailed hawks responded most strongly to the clustering index of trees at a scale of 500 m, responding positively to more dispersed juniper. However, confidence intervals overlapped zero (median β = 1.72, 90% Crl - 4.82, 8.02; 77% posterior direction). Red-tailed hawk occupancy was most strongly influenced by distance to a cliff, but differences in estimates of expected log predictive density (ELPD) suggest that this top model was only marginally more predictive than the null model. Red-tailed hawk occupancy declined as distance to cliff increased (median β = -4.09, 90% Crl -7.57, -1.08; 97.3% posterior direction; Figure 2.2; Table 2.5). Bayesian *p*-values suggest overdispersion in the models. We did not detect a statistically significant change in red-tailed hawk occupancy probability following juniper removal (Table 2.6).

Effect of prey on occupancy

Estimates of prey abundance alone did not influence habitat use for either ravens or red-tailed hawks (Appendix Tables 5 and 6). For ravens, models that included songbird relative abundance and small mammal density along with juniper cover ranked higher than the top-ranked model that included habitat structure only. However, as small mammal density increased raven occupancy probability decreased (β small mammals = -0.92, 90% Crl -1.76, -0.08) suggesting that ravens are less likely to use habitat with higher density of small mammal prey. For red-tailed hawks, neither individual prey groups nor the combined prey index influenced occupancy more than distance to cliff.

Discussion

Our results provide evidence that structures such as trees and cliffs have a stronger influence on occupancy by generalist avian predators than the abundance of some of their most common prey resources. Higher juniper cover and proximity to cliffs increased the probability of habitat use by ravens and red-tailed hawks, respectively, while we found no effects of individual prey resources or a pooled prey abundance index on habitat use by avian predators. Further, we found no evidence of an interaction between habitat structure and prey resources on habitat use by avian predators. For generalist predators such as ravens and red-tailed hawks, which have a high degree of diet plasticity, our results shed light on how habitat structure can influence habitat use whereas the abundance of any individual prey type may not. For example, in areas near agricultural fields, grains can make up the majority of raven diets (Engel and Young 1989), while in more natural types of vegetation cover, small mammals and songbirds can constitute the majority of raven diets (Stiehl and Trautwein 1991). Near roads, carrion is often consumed by both red-tailed hawks and ravens (Knight and Kawashima 1993, Preston and Beane 2020) Red-tailed hawks are also adaptable, with diet composition varying by region and prey abundance (Steenhof et al. 1988), and small passerines birds and medium and small mammals including deer mice can be an important part of red-tailed hawk diets. Therefore, habitat structures that increase the probability of habitat use by generalist predators may increase the risk of predation for a wide range of prey species.

Effect of habitat on occupancy

The establishment of trees and other woody vegetation in rangeland habitats is occurring globally as a consequence of altered fire regimes, climate change, enhanced atmospheric CO_2, and livestock grazing (Bond and Parr 2010, Ratajczak et al. 2012). Conifer trees have expanded into shrub-steppe habitats in southern Canada (Kranitz 2017), acacia (*Acacia saligna*) and pines (*Pinus spp.)* have become established in the fynbos shrublands of South Africa (Holmes and Cowling 1997, Rundel et al. 2014), and pines have invaded the high Andean paramos ecosystem (Hofstede et al. 2002). The establishment of trees in these systems has had negative impacts on some native wildlife associated with vegetation that existed before expansion. For example, the establishment of conifer trees in Mediterranean shrublands has increased predation of songbird nests by a generalist corvid species (Ben-David et al. 2019). As expansion of woody plants continues across the globe, understanding how expansion affects distributions of both predator and prey species and subsequent predator-prey dynamics will be an important part of conserving grassland and shrubland-dependent species. Where habitat structure can be modified through removal of expanding woody species, it will be important to assess whether there are limitations to the effectiveness of removal as a restoration technique, or if additional efforts are required. For instance, tree removal can increase cover of understory vegetation such as bunchgrasses and sagebrush shrubs (Williams et al. 2017). However, variation in soil condition, hydrologic factors, and the pre-removal dominance of conifer can limit the response of understory plants to conifer removal (Freund et al. 2020). Further, variation in plant responses to tree removal techniques (i.e., mastication, hand cutting, etc.) may lead to the establishment of invasive annual grasses and contribute to differences in the recovery of faunal communities (Young et al. 2015).

Effects of generalist predators are a widespread conservation concern for sensitive prey populations, and efforts to control predator populations can be difficult and controversial (Conover and Roberts 2017). Conversion of sagebrush habitat to juniper woodlands has reduced and fragmented habitat for sagebrush-obligate wildlife, and increased abundances of generalist predators can compound the negative effects of habitat loss on prey species (McMahon et al. 2020). For example, juniper expansion has been linked to population declines for greater sage-grouse and increased predator populations are suspected to play a role in these trends (Coates et al. 2017, Severson et al. 2017). However, evidence for an association between juniper expansion and numerical or functional responses of avian predators has been limited or speculative (e.g., Commons et al. 1999, Howe et al. 2014, O'Neil et al. 2018). Our results show that ravens are more likely to occupy sagebrush habitat experiencing conifer expansion, a relationship that has implications for the conservation of sagebrush-associated wildlife populations.

Subsidized populations of generalist predators can significantly impact prey populations because predation may continue even after the prey density becomes very low (Polis 1997). There are likely fewer anthropogenic subsidies at our study site than in many areas of the western U.S. given the low human density of Owyhee County, but raven populations more broadly have benefited from human development, leading to increased abundance in the Great Basin (Leu et al. 2008). Housing density is low at our site (0.02 houses/km^2), and two lightly used dirt roads run through the study site (road density is 0.08 km/km^2). There are no agricultural fields within 10 km (distance from a transect to agriculture ranged from 10 – 43 km) and no transmission lines within 21 km (distance from a transect to a transmission line ranged from 21-55 km) of the study site. As a result, the effects of natural structures on occupancy probability are less likely to be confounded by the positive effects of human subsidies and structures. Ravens are 'incidental' hunters, consuming a wide variety of prey including small mammals, songbirds, and lizards (Boarman and Heinrich 1999). As the amount of habitat used by ravens increases, the likelihood that ravens will incidentally prey on sage-grouse nests may also increase (Manzer and Hannon 2005, Bui et al. 2010, Coates et al. 2020).

We found that the probability of raven occupancy declined as distance to water increased, suggesting that riparian habitat may be more likely to be used by ravens. During our study, we observed mated pair behavior from ravens on multiple occasions, and in each case, the territory was near a streambed lined with juniper and willow. Wildlife biologists with the BLM observed ravens nesting in juniper trees at our site (S. Copeland, BLM, pers. comm.) and, in some habitats, nesting ravens tend to focus their hunting within a smaller area compared to non-nesting ravens (800 m; Harju et al. 2018). The use of mesic habitat by both ravens and prey species may have demographic consequences for prey. For example, sage-grouse hens select for habitat near mesic resources because forbs and insects that occur in these habitats are preferred by sage-grouse broods (Dinkins et al. 2014, Donnelly et al. 2016). Though primarily nest predators, ravens also prey on sage-grouse chicks (Conover and Roberts 2017). Therefore, ravens nesting near riparian areas may be more likely to incidentally prey on juvenile sage-grouse.

Red-tailed hawk occupancy was associated with cliffs, and watercourses at our study site are often at the base of steep cliffs. Though we did not find a relationship between juniper cover and red-tailed hawk occupancy, this species nests in juniper trees throughout the study site and we observed red-tailed hawks hunting from juniper trees and cliff edges near riparian habitat. Small sample sizes for red-tailed hawks may have contributed to overdispersion in models for this species. Overdispersion in models may limit our ability to make inferences on habitat characteristics for red-tailed hawks other than distance to cliff. Along with small sample sizes, overdispersion in the model may also be caused by spatial clustering of red-tailed hawk observations around nests.

For highly mobile species such as avian predators, violations of the assumption that animals remain in a survey location throughout a season may require that researchers consider the effects of habitat on an animal’s presence and availability to be observed (i.e., “availability”; McKenzie et al. 2003, Tyre et al. 2003). Availability is defined as the probability that an animal is present at a survey location and able to be observed. Ravens are large, conspicuous birds that are easily seen and heard over long distances. Previous studies have sometimes assumed that observer error in detecting ravens is close to zero and estimated availability of ravens in relation to habitat, often referred to as use (e.g., Coates et al. 2014b). When the objective is to estimate the effects of habitat on an observer’s ability to detect an avian predator, researchers most often test for effects of habitat features that can obscure avian predators, including trees or rough terrain (Bui et al. 2010). For example, O’Neil et al. (2018) found support for using a ‘viewshed index’ that factored tree cover and TRI into an observer’s ability to detect ravens. We found that juniper cover and TRI positively influenced detection of ravens, indicating that ravens are spending more time in habitat featuring juniper, regardless of whether or not ravens were being obscured from the observer by juniper or landscape features. At 0.43-0.58, our estimate of detection probability for ravens is higher than other studies (e.g., 35%, O'Neil et al. 2018). Given that we truncated our detections to 500 m, a smaller area than other studies (e.g., Bui et al. 2010, O'Neil et al. 2018), we assume that our ability to see and hear ravens was high and that our estimate of detection probability represents availability to a large degree. Therefore, the fact that both occupancy probability and availability are positively influenced by juniper cover provides further support for a relationship between juniper cover and raven habitat use.

Effect of prey on occupancy

Similar to others, our study suggests that habitat structure is more important than any specific prey resource for generalist avian predators (Beier and Drennan 1997, Rullman and Marzluff 2014). In fact, ravens were less likely to use habitat with higher densities of small mammals. Densities of small mammals at our site, largely driven by deer mice, are highest at 10% juniper cover and decline as juniper cover increases (Young 2021). Songbird abundance and diversity also increased in areas featuring early juniper expansion because the habitat can support sagebrush, ecotone, and conifer-associated songbirds (Krannitz 2007, Young 2021). Given the strong relationship we observed between raven habitat use and juniper woodlands, a disconnect between habitat use and prey abundance may be explained by the strong influence of vertical structure on habitat use (also reported in O'Neil et al. 2018).

Conclusion and Management Implications

Conifer removal may benefit wildlife species associated with sagebrush habitat by reducing the occupancy of a common generalist predator. The relationship documented in this study between increasing tree cover in a historically tree-limited habitat and changes in the abundance of a generalist predator species has corollaries in shrubland and grassland ecosystems globally. For instance, increased abundance of generalist predators have been shown to increase predation risk for small prey, such as in Australia where increased abundances of ravens and crows in rangelands decreased the abundance of shrub and ground-nesting songbirds (Rees et al. 2020). Moreover, direct and indirect effects of woody plant expansion on understory vegetation and interactions between trophic levels, respectively, may combine to alter rangeland wildlife communities and contribute to population declines of specialist species. As an example, changes to the structure of the small mammal community can affect seed dispersal, potentially affecting vegetation structure and composition (Kuprewicz 2013).

In our study, raven occupancy was most strongly influenced by juniper cover >20%, which is considered woodland habitat. This relationship has implications for habitat restoration efforts that focus primarily on removal of conifer cover that is < 20% (e.g., BOSH), while allowing conifer cover >20% stands to remain intact. The relationship between raven occupancy juniper cover <20% was highly variable and far less predictive than the effect of juniper woodlands on occupancy (Appendix A1; Figure 2). Sage-grouse avoid using habitat where the abundance of avian predators is high (Dinkins 2014), and our findings suggest that riparian habitat lined with juniper and near cliffs is likely to have the highest probability of use by avian predators at our site. Given that riparian habitat is important for sage-grouse during a vulnerable life stage, managing conifer expansion in and around riparian habitat may be particularly beneficial for sage-grouse populations.

Although areas with juniper cover < 20% are likely to have retained some shrub structure required by sagebrush wildlife, the association between ravens and juniper cover >20% suggests restoration efforts that do not remove dense juniper stands may not significantly alter the avian predator community. However, this is not to suggest removal of juniper cover < 20% may not have net benefits for sagebrush wildlife, as the mean occupancy of ravens was lowest in the year following removal of juniper cover and would likely represent a net reduction in avian predator density for sagebrush wildlife. Moreover, logistical considerations are also important, as a primary objective of tree removal is to prevent the continued expansion of juniper (BLM 2018). Restoration of rangeland habitat dominated by late-stage conifer development may not be as successful as restoration of earlier successional stages (Williams et al. 2017), and removal of trees from shrublands can be costly and require long-term management through regular retreatment (Fill et al. 2017). Finally, juniper woodlands are important for many wildlife species as well, and often feature high songbird diversity (Bombaci and Pejchar 2016). Though more research is needed on the implications of remaining juniper cover > 20% habitat in sagebrush, the benefits of removing juniper cover < 20% for sagebrush wildlife, and the potential decreases in habitat use by a common generalist predator, are important considerations for the conservation of sagebrush wildlife.

Given observed yearly variation in occupancy and abundance of avian predators, long-term monitoring, especially after tree removal, is required to better assess the impact of juniper removal on avian predators as well as predation rates for prey species. However, to our knowledge no long-term studies of habitat use by avian predators in a sagebrush-conifer woodland habitat exist. Therefore, our study represents a critical first step and provides unique and valuable information because the overall effect of juniper cover on raven occupancy suggests that juniper removal may be effective if the goal is to reduce habitat use by predators of sage-grouse.

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Tables

Table 2.1. Covariates used to test effects of habitat features on detection and occupancy probability of common ravens (*Corvus corax*) and red-tailed hawks (*Buteo jamaicensis)* in southwest Idaho, 2017-2020. We used a three-stage modeling approach, carrying over the top ranked model from each stage. We ranked models using leave one out cross validation and Bayesian p-values.

Detection	**Habitat Structure Models**	**Prey Models**
Null	Null	Structure model (sm)
Time of year	Juniper Cover	Small mammals
Terrain roughness index	Distance to cliff	Songbirds
	Distance to water	Ground squirrels
	Distance to stream	Distance to lek
	Distance to road	Prey index
	Distance to human dwelling	SMD + sm
	Distance to cliff + juniper	Songbirds + sm
	Distance to cliff + distance to stream	Ground squirrels + sm
	Distance to road + juniper	Distance to lek + sm
	Distance to water + juniper	Prey index + sm
	Distance to human dwelling + juniper	SMD*sm
	Small mammal density (SMD)	Songbirds*sm
	Juniper Removal	Distance to lek*sm
		Prey index*sm

Table 2.2 Sampling effort for occupancy surveys of common raven (Corvus corax) and red-tailed hawk (Buteo jamaicensis) in southwest Idaho, 2017-2020. We conducted surveys from 1 May – 15 July each year. In fall of 2019 juniper was removed from ~ 14,000 ha, so 2020 statistics represent post-removal conditions.

	2017	**2018**	**2019**	**2020**
Transects sampled	30	37	37	37
Surveys completed	76	111	111	111
Ravens				
# Observations[1]	35	236	205	161
% of Surveys [2]	32%	64%	57%	43%
% of transects[3]	50%	89%	91%	70%
Red-tailed hawks				
# detections	17	36	22	20
% of Surveys	18%	21%	24%	16%
% of transects	40%	45%	40%	37%
Transect juniper cover category (100 m)				
0%	5	5	6	17
1-10 %	16	21	20	12
10-20%	5	6	6	3
> 20%	4	5	5	5

[1] Total observations per year.

[2] Percentage of surveys where a species was detected.

[3] Unadjusted percentage of transects where a species was detected.

Table 2.3 Habitat model rankings for common raven (Corvus corax) occupancy in southwest Idaho, 2017-2020. We conducted 409 occupancy surveys at 37 transects. We used Bayesian multi-season models to test the effects of habitat variables on common raven occupancy and compared models using leave-one-out cross validation.

Model	**[1]elpd_diff**	**[2]se_diff**	**[3]*p*-value**
Juniper cover + water	0.00	0.00	0.35
Juniper cover	-0.80	1.48	0.31
Juniper cover + road	-4.30	1.38	0.29
Null	-6.83	2.00	0.23
Juniper cover + cabin	-7.05	1.94	0.29
Water	-7.40	1.59	0.21
Cliff + stream	-9.90	6.02	0.09
Juniper + cliff	-10.93	5.22	0.11
Cliff	-11.01	5.57	0.09
Stream	-11.74	2.46	0.14
Road	-12.17	2.52	0.14
Cabin	-12.52	2.81	0.15
Juniper removal	-14.67	3.07	0.13

[1] Expected log predictive density. Larger scores indicate the model is more predictive.

[2] Standard error of the difference in elpd between a model and the most predictive model.

[3] Bayesian p-value calculated using the Freeman-Tukey test statistic. Values closer to 0.5 indicate a better model fit.

Table 2.4 Derived parameters for the top-ranked common raven (Corvus corax) occupancy model in southwest Idaho, 2017-2020. Model covariates include juniper cover within 100 m of the survey location and distance to water. We conducted occupancy surveys (n = 409 surveys) at 30 transects in 2017 and 37 transects each year during 2018-2020 to test the effect of habitat features on occupancy and detection probability. Juniper removal occurred in fall 2019 at 21 of the 37 transects.

Parameter	Pre-removal 2017		Pre-removal 2018		Pre-removal 2019		Post-removal 2020	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE
[1]ψ	0.82	0.05	0.69	0.07	0.77	0.06	0.34	0.06
[2]p	0.43	0.01	0.45	0.01	0.58	0.01	0.58	0.01
[3] n.occ	28.21	0.93	36.16	0.37	37.74	0.84	30.00	0.53

[1] average occupancy probability

[2] mean detection probability

[3] estimated total number of occupied transects

Table 2.5 Habitat model rankings for red-tailed hawk (*Buteo jamaicensis*) occupancy in southwest Idaho, 2017-2020. We conducted 409 occupancy surveys at 37 transects. We used Bayesian multi-season models to test the effects of habitat variables on red-tailed hawk occupancy and compared models using leave-one-out cross validation.

Model	**[1]elpd_diff**	**[2]se_diff**	**[3]*p* value**
Cliff	0.00	0.00	0.07
Cliff + Tree Clustering	-0.26	1.36	0.07
Water + Tree Clustering	-0.69	5.29	0.10
Null	-1.45	3.97	0.15
Water	-1.55	4.42	0.11
Tree Clustering	-2.02	4.91	0.12
Treatment	-2.80	3.82	0.10
Cabins + Tree Clustering	-3.69	4.29	0.07
Distance to Road	-4.08	4.02	0.06
Distance to Cabins	-4.28	3.83	0.06
Distance to Streams	-5.10	3.93	0.06
Distance to Road + Tree Clustering	-5.39	4.88	0.05
Distance to Stream + Tree Clustering	-7.17	4.68	0.04

Table 2.6 Derived parameters for the top-ranked red-tailed hawk (*Buteo jamaicensis*) occupancy model in southwest Idaho, 2017-2020. We conducted occupancy surveys (n = 409 surveys) at 30 transects in 2017 and 37 transects from 2018-2020 to test the effect of habitat variables on occupancy and detection probability. Juniper removal occurred in fall 2019 from 21 of the 37 transects following the completion of surveys for the year.

Parameter	2017		2018		2019		2020	
	Est.	SE	Est.	SE	Est.	SE	Est	SE
[1]ψ	0.50	0.07	0.85	0.05	0.94	0.03	0.99	0.00
[2]p	0.18	0.01	0.24	0.01	0.23	0.01	0.16	0.00
[3]n.occ	31.70	0.45	31.98	0.24	32.02	0.29	37.73	0.12

[1] average occupancy probability

[2] mean detection probability

[3] estimated total number of occupied transects

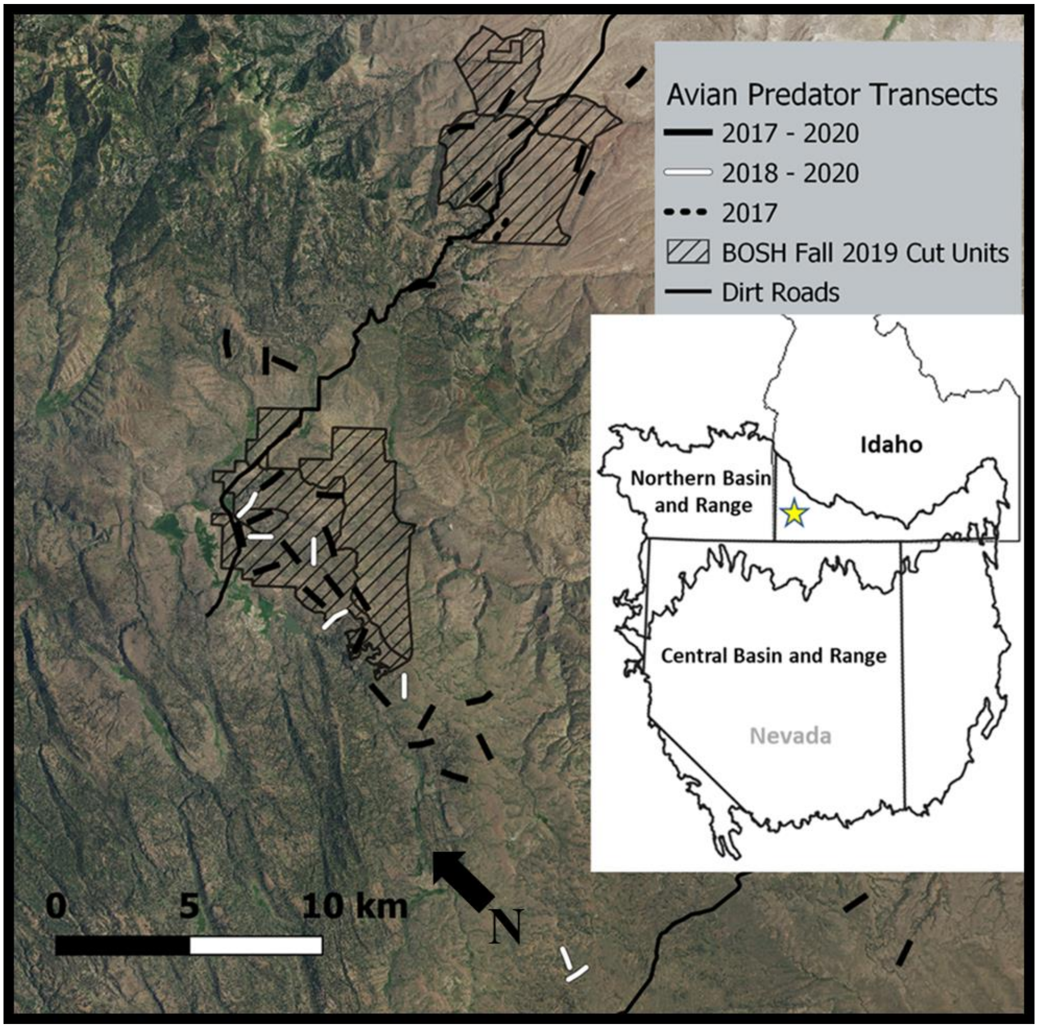

Figure 2.1. Study site for avian predator surveys in the Owyhee Mountains of southwestern Idaho. Surveys took place 2017-2020 along 800-m transects inside and outside areas of juniper removal. Juniper removal occurred in the fall of 2019. The inset map shows the location of the two U.S. EPA Level III ecoregions that comprise most of the Great Basin.

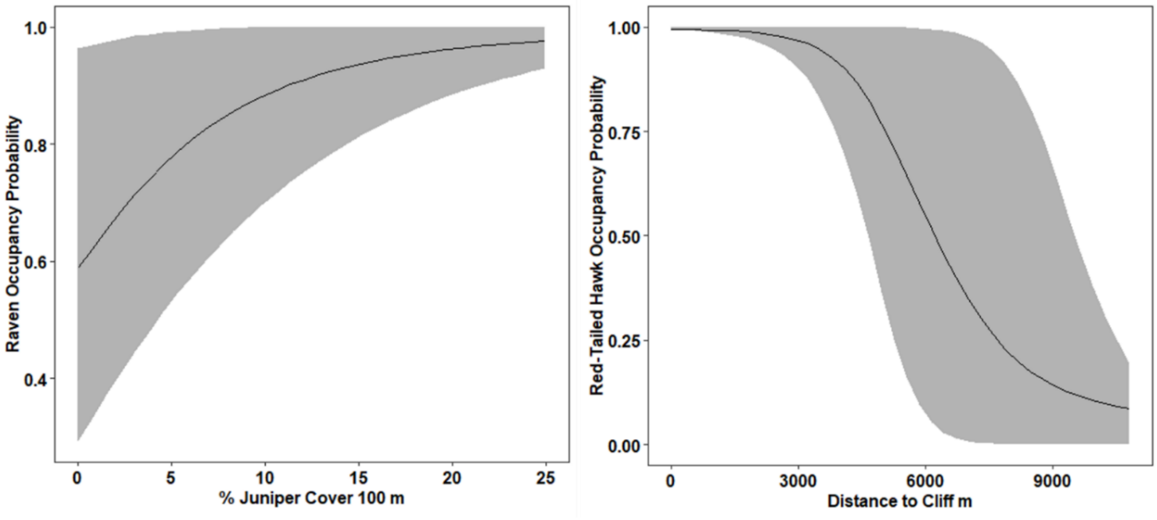

Figure 2.2. Occupancy probability for common ravens (*Corvus corax*) and red-tailed hawks (*Buteo jamaicensis*) in southwest Idaho from 2017-2020. We surveyed 29 transects for four years and eight transects for three years and tested the effect of juniper cover and other habitat characteristics on occupancy probability. A model that included percent juniper cover within 100 m of the survey transect was most predictive for ravens and a model that included distance to cliff was most predictive for red-tailed hawks.

Appendix A

Table A1. Model rankings for the effect of juniper (*Juniperus occidentalis*) on common raven (*Corvus corax*) occupancy in the Owyhee Mountains of southwestern Idaho, 2017-2020. We conducted 409 occupancy surveys at 37 transects. We tested nine spatial scales of percent juniper cover within 100 m to 3000 m. We tested quadratic models for each spatial scale. We also tested for an effect of the proportion of phases one (<10% juniper cover), two (10-20% juniper cover), and three (>20% juniper cover) at each spatial scale. Finally, we tested for an effect of tree clustering on raven occupancy using a nearest neighbor algorithm value generated using a 1 m resolution juniper layer at each spatial scale. We used Bayesian multi-season models and compared models using leave-one-out cross validation.

Model	**[1]elpd_diff**	**[2]se_diff**	**[3]*p* value**
[4]100 p3	0.00	0.00	0.35
250 p3	-1.41	5.43	0.31
100	-2.85	5.86	0.36
250	-4.53	5.89	0.32
750*750	-4.93	1.21	0.19
1000*1000	-5.53	1.92	0.19
100*100	-6.23	4.17	0.26
250*250	-7.18	3.59	0.24
500 p3	-7.89	5.42	0.21
100 p2	-8.11	5.50	0.24
500*500	-8.25	2.51	0.21
500	-9.65	5.90	0.23
250 p2	-10.34	5.52	0.20
750 p3	-11.51	5.43	0.17
750	-12.83	5.92	0.18
[5]500 cl	-12.94	4.88	0.19
750 cl	-13.41	4.83	0.18
3000 p2	-13.43	7.03	0.09
2000^2	-13.49	3.96	0.13
3000 cl	-13.72	4.66	0.17
1000 cl	-13.90	4.79	0.16
1000 p3	-13.94	5.52	0.14
2500 cl	-14.06	4.75	0.16
2500 p3	-14.12	5.71	0.12
1500 cl	-14.16	4.79	0.15
2000 p3	-14.19	5.73	0.12
2000	-14.21	6.15	0.14
2000 cl	-14.22	4.79	0.15
1500 p3	-14.26	5.61	0.12
1000	-14.32	5.96	0.16
500 p2	-14.32	5.85	0.13

3000 p1	-14.48	7.00	0.08
1500	-14.56	6.04	0.15
2500	-14.68	6.21	0.13
2500 p2	-14.70	6.72	0.08
3000	-14.80	6.28	0.12
3000 p3	-14.80	5.80	0.11
250 cl	-14.85	4.71	0.14
2500^2	-14.92	4.36	0.12
100 cl	-15.10	4.93	0.16
2000 p2	-15.22	6.54	0.09
2500 p1	-15.28	6.79	0.08
100 p1	-15.35	4.97	0.15
250 p1	-15.63	5.07	0.14
1000 p2	-15.84	5.95	0.10
750 p2	-15.90	5.95	0.10
2000 p1	-16.04	6.44	0.09
1500 p2	-16.10	6.09	0.09
750 p1	-16.70	5.58	0.11
500 p1	-16.70	5.65	0.11
1500 p1	-16.72	6.07	0.09
1000 p1	-16.73	5.76	0.10
3000*3000	-16.90	4.95	0.06

[1] Expected log predictive density. Larger scores indicate the model is more predictive.

[2] Standard error of the difference in elpd between a model and the most predictive model.

[3] Bayesian p value calculated using the Freeman-Tukey test statistic. Values closer to 0.5 indicate a better model fit, [4] Phase 1, Phase 2, Phase 3

[5] Tree Clustering

Table A2. Model rankings for the effect of juniper (*Juniperus occidentalis*) on red-tailed hawk (*Buteo jamacensis*) occupancy in the Owyhee Mountains of southwestern Idaho, 2017-2020. We conducted 409 occupancy surveys at 37 transects. We tested nine spatial scales of percent juniper cover within 100 m to 3000 m. We tested quadratic models for each spatial scale. We also tested for an effect of the proportion of phases one (<10% juniper cover), two (10-20% juniper cover), and three (>20% juniper cover) at each spatial scale. Finally, we tested for an effect of tree clustering on occupancy using a nearest neighbor algorithm value generated using a 1-m resolution juniper layer at each spatial scale. We used Bayesian multi-season models and compared models using leave-one-out cross validation.

Model	**[1]elpd_diff**	**[2]se_diff**	**[3]*p* value**
[4]500 cl	0.00	0.00	0.12
750 cl	-0.50	3.55	0.12
500*500	-0.60	0.87	0.06
250 cl	-1.53	3.95	0.09
3000 cl	-2.13	3.75	0.10
3000*3000	-2.22	2.39	0.06
100 cl	-2.46	3.16	0.11
[5]500 p2	-2.59	2.72	0.08
1000 cl	-2.98	3.15	0.10
250 p2	-3.45	2.75	0.07
2500 p1	-3.51	3.87	0.08
1500*1500	-3.51	2.46	0.04
3000 p1	-3.53	4.17	0.07
750 p2	-3.57	2.76	0.07
1500 cl	-3.59	3.54	0.08
2000 cl	-3.62	3.63	0.08
3000	-3.63	3.13	0.07
500 p3	-3.68	3.25	0.09
100 p3	-3.79	3.19	0.09
750 p3	-3.80	3.33	0.08
250*250	-3.82	2.16	0.05
2500 cl	-3.84	3.61	0.08
750	-3.84	3.23	0.08
1000 p3	-3.90	3.32	0.08
2000 p1	-3.91	3.64	0.08
500	-3.92	3.22	0.08
100	-3.92	3.21	0.08
250	-3.99	3.24	0.08
1000 p2	-3.99	2.88	0.07
1500 p1	-4.07	3.52	0.08
1500	-4.08	3.21	0.08
100 p2	-4.08	3.13	0.08

1000	-4.11	3.24	0.08
1500 p3	-4.12	3.27	0.08
2000	-4.13	3.18	0.08
2000 p2	-4.16	3.25	0.08
2000 p3	-4.17	3.30	0.08
250 p1	-4.19	2.64	0.06
1000*1000	-4.22	2.33	0.05
750 p1	-4.25	3.03	0.07
100 p1	-4.26	3.08	0.07
3000 p2	-4.26	3.38	0.08
3000	-4.30	3.18	0.08
2500 p3	-4.36	3.27	0.08
250 p3	-4.37	3.25	0.08
1000 p1	-4.42	3.14	0.07
2500*2500	-4.45	2.43	0.05
500 p1	-4.49	3.02	0.07
2500 p2	-4.50	3.36	0.07
1500 p2	-4.55	3.23	0.07
2000*2000	-4.58	2.39	0.05
3000 p3	-4.65	3.28	0.07
750*750	-5.15	2.32	0.04
100*100	-5.79	2.71	0.04

[1] Expected log predictive density. Larger scores indicate the model is more predictive.

[2] Standard error of the difference in elpd between a model and the most predictive model.

[3] Bayesian p value calculated using the Freeman-Tukey test statistic. Values closer to 0.5 indicate a better model fit.

[4] Phase 1, Phase 2, Phase 3

[5] Tree Clustering

Table A3. Model rankings for common raven (*Corvus corax*) detection in southwest Idaho, 2017-2020. We conducted 409 occupancy surveys at 37 transects. We used Bayesian multi-season models to test the effects of habitat variables on common raven detection and compared models using leave-one-out cross validation.

Model	[1]**elpd_diff**	[2]**se_diff**	**Bayesian *p*-value**
Terrain Roughness Index	0.00	0.00	0.22
Null	-1.30	2.70	0.19
Time of Year	-2.70	2.80	0.19

[1] Expected log predictive density. Larger scores indicate the model is more predictive.

[2] Standard error of the difference in elpd between a model and the most predictive model.

Table A4. Model rankings for red-tailed hawk (*Buteo jamaicensis*) detection in southwest Idaho, 2017-2020. We conducted 409 occupancy surveys at 37 transects. We used Bayesian multi-season models to test the effects of habitat variables on red-tailed hawk detection and compared models using leave-one-out cross validation.

Model	**[1]elpd_diff**	**[2]se_diff**
Null	0.00	0.00
Time of Year	-0.50	0.90
[3]Terrain Roughness Index	-1.3	0.60

[1] Expected log predictive density. Larger scores indicate the model is more predictive.

[2] Standard error of the difference in elpd between a model and the most predictive model.

Table A5. Prey model rankings for common raven (*Corvus corax*) occupancy in southwest Idaho 2017-2020. We conducted 409 occupancy surveys at 37 transects. We used Bayesian multi-season models to test the effects of habitat variables on common raven occupancy and compared models using leave-one-out cross validation.

Model	**[1]elpd_diff**	**[2]se_diff**	**[3]*p* value**
[4]Songbirds + [5]Juniper	0	0	0.35
[6]Small Mammals + Juniper	-0.30	2.69	0.37
Juniper + [7]Water	-2.39	2.24	0.35
Songbirds*Juniper	-3.71	0.52	0.31
Small Mammals*Juniper	-4.72	2.83	0.32
[8]Ground Squirrels + Juniper	-6.26	3.58	0.24
[9]Lek + Juniper	-6.64	2.34	0.27
Lek*Juniper	-9.89	2.64	0.22
[10]Prey + Juniper	-10.79	2.27	0.23
Prey*Juniper	-12.13	2.73	0.16
Prey	-12.42	4.32	0.08
Small Mammals	-13.78	3.08	0.17
Lek	-14.16	3.31	0.13
Songbirds	-14.42	2.90	0.16
Ground Squirrels	-15.49	3.62	0.13

[1] Expected log predictive density. Larger scores indicate the model is more predictive.

[2] Standard error of the difference in elpd between a model and the most predictive model.

[3] Bayesian p value calculated using the Freeman-Tukey test statistic. Values closer to 0.5 indicate a better model fit, [4] Unadjusted count, [5] % *Juniperus occidentalis* cover 100 m, [6] Density/ha, [7] Distance m, [8] Presence/absence, [9] Distance m, [10] Index of all prey groups

Table A6. Prey model rankings for red-tailed hawk (*Buteo jamaicensis*) occupancy in southwest Idaho, 2017-2020. We conducted 409 occupancy surveys at 37 transects. We used Bayesian multi-season models to test the effects of habitat variables on red-tailed hawk occupancy and compared models using leave-one-out cross validation.

Model	**[1]elpd_diff**	**[2]se_diff**	**[3]*p* value**
[4]Songbird*[5]Cliff	0.00	0.00	0.07
[6]Lek*Cliff	-1.35	1.39	0.08
[7]Prey*Cliff	-2.41	1.47	0.06
Lek + Cliff	-3.49	2.03	0.07
[8]Small Mammal*Cliff	-4.18	2.09	0.07
Cliff	-4.96	2.40	0.07
Prey + Cliff	-5.01	2.16	0.06
Small Mammal + Cliff	-5.29	2.45	0.07
Small Mammals	-5.57	2.50	0.07
[9]Ground Squirrels + Cliff	-5.58	2.01	0.06
Prey	-6.88	5.38	0.13
Lek	-8.69	5.30	0.11
Ground Squirrels	-9.83	5.24	0.08
Songbirds + Cliff	-11.50	4.12	0.04
Songbirds	-15.91	5.32	0.02

[1] Expected log predictive density. Larger scores indicate the model is more predictive.

[2] Standard error of the difference in elpd from the most predictive model.

[3] Bayesian p value calculated using the Freeman-Tukey test statistic. Values closer to 0.5 indicate a better model fit.

[4] Unadjusted count, [5] Distance m, [6] Distance m, [7]Index of all prey groups, [8]Density/ha , [9] Presence/absence

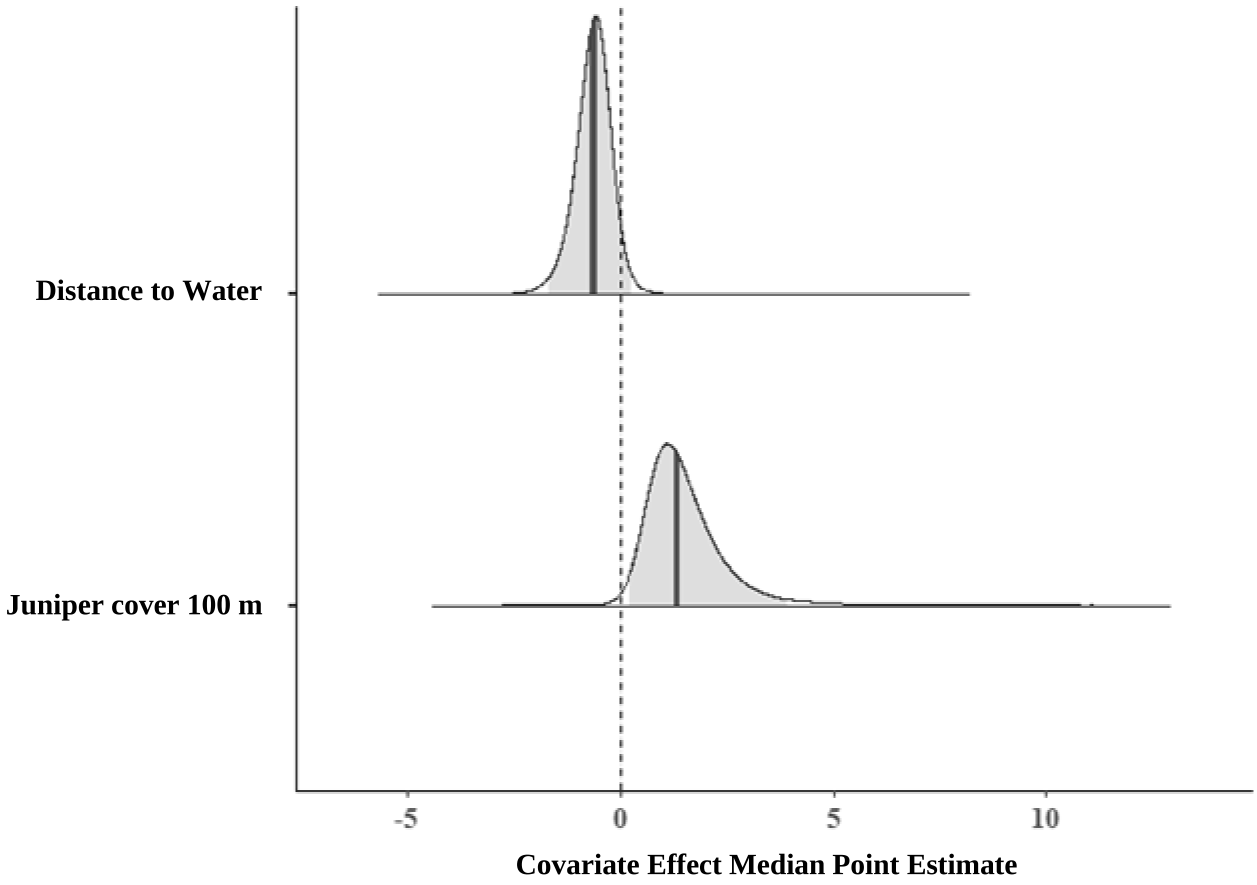

Figure A1. Posterior distributions for covariate effects on common raven (*Corvus corax*) occupancy in southwest, Idaho, 2017-2020. We modeled occupancy at 37 transects using a multi-season occupancy model. The solid line is the median point estimate for covariate effects. The shaded region is the 90% credible interval, and the dashed line is zero covariate effect.

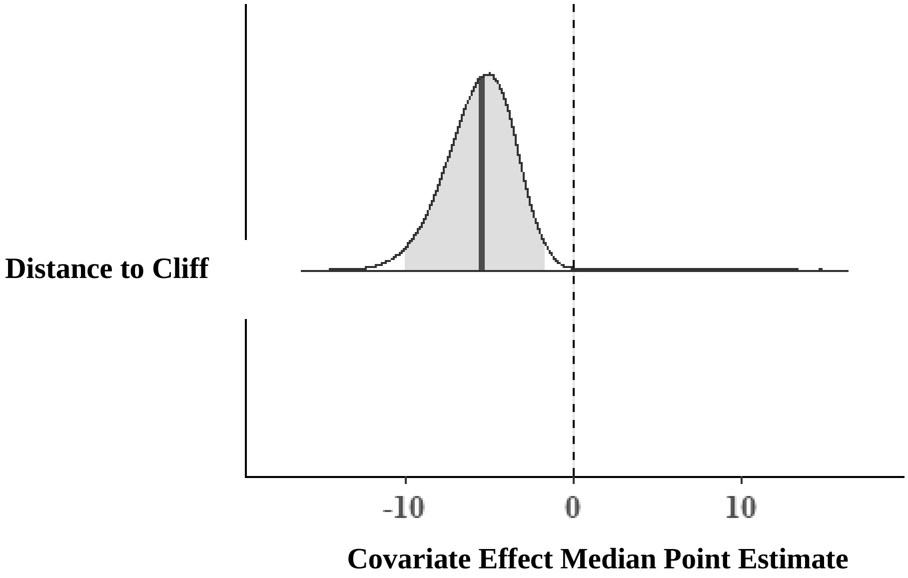

Figure A2. Posterior distributions for covariate effects on red-tailed hawk (*Buteo jamaicensis*) occupancy in southwest, Idaho, 2017-2020. We modeled occupancy at 37 transects using a multi-season occupancy model. A model that included distance to cliff (m) was the most predictive model for red-tailed hawk occupancy. The solid line is the median point estimate for covariate effects. The shaded region is the 90% credible interval, and the dashed line is zero covariate effect.

Chapter 3: Expanding and invading plants in sagebrush steppe effect multiple aspects of small mammal ecology

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Abstract

Invasion and expansion of nonnative and native plants, respectively, have altered vegetation structure in many terrestrial ecosystems. For small mammals, an important group that influences multiple ecosystem processes through their roles as both ecosystem engineers and prey, changes to vegetation structure can affect habitat use, community composition, and predator/prey interactions. In the sagebrush shrublands of the western United States, invasions by nonnative grasses and expansion of conifer trees beyond their historic range has altered vegetation structure, potentially affecting species interactions and distributions of deer mice (*Peromyscus maniculatus*), a generalist omnivore, or Great Basin pocket mice (*Perognathus parvus*), a specialized herbivore. To assess the extent to which altered habitat affects small mammal density, survival, and home-range size, we examined these aspects of small mammal ecology along a gradient of cheatgrass (*Bromus tectorum*), a nonnative annual grass, and western juniper (*Juniperus occidentalis*) establishment in a sagebrush shrubland in southwestern Idaho. Over three years, we used a spatially explicit mark-recapture design to examine attributes of small mammal ecology along an invasion gradient. We did not find support for an effect of cheatgrass cover on density or survival of either species. However, home-range size of deer mice was 2.3 times smaller in areas where 60% of the site had been invaded by cheatgrass compared to areas with no cheatgrass cover. Density of deer mice was highest (5/ha) in areas with 10% juniper cover and decreased with increasing juniper cover whereas density of pocket mice was positively influenced by shrub cover. The use of habitat featuring juniper may represent an ecological trap for deer mice because survival for this species decreased with increasing juniper stem density. Conversely, survival of pocket mice increased with increasing juniper stem density. We found evidence for interspecific interactions between these two species, in the form of a density-dependent effect of deer mice on pocket mouse home-range size. Home-range size for pocket mice was two times smaller in areas with the highest estimated density of deer mice compared to areas with low densities of deer mice. Efforts to stem the negative effects of native plant expansion, including removal of conifer from sagebrush habitat, and nonnative invasions on wildlife populations may benefit small mammal populations, or at the very least impact community composition. Our data provides unique information about how small mammals in sagebrush

steppe are affected by expanding and invasive plants the potential ways that habitat restoration, in the form of conifer removal, may impact small mammals.

Introduction

One of the most common forms of habitat degradation worldwide is native and non-native plants that expand beyond their historic ranges (Westbrook 1998, Briske 2017). Changes in plant composition and structure can affect many aspects of ecosystem function, including nutrient and water cycling, fundamentally altering the availability of resources for which plants and wildlife in pre-expansion communities are adapted (Evans et al. 2001, Briske et al. 2008, Wilcox et al. 2017). Plant expansions may influence species richness, abundance, and diversity, or can facilitate the establishment of new fauna species, resulting in novel ecosystems (Bestelmeyer et al. 2017). However, changes to ecosystem function caused by plant expansions are not necessarily linear. As novel plants become established, changes to ecosystem function may create positive feedback allowing further establishment of the expanding plant until a threshold is reached and a state transition takes place (Lee et al. a process we refer to here as the "invasion gradient" Changes to ecosystem structure and function along the invasion gradient have implications the conservation of species dependent on the affected ecosystem.

Plant invasions often have effects on the broader food web (Garden et al. 2007, Heleno et al. 2009, Bachen et al. 2018). Although the composition of the plant community is important for herbivores that may use specific plant species as food, the physical structure of vegetation is also important to many animals (Patterson and Best 1996). Vegetation structure can influence habitat use independently of food resources by providing protection from predation, thermal regulation, and by impeding or facilitating animal movements (With and Crist 1995). If changes to vegetation structure provide resources to predators or competitors, species adapted to pre-invasion conditions may experience population reduction or extirpation (Tylianakis et al. 2008). For example, invasion of shrubs into prairie vegetation indirectly reduces survival for songbirds via improved thermal cover for snakes that results in increased snake density (Klug et al. 2010, Young et al. 2019). Plant invasions can also lead to changes in intra-trophic competition caused by increased abundance of a species already present in the community or the colonization of new species (Didham et al. 2007, Litt and

Pearson 2013). Plant invasions leading to increased competition has been shown in diverse settings, including songbirds (Maron et al. 2011) and aquatic ecosystems (Boström-Einarsson et al. 2014, Calizza et al. 2017). In these cases, increased competition led to lower abundance and diversity of the pre-invasion community.

The Great Basin of the western United States has arguably experienced some of the most extensive and damaging changes from invasive non-native and expanding native plant species. The sagebrush ecosystem that dominates the Great Basin has undergone widespread changes to vegetation structure due to invasions by cheatgrass (*Bromus tectorum*) and expansion of conifer (*Juniperus spp. and Pinus spp.)* trees into areas of previously contiguous sagebrush (Davies et al. 2011, Miller et al. 2019). These changes have negatively affected some sagebrush-obligate birds (Knick et al. 2003, Coates et al. 2017). However, responses among wildlife species to cheatgrass and conifer will depend on the magnitude of ecological change that has occurred, i.e., the invasion gradient (Archer et al. 2017). At one end of the invasion gradient habitat is dominated by conifer trees with minimal shrub and grass layers and the abundance of sagebrush-associated wildlife is low. At the other end of the invasion gradient, habitat is dominated by sagebrush shrubs with an intact layer of native grasses and forbs and should support a diverse community of sagebrush-associated wildlife. In sagebrush ecosystems in the Great Basin, habitat between these two extremes often features varying degrees of cheatgrass and conifer cover that has reduced, but not eliminated, the sagebrush and native perennial herbaceous layers (Coultrap et al. 2008).

Small mammals are an important component of the sagebrush ecosystem because they serve as both prey and predators and influence vegetative structure and composition through herbivory (Merritt 2010). The joint effects of conifer expansion and cheatgrass invasion on small mammals in sagebrush ecosystems are likely complex, but many aspects of small-mammal ecology in such altered sagebrush habitat remain unknown. Increases in cheatgrass and juniper cover over the last 100 years coincide with declines in diversity, richness, and evenness of the small-mammal community (Phillips 2018), and abundance and diversity of small mammals are lower in juniper woodlands than sagebrush habitat (O’Meara et al. 1981, Peterson et al. 2017, Hamilton et al. 2019). However, for many species information on the population level effects of vegetation change is lacking. Reductions in shrub and grass cover associated with juniper expansion may increase the susceptibility of small mammals to predation by visual hunters, as well as reduce the availability of small mammal food (Loggins et al. 2019). Juniper may also increase the hunting efficiency of avian predators by providing perches (Coates et al. 2014, Severson et al. 2017, Andersson et al. 2019). Cheatgrass can reduce survival of small mammals, an effect ameliorated by the presence of native shrubs (Ceradini and Chalfoun 2017), and small mammal abundance and diversity is lower in habitat invaded by cheatgrass (Ostoja et al. 2009, Hall 2012, Kluever et al. 2019). The combined effects of juniper expansion, which may alter habitat use by predators, and cheatgrass, which may affect predation risk for small mammals by inhibiting movements, on survival of small mammals has not been examined to our knowledge. Understanding how these changes to sagebrush habitat affect the small-mammal community will be important for understanding the overall effect of invasion on the sagebrush ecosystem.

Given the broad scale and ongoing changes to sagebrush habitat from expanding and invading plants and the importance of small mammals to ecosystem function, understanding population-level responses from small mammals will be important for conservation of the sagebrush biome. Our study consisted of two objectives: 1.) evaluate the effects of a gradient of conifer and cheatgrass cover on small mammal density; 2.) test the effect of habitat features including conifer and cheatgrass cover, and intra/inter-specific density on small mammal survival and home-range size. We hypothesized that understory vegetation (herbaceous and shrub layers) would be the primary influence on small mammal habitat use; therefore, the density of species that are specialist herbivores will be highest in areas with higher cover of native bunchgrasses and shrubs. We also predicted that small mammal survival will decrease with increasing conifer, cheatgrass, and low shrub cover due to changes in predator/prey interactions that are mediated by habitat structure. Finally, we expect that small mammal home ranges will be smaller in areas featuring conifer expansion and higher cheatgrass cover due to changes in either perceived or actual predation risk.

Methods

Study area

We trapped small mammals in Owyhee County, southwestern Idaho habitat consisting of sagebrush steppe and juniper woodland (Figure 3.1). The study area is in the Northern Basin and Range ecoregion (McGrath et al. 2002) and is composed primarily of big (*Artemisia tridentata*) and low (*A. arbuscula*) sagebrush interspersed with western juniper (*Juniperus occidentalis;* hereafter, juniper). Elevation ranges 1,250–1,920 m and topography varies with low-lying riparian areas, open sagebrush tablelands, and rocky ridgelines. Dense juniper is found along ridgetops and in drainages and has expanded into sagebrush communities, forming a gradient of tree cover across the landscape. Sandberg bluegrass (*Poa secunda*) is the dominant grass at higher elevations, and cheatgrass (*Bromus tectorum*) is dominant at lower elevations. Other common shrub species include antelope bitterbrush (*Purshia tridentata*) and green rabbitbrush (*Chrysothamnus viscidiflorus*). Juniper at the site is classified into three phases based on the degree to which sagebrush and juniper dominate ecosystem processes. In phase 1, juniper cover is <10% but sagebrush is still the dominant plant cover. In phase 2, juniper (10-20% cover) and sagebrush codominate ecosystem processes. In phase 3 juniper cover is> 20%and juniper dominates ecosystem processes,and cover of sagebrush and grass have been greatly reduced (Miller et al. 2005, Falkowski and Evans 2012).

Data collection

We selected trapping sites (*n* = 14) from a pool of randomly generated sampling locations (*n* = 111; Figure 1). First, to generate trapping sites randomly across a gradient of juniper expansion, we stratified the study area by juniper cover categories (pre-expansion and phases 1 and 2) and placed trapping sites within pre-expansion and phases 1 and 2 using the random points tool in ArcGIS. We selected a subset of trapping sites within each juniper cover category based on accessibility and habitat characteristics such as juniper cover, sagebrush structure, and grass composition. We selected trapping sites that featured a range of juniper cover within phases 1 and 2, as well as varying amounts of cheatgrass cover both within and across trapping site. Using visual estimation, we selected trapping sites that featured a gradient of cheatgrass cover, from no cheatgrass to dominated by cheatgrass. At trapping sites, average juniper cover ranged from 0 – 17% (Figure 3.2), average cheatgrass cover ranged from 2 – 12%, and average big sagebrush cover ranged from 8 – 17%. In 2017 at five trapping sites, we deployed 148 traps in a radial design with a diameter of 200 m covering an area of 3.13 ha, as described in the distance sampling design of Anderson et al. (1983; Figure 3.3). Due to low capture rates, we expanded the number of trapping sites sampled in 2018 to 14, including the original five, and we re-sampled all 14 trapping sites in 2019. In 2018 and 2019, we deployed 64 traps at each trapping site, arrayed in a square grid with traps spaced 15 m equidistant covering an area of 1.1 ha (Hamilton et al. 2019; Figure 3). In total, we sampled five trapping sites for three years and nine trapping sites for two years. To account for changing density over each year's sampling period, we sampled twice each year. The first trapping session consisted of five nights in May or June, and the second consisted of four nights in July or August. We used 7.6 x 8.9 x 22.9 cm Sherman traps (H.B. Sherman Traps, Tallahassee, FL, USA) baited with peanut butter, rolled oats, apples, and carrots. We placed polyester batting material in each trap as bedding. We opened traps each evening before sunset and checked traps each morning at sunrise. We identified captured animals to species, and recorded sex and age. We individually marked animals with an 8 mm passive integrated transponder (PIT.; Biomark, Boise, ID, USA) tag and released animals at their capture location.

Vegetation characteristics

We assessed vegetation characteristics and juniper cover at trapping sites in multiple ways. We calculated the percent cover of juniper at each trapping site in ArcGIS (ESRI 2018, Redlands, CA: Environmental Systems Research Institute) using a 1-m juniper classification obtained from a National Agriculture Inventory Program aerial photograph (NAIP, 2016). We identified juniper using a supervised classification and manually corrected any misidentifications for each trapping location using visual inspection and ground truthing.

Density and home range

To assess the effect of vegetation structure on population processes for small mammals, we characterized trapping-grid vegetation in two ways. Our approach to estimating mammal density and home-range size required information about habitat outside of the trapping area to quantify the spatial distribution of individual animals (Effords 2016).

Therefore, we examined the effects of shrub and grass cover on the distribution of small mammals using spatial layers from the National Land Cover Database 2016 (NLCD). First, we created a buffer around each trapping grid to ensure that the effective sampling area was large enough to include habitat for captured animals whose home ranges only partially overlap the trapping grid. The size of the effective sampling area (i.e., how far the sampled area extends beyond the trapping grid) is calculated using empirical animal movement data from capture events, and habitat measurements are required for the entire sampling area (Effords 2016). We tested effects of the following fine-scale habitat features on habitat use using NLCD spatial layers: percent non-native and native grass cover, big sagebrush cover and height, litter cover, the fraction of the habitat classified as shrubs, the fraction of the habitat classified as sagebrush, % cover of bare ground, and non-sagebrush shrub height. Additionally, for each trap in our trapping grids (2017 *n* =740, 2018-2019 *n* = 896) we estimated juniper cover at four spatial scales using our 1-m resolution juniper classification. We estimated mean juniper cover within 10, 20, 50, and 100 m^2 of each trap location using a moving windows analysis in R (Hijman and Van Etten 2012). Therefore, each trap received a unique juniper cover estimate at four different scales. We chose these scales based on estimates of distances that animals moved between capture events obtained from a null model.

Survival

To address effects of habitat structure on survival of small mammals, we first characterized grass, shrub, and tree cover at each trapping grid by directly estimating vegetation features in the field within a one-meter radius of each trap (hereafter 'trap-level vegetation'; 2017 *n* = 148 traps per grid, 2018 *n* = 64 traps per grid, 2019 *n* = 64 traps per grid). We recorded the species and height of each shrub whose canopy at least partially covered the trap sampling area and categorized native and non-native grass into five cover categories using ocular estimates (0, 10-20, 30-50, 60-90, 90-100%). Finally, we classified each trap location as having a rocky component if rocks covered > ~25% of the 1-m radius. We then summarized the following habitat characteristics for each trapping grid using all trap locations in a grid: mean shrub density and height, percentage of trap locations in each grid that were classified as having annual grass cover > 10%, percentage of trap locations in each grid that were classified as native grass cover > 30%, and the percentage of trap locations in each grid classified as rocky. We chose these values based on the distribution of cover estimates within trapping sites.

To assess the effect of juniper on the survival of small mammals, we evaluated the relationship between survival and several measures of juniper. First, we estimated percent juniper cover at four scales using our 1-m resolution juniper classification: 50 m, 100 m, 150 m, and 200 m. These scales represent a radius from the center of each trapping grid. We also counted individual juniper stems within a 50 m radius of the center of each trapping grid and recorded the height (m) of each tree using a laser inclinometer (Nikon Forestry Pro II).

Small mammal density analysis

To examine the relationship between habitat features and the density of small mammals, we conducted a spatially explicit capture-recapture analysis (SECR; Borchers and Efford 2008, Romairone et al. 2018). This SECR analysis uses the capture histories of marked individuals and the movement of animals between capture events to account for individual heterogeneity in capture probability. Spatially explicit capture-recapture models estimate density as the response variable to habitat predictor variables. These models also account for factors that may affect detection using a capture-probability parameter. We tested the effect of habitat features on small mammal density using a set of candidate models with different combinations of habitat-related predictor variables. We included year as a fixed effect in each model that we tested to account for yearly variation in small mammal populations. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) to select the model that most parsimoniously fit the data (Burnham and Anderson 1998).

Model selection proceeded in three stages: first, we compared a model set including predictors unrelated to habitat that may affect capture probability ($g0$). We tested for an effect of learned behavior on capture probability, because for some individuals capture probability may change following the first capture event (Pollock 1982). Small mammal activity may vary seasonally, so we tested for an effect of time within each year (O'Farrell et al. 1975). We also tested a null model. In the second stage of modeling, we compared a model set including linear and non-linear juniper cover estimates at four spatial scales (10 m, 20 m, 50 m, and 100 m). We retained the top detection covariate for these juniper models and carried the juniper model that best fit the data forward into the final stage of modeling.

In the final stage of modeling, we retained the top detection and juniper covariates from the first and second stages and tested univariate and multivariate models containing habitat structure variables obtained from the NLCD landcover dataset and a juniper cover classification. We tested both linear and quadratic forms of NLCD predictor variables for a total of 18 candidate models (Table 1). We did not test models with more than one NLCD covariate because NLCD covariates were highly spatially correlated, and models did not converge due to small sample size. Therefore, the only multivariate models we tested included one NLCD covariate and one juniper cover covariate. To ensure convergence of models and avoid issues of scale between predictor covariates, we transformed predictor variables to a mean of zero and a standard deviation of one (Zuur et al. 2007). We conducted density analyses in program R (R Core Team 2020) using package SECR (Efford 2016).

Small mammal survival analysis

To examine effects of habitat features on small mammal survival, we used a Cormack-Jolly-Seber (CJS) model design (Lebreton et al. 1992, Kendall et al. 1995). A CJS survival model design assumes that the population is open to death and emigration during the sampling period and uses individual encounter histories to estimate apparent survival (φ) and capture probability (p). Apparent survival is a joint estimate of true survival and emigration because the two parameters cannot be estimated separately with the data we collected (White and Burnham 1999). Factors such as year, time of season, and learned behavior can affect estimates of capture probability for small mammals; thus, we first compared a detection model set including time and behavior-related covariates for p (Table A2). We included the covariate from the top detection model in all subsequent models testing the effects of habitat features on survival. We tested habitat features that we *a priori* suspected may influence predation risk. To limit the size of our set of candidate models, we first compared a set of univariate models that included linear and quadratic effects of juniper cover and stem density. We carried the form of the juniper variable with the most support forward into the candidate model set that included other habitat variables. We included big sagebrush (*A. tridentata*) density and shrub density for all species combined (*A. tridentata, A. arbuscula,* and *Purshia tridentata*) in our candidate model set. We also included covariates for the percent of each grid where cheatgrass was present and the percent of each grid with native grass cover greater than 30%. Of our 14 grids, two grids (15%) had low native grass cover (<35% of the grid classified as >30% native grass cover), six (42.5%) had medium native grass cover (40-60% of the grid classified as >30% native grass cover), and six (42.5%) had high native grass cover (70-90% of the grid classified as >30% native grass cover). Finally, we included covariates for the percent of each grid classified as rocky because rocky crevices can provide protection from predation (Table 2).

To address our objective of examining the effect of inter- and intra-specific density on survival, we tested for effects of species interactions between deer mice (*Peromyscus maniculatus,* a generalist omnivore) and pocket mice (*Perognathus parvus,* a specialist herbivore) on survival of each species using a predicted density surface generated from our top habitat density model. We used estimates from the top density model for deer mice to predict the average density of deer mice at each trapping grid. After calculating predicted density for each grid, we compared our top survival habitat model to a model that included only predicted deer mouse density as well as a model that included both the best supported habitat covariates and predicted deer mouse density. All covariates were scaled and centered, and we conducted survival analyses using package RMark (Laake 2013).

Home-range size analysis

Detection probability is estimated in SECR models using two parameters; *g*0 is the capture probability when distance to traps equals zero, and sigma is the range parameter. Range is derived from empirical animal movements between capture events and is an estimate of the average capture probability as a function of increasing distance from an animal’s activity center. Thus, range is analogous to mean home-range size (Efford et al. 2016). We tested for effects of species interactions and habitat on range using the predicted intra- and inter-specific densities of pocket mice and deer mice for each trapping grid and habitat features that may influence movement, including food resources and cover.

To examine the relationship between range and habitat characteristics, including species interactions, we tested the relative effects of habitat structure and inter- and intra-species density on range using SECR models to assess variation in home range across our trapping grids (Bogdziewicz et al. 2016, Casula et al. 2019). We allowed the range parameter to vary as a function of habitat features that we *a priori* hypothesized may influence movement of small mammals. To aid in model convergence we constrained *g*0 to the intercept so that capture probability represents the mean of the population across all trapping sites for each species. We included annual and native grass covers as covariates as well as shrub cover. We also evaluated the effect of juniper cover on range size because juniper may lead to reduced movement through increases in perceived or actual predation risk if avian predators use juniper as hunting perches (Andersson et al. 2009). Finally, we included the percent cover of rocky areas because rocky areas may provide escape cover for small mammal while increasing distances that animals need to move to access food (Reichman and Price 1993, Melaschenko et al. 2020). We used trap-level vegetation measurements (*n* = 896) to obtain mean values for each trapping grid to construct a set of models that tested for the following effects on home range: 1.) structural effects only, 2.) structural and interspecific density effects, 3.) structural and intraspecific density effects, and 4.) structural, inter, and intraspecific density effects. We used mean estimated densities from our top density models for each species. We scaled and centered all covariates.

Results

We captured 583 individuals of eight small mammal species from May-August 2017-2019. Most captures were deer mice (66% of captures, *n* = 387 individuals) and Great Basin pocket mice (26% of captures, *n* = 158 individuals). Other species captured included least chipmunk (*Tamias minimus*; 3%), western harvest mouse (*Reithrodontomys megalotis*; 2%), sagebrush vole (*Lemmiscus curtatus*; 1%), long-tailed vole (*Microtus longicaudus*; 0.6%), pocket gopher (*Thomomys spp.*; 0.3%), and Ord’s kangaroo rat (*Dipodomys ordii*; 0.2%). Deer mice and Great Basin pocket mice were the only species with adequate captures for analyses.

Effect of habitat gradients on density

The density of deer mice increased to a maximum at 10% juniper cover and decreased as juniper increased beyond 10% cover (main effect β = 0.43, 95% CI 0.26, 0.60; Table 3.1, Figure 3.4). Estimated density of deer mice was highest in 2017 (3.49 individuals/ha, 95% CI

2.41, 5.31) and lowest in 2019 (1.71 individuals/ha, 95% CI 1.20, 2.41). For deer mice, we observed an effect of learned behavior on capture probability (β = 2.32, 95% CI 1.97, 2.67).

The quantity of sagebrush cover positively influenced the density of pocket mice, which increased between 10-20% sagebrush cover (main effect β = 3.84, 95% CI 1.24, 6.44; Table 3.1, Figure 3.4). Beyond 20% fractional cover of sagebrush, wide confidence intervals for density of pocket mice make prediction unreliable. Estimated density for pocket mice was lowest in 2017 (2.13/ha, 95% CI 0.97, 4.67) and highest in 2019 (5.61/ha 95% CI 2.52, 12.44). We observed an effect of learned behavior, which positively affected capture probability (β = 2.14, 95% CI 1.17, 3.11). Capture probabilities for pocket mice (*g*0 intercept = 0.0056, 95% CI 0.0021, 0.014) were lower than for deer mice (*g*0 intercept = 0.020, 95% CI 0.017, 0.024).

Effects of habitat gradients on survival

Survival of deer mice declined as the stem density of juniper increased (β = - 0.18, 95% CI = -0.35, -0.098; Table 3.1, Figure 3.5). For deer mice, we observed an effect of learned behavior on detection probability (β = 0.57, 95% CI 0.09, 1.05).

Survival of pocket mice declined as density of big sagebrush increased (β = - 0.30, 95% CI = - 0.57, - 0.03) and increased as height of sagebrush increased (β = 0.49, 95% CI = 0.21, 0.77). There was one competitive model for pocket mice that included a quadratic effect of juniper stem density (main effect β = 1.34, 95% CI = 0.46, 2.23; Table 3.1, Figure 3.5). We identified no variables that affected detection probability for pocket mice. There was no effect of deer mouse density on pocket mouse survival.

Effects of habitat gradients and density-dependent interactions on movement

For deer mice, density of big sagebrush (β = -0.09, 95% CI -0.16, -0.03), cheatgrass cover (β = -0.20, 95 CI -0.27, -0.14), and conspecific density (β = -0.14, 95% CI -0.20, -0.07; Table 3.1, Figure 3.6) reduced home-range size. There was no effect of pocket mice density on the home-range size of deer mice. Increased density of deer mice reduced the home-range size of pocket mice (β = -0.32, 95% CI -0.42, -0.21), whereas rock cover (β = 0.17, 95% CI 0.08, 0.27) and conspecific density (β = 0.35, 95% CI 0.25, 0.44; Table 3.1, Figure 3.6) increased home-range size for pocket mice. On average, pocket mice moved shorter (41%)

distances between captures than deer mice (pocket mice: range intercept = 24.0 m, 95% CI 21.79, 26.41; deer mice range intercept: = 34.1 m, 95% CI 31.52, 36.80).

Discussion

We found that western juniper and big sagebrush cover were more important influences on multiple aspects of small mammal ecology in sagebrush-juniper habitat than grass cover. The inverse relationship between density and survival of deer mice in response to juniper cover suggests the possibility of an ecological trap at certain points along the expansion gradient. Inter-specific, density-dependent effects of a common generalist may contribute to habitat degradation for a more specialist herbivore as evidenced by our finding of reductions in range size for the specialist pocket mouse as density of the generalist deer mouse increased. Our findings highlight the potentially complex interactions that may arise for small mammals as habitat structure changes along a gradient.

Effects of habitat gradients on density

Contrary to our prediction, grass cover and composition did not influence densities of either species we examined. The non-linear relationship we observed for density of deer mice in relation to juniper cover could be influenced by changes in vegetation structure around juniper trees. In phase-1 juniper, lower grass cover around juniper trees may facilitate movement, while shrub structure remains intact enough to provide protected foraging sites. It may also be that in phase 1, juniper is small enough to provide protection from predation (under trees) because cover is higher closer to the ground compared to areas with taller trees. Juniper berries are used as food by deer mice, so smaller trees that feature berries closer to the influence habitat use by deer mice. For example, caches of juniper berries made by small mammals are more common under juniper canopies than in open areas (Dimiti and Longland 2017). In areas where juniper cover was greater than 10%, reductions in deer mouse densities may be tied to reductions in shrub structure and food resources associated with increases in juniper cover. Though we did not examine the importance of specific food resources for distributions of small mammals, our study found that structural resources, including juniper, influence species distributions.

The density of pocket mice at our site was associated with sagebrush cover but not juniper cover. Pocket mice are reliant on shrub cover because they forage and consume seeds underneath sagebrush shrubs, moving quickly through open areas between shrubs (Reichman and Price 1993). Pocket mice at our site do not use habitat with less than 10% sagebrush cover, and densities of pocket mice are highest at 20% sagebrush fractional cover, suggesting that reductions in the shrub layer associated with juniper expansion have been detrimental to pocket mice.

Habitat structure facilitating increased densities of a generalist species can lead to indirect effects on other species in the community. Higher densities of deer mice in phase-1 juniper may have implications for sagebrush species that tolerate juniper at low densities. Brewer’s sparrows (*Spizella breweri*) is one such species, considered to be sagebrush obligates but occurring in areas with up to 20% juniper cover (A.C. Young 2021). In Wyoming, deer mice were the most common predator of Brewer’s sparrow nests (Hethcoat and Chalfoun 2011). Increased densities of a common nest predator may have implications for sagebrush songbirds, which have undergone declines (Knick et al. 2017). Increased density of small mammals can also influence habitat use by generalist predators such as the common raven (*Corvus corax*), which may indirectly affect other prey species (Ims et al. 2013). Small mammals can make up a large proportion of raven diets (Stiehl and Trautman 1991), and ravens are also nest predators of the greater sage-grouse (Coates et al. 2014). Incidental predation may occur if generalist predators increase habitat use in response to the abundance of one prey type and incidentally observe another (Schmidt et al. 2001, Latham et al. 2011). Increased abundances of predators associated with juniper cover would therefore have implications for a wide range of sagebrush wildlife.

Effects of habitat gradients on survival

Our findings supported our prediction that juniper cover would influence survival. However, juniper negatively influenced survival for one species and positively influenced survival for the other. The use of sagebrush habitat that includes a low density of juniper trees may have fitness consequences for deer mice because apparent survival of deer mice is negatively associated with juniper-stem density. This pattern could be influenced by the relationship between juniper expansion into sagebrush habitat and changes in the predator community, which are not well understood. Juniper may provide structural or food resources to predators such as raptors, ravens, and coyotes, thereby increasing the likelihood of habitat use by these predators (Severson et al. 2017, Stricklan 2019, Kendall 2020, Young 2022).

Contrary to our prediction, juniper cover had a positive effect on survival of pocket mice. Higher survival of pocket mice in phase 1 juniper cover may be attributed to several factors. First, increased densities of deer mice and a low density of pocket mice in phase-1 juniper make it more likely that predators encounter deer mice in this habitat, thereby resulting in a higher likelihood of depredating deer mice (Nordberg and Schwarzkopf 2019), a type III functional response. Further, pocket mice may be better able to evade predation by avian predators than deer mice because of differences in predator avoidance behaviors. Pocket mice experimentally exposed to owl predation were three times as likely to avoid capture as deer mice due to erratic jumping compared to the quadruped escape tactics of deer mice (Longland and Price 1991, Deggan 1997). It may be that pocket mice foraging in areas with tall shrubs and juniper are better able to evade predators than deer mice, and as a result avian predators are more likely to prey on deer mice. An association between sagebrush height and survival of pocket mice suggests that tall sagebrush lowers the risk of predation by obscuring more of the ground from aerial predators (Smallwood 1987). However, avian predators are not the only predator of small mammals. Lower survival of pocket mice in areas of dense sagebrush suggest that other predators, such as snakes or mammals, which hunt using olfactory cues, use the cover of sagebrush to hunt and that pocket mice are susceptible to predation in these areas. For example, pocket mice made up a larger proportion of coyote diets in open sagebrush habitat than juniper-sage habitat in Oregon (Kendall 2020).

Effects of habitat gradients on home-range size

Cheatgrass reduced home-range size for one of the species we examined, but contrary to our prediction, juniper did not influence home-range size for either species. Home ranges of deer mice were smaller as cheatgrass cover increased. Cheatgrass is thought to affect perceived predation risk for deer mice because they are more detectable to predators and are less able to evade capture (Bachen 2014, Cerandi and Chalfoun 2017). Structural changes to habitat resulting from invasive and expanding plants can affect home-range size because of altered predation risk or ability of an animal to physically move (Cerandi and Chalfoun

2017). Reductions in home-range size may therefore be expected if cheatgrass increases predation risk or physically inhibits movements. However, the distribution and abundance of food resources likely also play a part in home-range size (Schoepf et al. 2015).

Cheatgrass may influence small mammals via trophic effects because seeds can also be an important part of small mammal diets (Richardson et al. 2013). If cheatgrass seeds are an abundant food source, home-range size would likely decrease because the animal can travel shorter distances to get food (Schoepf et al. 2015). However, unlike pocket mice, deer mouse diets are not known to include cheatgrass seeds (Evert et al. 1978). Therefore, a smaller home-range size associated with cheatgrass was likely not a function of enhanced food availability. Instead, a large proportion of the deer mouse diet throughout the summer consists of invertebrates (Tabacaru et al. 2010). Little is known about the effects of cheatgrass invasion on the invertebrate community (Smith et al. 2019). Invertebrate species diversity may be lower in habitat with cheatgrass, although the implications for small mammal diets is unknown (Fielding and Brusyen 1993, Ostoja et al. 2009). Finally, increases in density of big sagebrush are associated with smaller home ranges for deer mice at our site, possibly because of increases in food resources. Taken together with our results, this suggests that deer mice may restrict their movements in areas invaded by cheatgrass to limit predation risk.

Density-dependent effects on movement and density

Density-dependent interactions can play a strong role in structuring ecological communities (Chock 2018) and complementary density estimates between species in each year at our site suggest a density-dependent relationship between pocket mice and deer mice. Further, in habitat with higher densities of deer mice, pocket mice moved on average shorter distances between captures, a pattern that further suggests density-dependent interactions between these two species. Interactions between territorial species can limit home-range size, and pocket mice are intolerant of heterospecifics as well as conspecifics (Kritzman 1974). The movement patterns we observed suggest that pocket mice may be excluded from entering conspecific territories and limit home-range size to avoid interspecific interactions. Larger home-range sizes in rocky areas, which feature less vegetation cover, would increase the distance that pocket mice need to travel to obtain food and find protection from predation.

In the early spring, pocket mouse diets may include invertebrates, and at this time pocket mouse diets can overlap with deer mouse diets (Kritzman 1974). Diet overlap during the early spring could lead to competition in habitat with high densities of deer mice if invertebrate availability is limited, though we did not test for competitive exclusion.

Conclusion

Our study sheds light on how gradients of both invasive and expanding plants can affect habitat use and demography for two species of small mammal. The expansion of juniper at low densities (10% cover) is likely to benefit, or be tolerated by, generalist species such as deer mice, and the resulting changes in habitat availability and species interactions are likely to have a negative effect on populations of specialists and overall species diversity. Dominance of the small mammal community at our site by a common generalist species may be a result of earlier changes to habitat structure because cheatgrass and juniper have expanded in the area over the last 50 years (Davies et al. 2011), and species diversity and abundance of small mammals have declined in the Great Basin over that same period (Phillips 2018). Our study suggests that juniper removal, a common management strategy throughout the Great Basin, may have implications for the most common small mammals at our site. Increases in shrub structure within six years following juniper removal may lead to increased densities of herbivores such as pocket mice (Willams et al. 2017). Conversely, removal of juniper may decrease densities of a predatory omnivore. Given the important functional role of small mammals, any changes occurring to the community composition of small mammals facilitated by juniper removal may have implications for the entire food web.

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Table 3.1. Top models predicting deer mice (*Peromyscus maniculatus*, n = 387 individuals) and Great Basin pocket mice (*Perognathus parvus*, n = 158 individuals) density, survival, and home-range size in southwestern Idaho from 2017-2019. We ranked models using Akaike's Information Criterion adjusted for small sample size. Only models with a ΔAICc less than two are shown.

Species	Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
	Density				
Deer Mouse	[5]Juniper 100 m*Juniper 100 m	8	10447.54	0.00	1
Pocket Mouse	[6]Sagebrush FC*Sagebrush FC	8	4269.40	0.00	0.94
	Survival				
Deer Mouse	[7]Juniper Den	6	1594.46	0.00	0.19
	Juniper Den + [8]AT Den	7	1595.20	0.74	0.13
	Juniper Den + [9]Cheatgrass	7	1596.19	1.73	0.08
Pocket Mouse	AT Den + [10]AT Height	6	691.36	0.00	0.29
	AT Den*AT Height	7	693.09	1.73	0.12
	Juniper Den*Juniper Den	6	693.16	1.80	0.12
	Home Range				
Deer Mouse	AT Den + Cheatgrass + [11]Intra	5	10866.17	0	0.67
Pocket Mouse	[12]Rock + Intra + [13]Inter	5	4274.21	0.00	0.65

[1] Number of model parameters, [2] Akaike's Information Criterion score for small sample sizes, [3] Difference in Akaike's Information Criterion score from the top model.
[4] Akaike's model weights, [5] Continuous cover of *Juniperus occidentalis* within 100 m of traps, [6] Fractional cover of *Artemisia tridentata*
[7] Stem density (count) of *Juniperus occidentalis* within 50 m of trapping grid center
[8] Mean density of *Artemisia tridentata,* [9] Percent cover of *Bromus tectorum*,
[10] Mean height of *Artemisia tridentata,* [11] Intraspecific density,
[12] Proportion of trapping grid classified as rocky, [13] Interspecific density

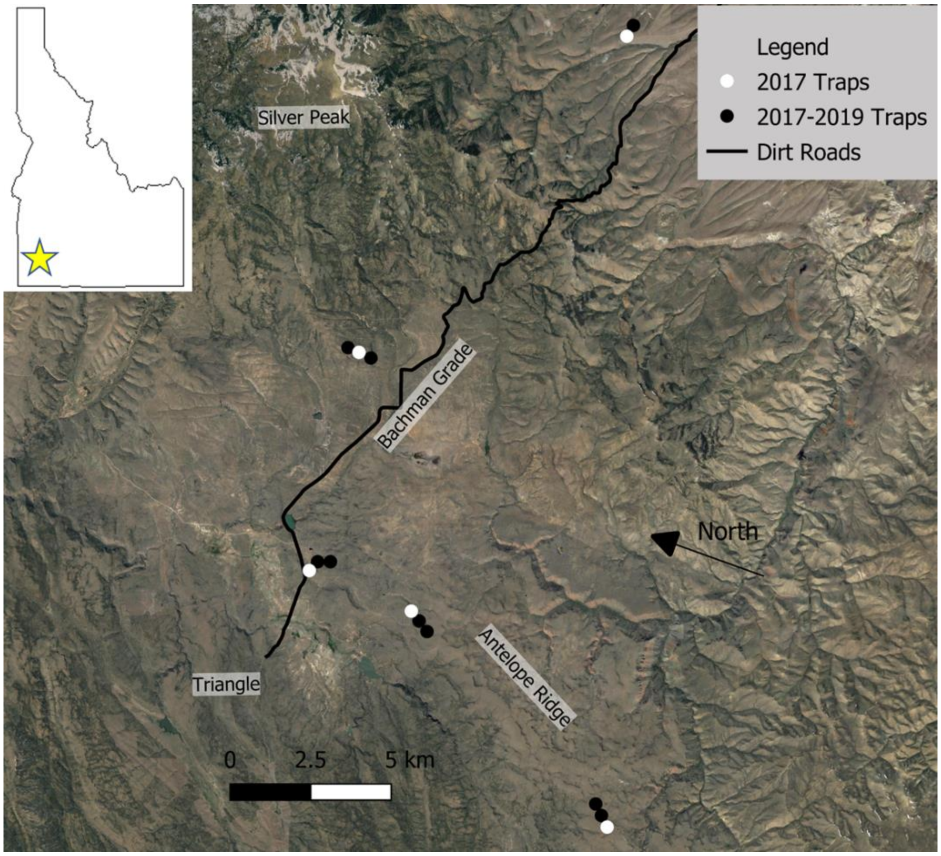

Figure 3.1. Small mammal trapping grids in the Owyhee Mountains of southwestern Idaho. Small mammal density, survival, and home-range size was estimated from 2017-2019 at 14 trapping sites located along gradients of western juniper (*Juniperus occidentalis*) expansion and cheatgrass (*Bromus tectorum*) invasion.

Figure 3.2. East and west view of a representative area with ~ 7% conifer cover in the Owyhee Mountains of southwestern Idaho, 2019. We estimated western juniper (*Juniperus occidentalis*) cover using a supervised classification, ground truthing, and visual inspection in ArcGIS (ESRI 2020). These photos were taken at the center of a 100-m radius plot.

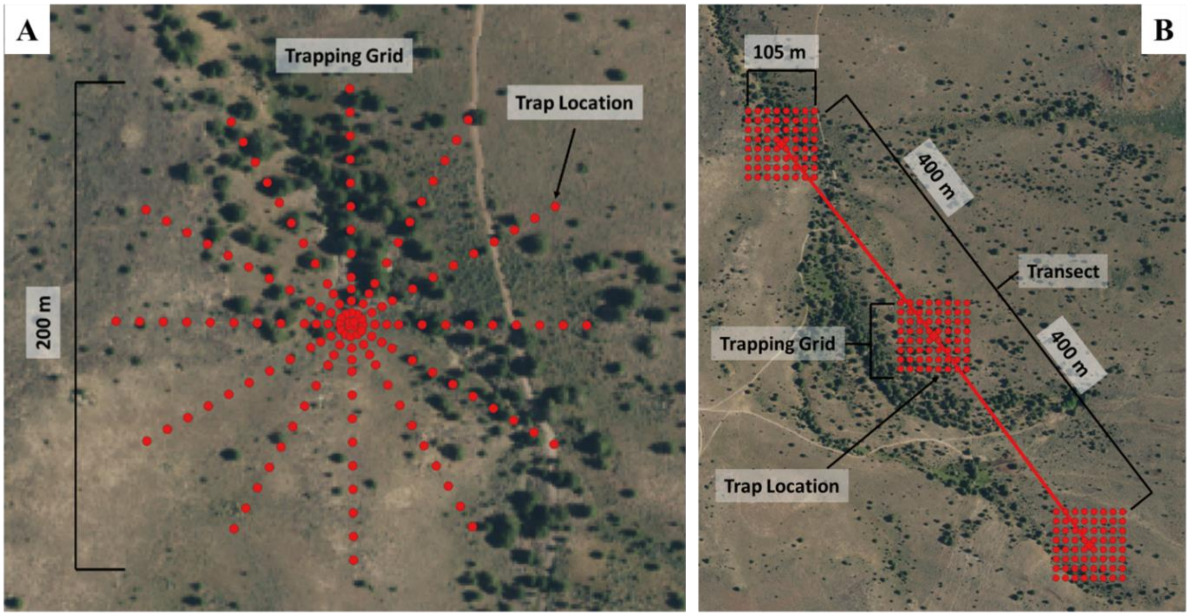

Figure 3.3. Trapping design for estimation of small mammal density, survival, and movement in the Owyhee Mountains of southwestern Idaho, May – August in A.) 2017, and B.) 2018 - 2019. We survey locations placed randomly for a separate study of songbird and avian predators. Five locations were selected that featured a range of juniper (*Juniperus occidentalis*) cover, sagebrush (*Artemisia spp*.) structure, and grass composition.

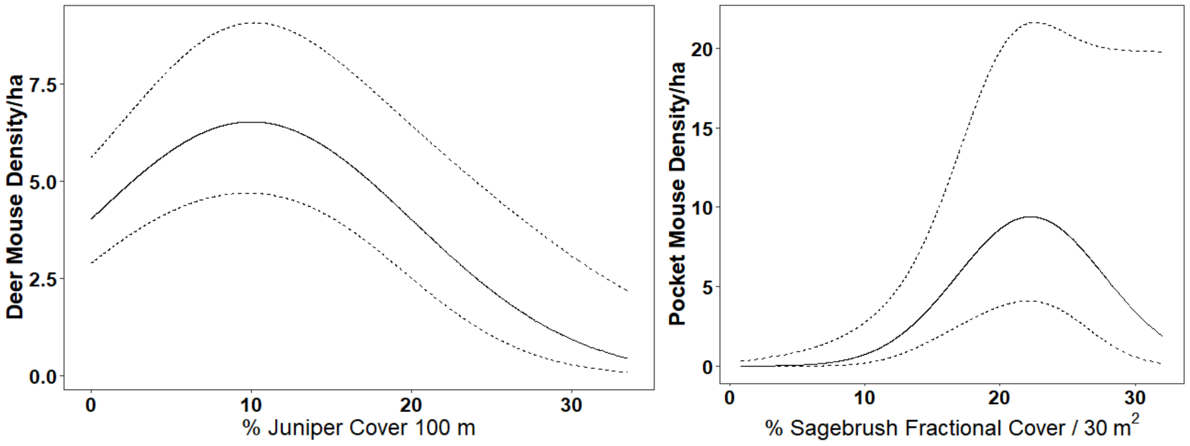

Figure 3.4. Predicted density of deer mouse (*Peromyscus maniculatus*) and Great Basin pocket mouse (*Perognathus parvus*) in southwestern Idaho in 2019. Deer mouse (n = 387 individuals) density is shown as a function of western juniper (Juniperus occidentalis) cover within 100 m. Pocket mouse (n = 158 individuals) density is shown as a function of percent sagebrush (*Artemisia spp*.) fractional cover within 30 m2. Dashed lines represent 95% confidence intervals.

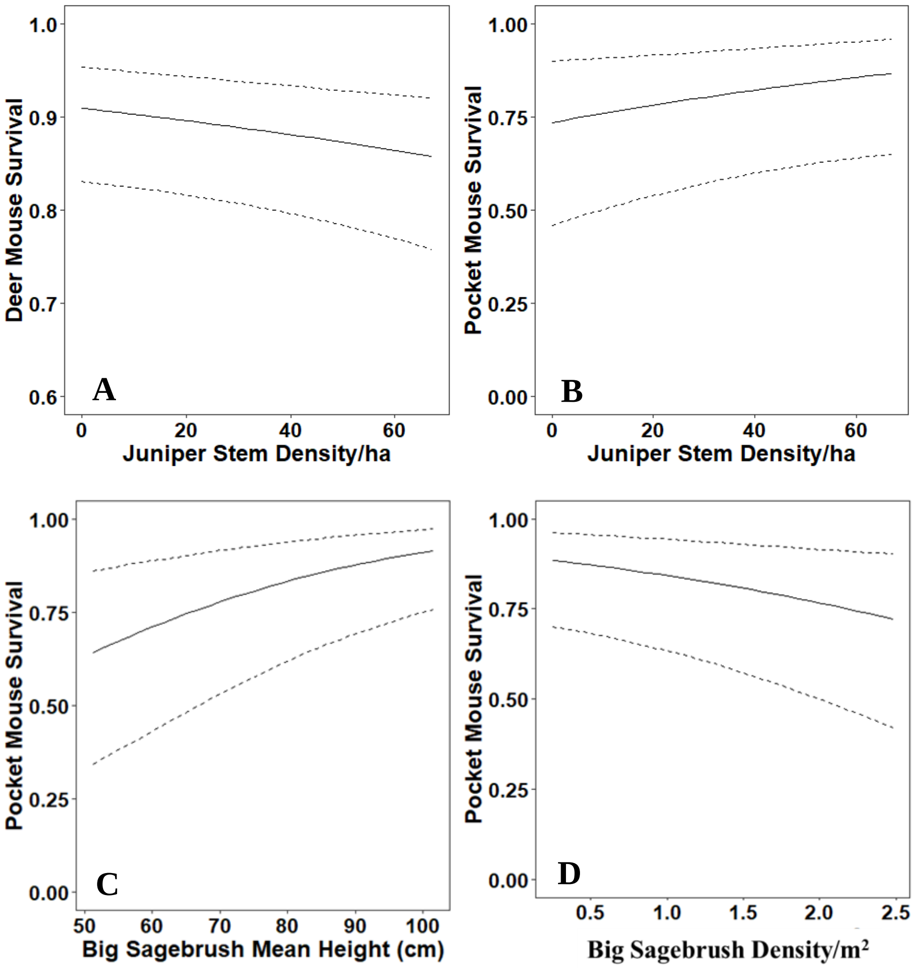

Figure 3.5. Predicted survival of small mammals in southwestern Idaho from 2017-2019. We estimated deer mouse (*Peromyscus maniculatus, n* = 387 individuals) and pocket mouse (*Perognathus parvus, n* = 158 individuals) survival using a Cormack-Jolly-Seber analysis. Dashed lines represent 95% confidence intervals. Deer mouse (A) and pocket mouse (B) survival rate was predicted by juniper (*Juniperus occidentalis*) stem density within 50 m of the center of a trapping grid. Pocket mouse survival rate (C.) was predicted by mean big sagebrush (*Artemisia tridentata*) height within each trapping grid. Pocket mouse survival rate (D.) was also predicted by mean big sagebrush (*Artemisia tridentata*) density in a trapping grid.

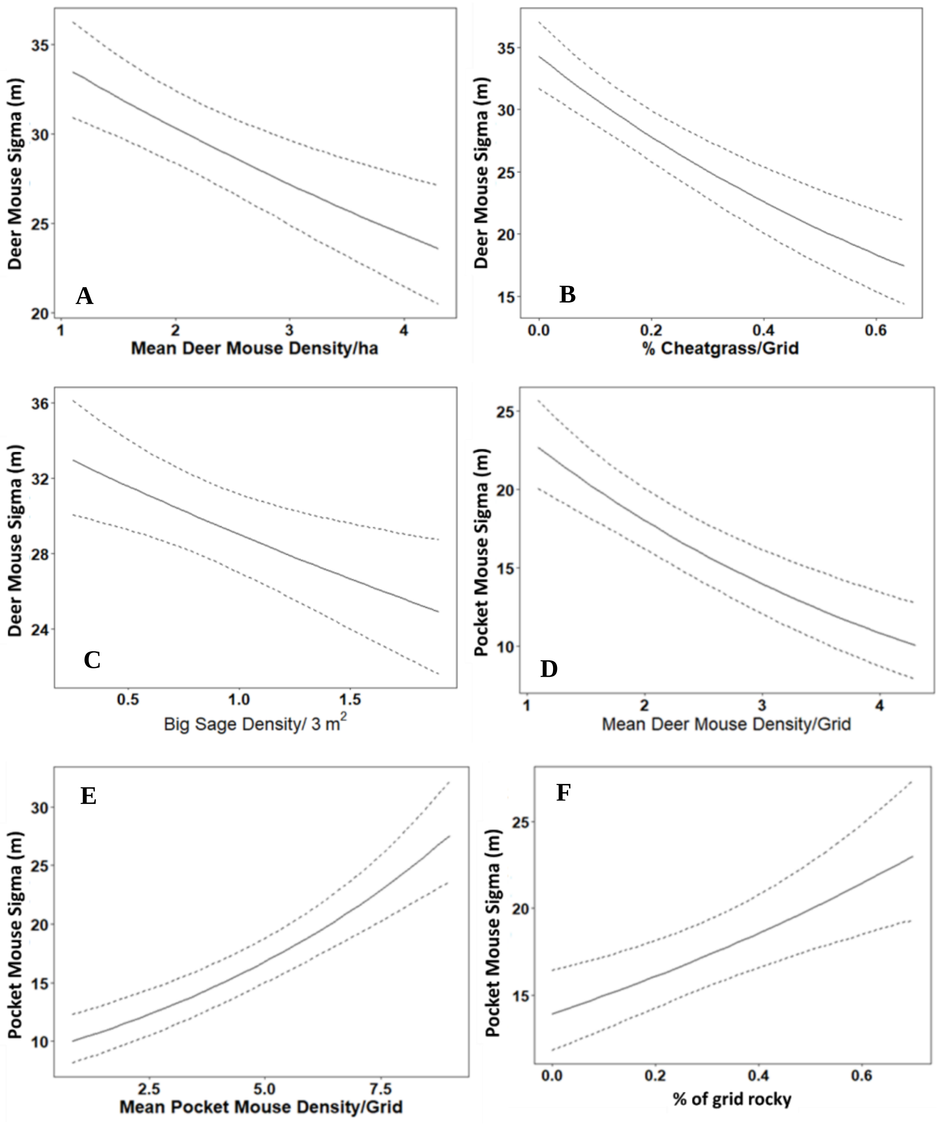

Figure 3.6. Predicted home-range sizes of small mammals in southwestern Idaho from 2017-2019. We analyzed deer mouse (*Peromyscus maniculatus*, *n* = 387) and pocket mouse (*Perognathus parvus*, *n* = 158) movements using spatial capture-recapture models. Dashed lines represent 95% confidence intervals and solid lines represent covariate relationships. Sigma (σ) is the range parameter derived from empirical animal movements between capture events and is an estimate of the average capture probability for all animals as a function of increasing distance from an animal's activity center. We allowed range to vary as a function of A. and E.) Mean intraspecific density for each trapping grid B.) The percent of each grid with cheatgrass >= 10% cover C.) Mean big sagebrush density for each trapping grid D.) Mean interspecific density for each trapping grid and F.) The percent of each grid classified as rocky

Appendix B

Table B1. Final rankings for deer mouse (*Peromyscus maniculatus)* detection models in southwestern Idaho from 2017-2019. We conducted spatial capture-recapture analyses for deer mice (n=357) captured between May and August at a total of 14 trapping grids.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
[5]Learned Behavior	6	10475.33	0.00	1.00
[6]Time	6	10695.85	220.52	0.00
Null	5	10932.03	456.70	0.00

[1] number of model parameters
[2] Akaike's Information Criterion score for small sample sizes
[3] Difference in Akaike's Information Criterion score from the top model.
[4] Akaike's model weights
[5] A change in capture probability following the initial capture event
[6] Study date

Table B2. Final rankings for Great Basin pocket mouse (*Perognathus parvus*) detection during density modeling in southwestern Idaho from 2017-2019. We conducted spatial capture-recapture analyses for pocket mice (n=158) captured between May and August at a total of 14 trapping grids.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
[5]Learned Behavior	6	4306.47	0.00	1.00
[6]Time	6	4384.63	78.17	0.00
Null	5	4389.58	83.11	0.00

[1] number of model parameters

[2] Akaike's Information Criterion score for small sample sizes

[3] Difference in Akaike's Information Criterion score from the top model.

[4] Akaike's model weights

[5] A change in capture probability following the initial capture event

[6] Study date

Table B3. Final rankings for deer mouse (*Peromyscus maniculatus*) detection during survival modeling in southwestern Idaho from 2017-2019. We conducted Cormack-Jolly-Seber survival analyses for deer mice (n=387) captured between May and August at a total of 14 trapping grids.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
[5]Learned Behavior	5	1596.73	0.00	0.49
[6]Year + Learned Behavior	7	1598.01	1.28	0.26
Null	4	1599.95	3.21	0.10
Year	6	1600.95	4.22	0.06
Moon	5	1600.95	4.22	0.06
Year + Moon	7	1602.01	5.28	0.03

[1] number of model parameters
[2] Akaike's Information Criterion score for small sample sizes
[3] Difference in Akaike's Information Criterion score from the top model.
[4] Akaike's model weights
[5] A change in capture probability following the initial capture event
[6] Study year

Table B4. Final rankings for Great Basin pocket mice (*Perognathus parvus*) detection models in southwestern Idaho from 2017-2019. We conducted Cormack-Jolly-Seber survival analyses for pocket mice (n =158) captured between May and August at a total of 14 trapping grids.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
Null	4	701.72	0.00	0.24
[5]Year	6	701.81	0.08	0.23
[6]Learned Behavior	5	702.14	0.42	0.20
Year + Learned Behavior	7	702.62	0.90	0.16
Moon Phase	5	703.78	2.06	0.09
Year + Moon Phase	7	703.89	2.17	0.08

[1] number of model parameters,
[2]Akaike's Information Criterion score for small sample sizes
[3] Difference in Akaike's Information Criterion score from the top model, [4] Akaike's model weights, [5] Study year
[6] A change in capture probability following the initial capture event

Table B5. Final rankings for models predicting deer mice (*Peromyscus maniculatus*) density in southwestern Idaho from 2017-2019. We conducted spatial capture-recapture analyses for deer mice (= 387) captured between May and August at 14 trapping grids. We classified juniper cover at the 1 m scale and then aggregated cells to the 10 m scale. We obtained all other habitat variables from the 30 m scale National Landcover Database. We ranked models using Akaike's Information Criterion adjusted for small sample size.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
Juniper 100 m*Juniper 100 m	8	10447.54	0.00	1
Juniper 50 m*Juniper 50 m	8	10462.34	14.80	0
[5]Annual Grass PC	7	10467.67	20.13	0
Annual Grass PC*Annual Grass PC	8	10467.82	20.28	0
[6]AT Height	7	10473.76	26.23	0
[7]AT PC	7	10474.00	26.47	0
AT Height*AT Height	8	10474.74	27.21	0
Juniper 20 m*Juniper 20 m	8	10475.17	27.64	0
[8]Shrub FC	7	10475.44	27.90	0
Juniper 10 m*Juniper 10 m	8	10475.71	28.18	0
Shrub FC*Shrub FC	8	10475.80	28.26	0
AT PC*AT PC	8	10476.04	28.51	0
[9]Shrub Height	7	10476.63	29.09	0
Juniper 50 m	7	10476.84	29.31	0
Juniper 100 m	7	10477.05	29.52	0
Juniper 10 m	7	10477.14	29.60	0
Juniper 20 m	7	10477.15	29.61	0
[10]Sagebrush FC	7	10477.15	29.62	0
[11]Herbaceous FC	7	10477.28	29.75	0

[12]Litter PC	7	10477.34	29.80	0
Sagebrush FC*Sagebrush FC	8	10477.70	30.16	0
Shrub Height*Shrub Height	8	10478.71	31.17	0
Litter PC*Litter PC	8	10479.28	31.74	0
Herbaceous FC*Herbaceous FC	8	10488.85	41.31	0
Null	6	10749.00	301.47	0

[1] Number of model parameters
[2] Akaike's Information Criterion score for small sample sizes
[3] Difference in Akaike's Information Criterion score from the top model.
[4] Akaike's model weights
[5] Percent cover of annal grass
[6] Mean height of *Artemisia tridentata*
[7] Percent cover of *Artemisia tridentata*
[8] Fraction of habitat classified as shrub cover
[9] Mean height of all shrub species
[10] Fraction of habitat classified as sagebrush
[11] Fraction of habitat classified as herbaceous cover
[12] Percent litter cover

Table B6. Final rankings for models predicting Great Basin pocket mice (*Perognathus parvus*) density in southwestern Idaho from 2017-2019. We conducted spatial capture-recapture analyses for pocket mice (n =158) captured between May and August at a total of 14 trapping grids. We classified juniper cover at the 1 m scale and then aggregated cells to the 10 m scale. We obtained all other habitat variables from the 30 m scale National Landcover Database. We ranked models using Akaike's Information Criterion adjusted for small sample size.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
[5]Sagebrush FC*Sagebrush FC	8	4269.40	0.00	0.94
Sagebrush FC	7	4275.05	5.65	0.06
[6]Litter*Litter	8	4283.06	13.66	0.00
Shrub FC*Shrub FC	8	4284.27	14.86	0.00
[7]AT Height*AT Height	8	4287.63	18.23	0.00
[8]Annual Grass PC	7	4295.13	25.73	0.00
Annual Grass PC*Annual Grass PC	8	4295.70	26.30	0.00
[9]AT PC	7	4300.07	30.67	0.00
[10]Herbaceous FC	7	4300.08	30.68	0.00
Herbaceous FC*Herbaceous FC	8	4300.36	30.96	0.00
AT PC*AT PC	8	4301.91	32.50	0.00
[11]Shrub Height	7	4302.62	33.22	0.00
[12]Shrub FC	7	4303.62	34.21	0.00
Null	6	4306.47	37.06	0.00
Juniper 50 m	7	4307.99	38.59	0.00
Juniper 20 m	7	4308.05	38.65	0.00
Juniper 10 m	7	4308.10	38.70	0.00
Litter PC	7	4308.40	39.00	0.00
Juniper 100 m	7	4308.42	39.02	0.00
Juniper 10 m*Juniper 10 m	8	4308.88	39.47	0.00
Juniper 20 m*Juniper 20 m	8	4309.47	40.07	0.00
Juniper 100 m*Juniper 100 m	8	4311.57	42.17	0.00

[1] Number of model parameters

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[2] Akaike’s Information Criterion score for small sample sizes
[3] Difference in Akaike’s Information Criterion score from the top model.
[4] Akaike’s model weights
[5] Fraction of habitat classified as sagebrush
[6] Percent litter cover
[7] Percent cover of *Artemisia tridentata*
[8] Percent cover of annal grass
[9] Percent cover of *Artemisia tridentata*
[10] Fraction of habitat classified as herbaceous cover
[11] Mean height of all shrub species
[12] Fraction of habitat classified as shrub cover

Table B7. Final rankings for models predicting deer mouse (*Peromyscus maniculatus*) survival in southwestern Idaho from 2017-2019. We conducted Cormack-Jolly-Seber survival analyses for deer mice (*n* =387) captured between May and August at a total of 14 trapping grids. We ranked models using Akaike's Information Criterion adjusted for small sample size.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
[5]Juniper Den	6	1594.46	0.00	0.19
Juniper Den + [6]AT Den	7	1595.20	0.74	0.13
Juniper Den + [7]Cheatgrass PC	7	1596.19	1.73	0.08
Juniper Den + [8]Shrub Den	7	1596.48	2.02	0.07
Year	5	1596.73	2.27	0.06
[9]AT Height	6	1596.92	2.46	0.05
Juniper Den*[10]Juniper Height	8	1597.70	3.24	0.04
Shrub Den	6	1597.88	3.42	0.03
[11]Native Grass PC	6	1598.00	3.54	0.03
Juniper Den + Cheatgrass PC + Native Grass PC	8	1598.22	3.76	0.03
[12]Rock	6	1598.24	3.78	0.03
AT Den*AT Height	8	1598.25	3.79	0.03
Cheatgrass PC	6	1598.30	3.84	0.03
AT Den + AT Height	7	1598.58	4.12	0.02
AT Den	6	1598.73	4.27	0.02
Juniper Den + Cheatgrass PC + AT Den	9	1598.77	4.31	0.02
Cheatgrass PC + Native Grass PC	7	1599.67	5.21	0.01
AT Den + Cheatgrass PC + Native Grass PC	8	1601.31	6.85	0.01

[1] Number of model parameters

[2] Akaike's Information Criterion score for small sample sizes

[3] Difference in Akaike's Information Criterion score from the top model.

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[4] Akaike's model weights
[5] Juniper stem density within a 50 m radius of the center of the trapping grid
[6] Mean density/m^2 of *Artemisia tridentata*
[7] Percent of each trapping grid with *Bromus tectorum* present
[8] Mean density/m^2 for all shrub species
[9] Mean height of *Artemisia tridentata*
[10] Mean juniper height
[11] Percent of each trapping grid visually classified as >30% native grass cover
[12] Proportion of trapping grid classified as rocky

Table B8. Final rankings for models predicting Great Basin pocket mice (*Perognathus parvus*) survival in southwestern Idaho from 2017-2019. We conducted Cormack-Jolly-Seber survival analyses for pocket mice (*n* =158) captured between May and August at a total of 14 trapping grids. We ranked models using Akaike's Information Criterion adjusted for small sample size.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
[1]AT Den + [2]AT Height	6	691.36	0.00	0.29
AT Den*AT Height	7	693.09	1.73	0.12
[7]Juniper Den*Juniper Den	6	693.16	1.80	0.12
Juniper Den*Juniper Den + [8]Cheatgrass PC	7	693.71	2.35	0.09
AT Height	5	694.11	2.75	0.07
Juniper Den*Juniper Den + [9]Shrub Den	7	694.69	3.33	0.05
Juniper Den*Juniper Den + AT Den	7	694.80	3.44	0.05
Juniper Den*Juniper Den + Cheatgrass PC + [10]Native Grass PC	8	694.90	3.55	0.05
Native Grass PC	5	698.43	7.07	0.01
Juniper Den*[11]Juniper Height	7	699.52	8.17	0.00
Cheatgrass PC + Native Grass PC	6	700.20	8.84	0.00
AT Den	5	700.72	9.36	0.00
Shrub Den	5	701.32	9.96	0.00
Year	4	701.72	10.36	0.00
AT Den + Cheatgrass PC + Native Grass PC	7	702.12	10.76	0.00
[12]Rock	5	702.26	10.91	0.00
Cheatgrass PC	5	703.39	12.03	0.00

[1] Number of model parameters
[2] Akaike's Information Criterion score for small sample sizes
[3] Difference in Akaike's Information Criterion score from the top model.

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[4] Akaike's model weights
[5] Mean density/m^2 of *Artemisia tridentata*
[6] Mean height of *Artemisia tridentata*
[7] Juniper stem density within a 50 m radius of the center of the trapping grid
[8] Percent of each trapping grid with *Bromus tectorum* present
[9] Mean density/m^2 for all shrub species
[10] Percent of each trapping grid visually classified as >30% native grass cover
[11] Mean juniper height
[12] Proportion of trapping grid classified as rocky

Table B9. Final rankings for models predicting deer mouse (*Peromyscus maniculatus*) home-range size (range) in southwestern Idaho from 2017-2019. We conducted spatial capture-recapture analyses for pocket mice (*n* =158 individuals) and deer mice (*n* =387 individuals) captured between May and August at a total of 14 trapping grids. We estimated density for deer mice and pocket mice using maximum likelihood estimation and calculated mean density for each trapping grid using estimates from the top model for each species. We used mean density estimates and habitat covariates for conditional likelihood models testing the effects of habitat and species interactions on the range. We ranked models using Akaike's Information Criterion adjusted for small sample size.

Model	[1]npar	[2]AICc	[3]ΔAICc	[4]ω_i
[5]AT Den + [6]Cheatgrass + [7]Intra	5	10866.17	0	0.67
AT Den + Cheatgrass + Intra + [8]Inter	6	10868.20	2.03	0.24
Cheatgrass + Intra	4	10872.57	6.40	0.03
[9]Juniper Den + Cheatgrass + Intra	5	10873.69	7.52	0.02
[10]Native Grass PC + Cheatgrass + Intra	5	10874.10	7.93	0.01
Juniper Den + Cheatgrass + Inter + Intra	6	10874.38	8.21	0.01
[11]Juniper 100 m + Cheatgrass + Intra	5	10874.46	8.28	0.01
Cheatgrass + Inter + Intra	5	10874.51	8.33	0.01
Native Grass PC + Cheatgrass + Inter + Intra	6	10875.77	9.60	0
Juniper 100 m + Cheatgrass + Inter + Intra	6	10876.49	10.32	0
Juniper 100 m + Cheatgrass + Inter	5	10878.80	12.63	0
Cheatgrass	3	10878.96	12.79	0
Cheatgrass + Inter	4	10879.53	13.36	0
Juniper Den + Cheatgrass + Inter	5	10880.02	13.85	0
AT Den + Cheatgrass + Inter	5	10880.26	14.09	0
Native Grass + Cheatgrass + Inter	5	10881.22	15.04	0

AT Den + Inter + Intra	5	10893.56	27.39	0
AT Den*[12]AT Height + Inter + Intra	7	10893.58	27.41	0
Juniper Den + AT Den + Intra	5	10894.44	28.27	0
Juniper 100 m + AT Den + Inter + Intra	6	10894.65	28.48	0
Juniper Den + AT Den + Inter + Intra	6	10894.71	28.54	0
[13]Rock + Intra	4	10895.24	29.07	0
Rock	3	10896.17	30.00	0
[14]Year + Inter + Intra	6	10896.27	30.10	0
Rock + Inter + Intra	5	10896.81	30.63	0
Year + Intra	5	10897.18	31.01	0
AT Den + Intra	4	10897.32	31.15	0
AT Height + Inter	4	10897.47	31.30	0
AT Height + Inter + Intra	5	10897.73	31.55	0
[15]Shrub Den + Inter + Intra	5	10897.80	31.63	0
Rock + Inter	4	10898.18	32.01	0
Juniper Density + Intra	4	10898.84	32.67	0
Juniper 100 m + AT Density + Intra	5	10898.99	32.82	0
AT Density*AT Height + Inter	6	10899.21	33.04	0
Juniper Den + Inter + Intra	5	10899.39	33.22	0
Juniper 100 m + Inter + Intra	5	10900.41	34.24	0
Native Grass PC + Inter + Intra	5	10900.43	34.26	0
AT Den*AT Height + Intra	6	10900.54	34.37	0
Intra	3	10902.00	35.83	0

Juniper 100 m + Intra	4	10902.62	36.44	0
Shrub Den + Intra	4	10902.73	36.56	0
Year	4	10902.96	36.79	0
Native Grass + Intra	4	10903.33	37.16	0
AT Height + Intra	4	10904.04	37.87	0
Juniper 100 m + AT Den + Inter	5	10904.18	38.01	0
Year + Inter	5	10904.38	38.21	0
Juniper Den + AT Density + Inter	5	10904.70	38.53	0
AT Den*AT Height	5	10905.15	38.98	0
Juniper Den + Inter	4	10905.17	39.00	0
Juniper 100 m + Inter	4	10905.45	39.27	0
AT Height	3	10905.65	39.48	0
Null	2	10906.79	40.62	0
Inter	3	10906.98	40.81	0
Shrub Den + Inter	4	10907.37	41.20	0
Shrub Den	3	10907.60	41.43	0
AT Den	3	10908.08	41.91	0
Juniper Density	3	10908.35	42.18	0
Juniper 100 m	3	10908.45	42.28	0
AT Den + Inter	4	10908.62	42.44	0
Native Grass PC	3	10908.78	42.61	0
Native Grass PC + Inter	4	10908.95	42.78	0

[1] Number of model parameters

[2] Akaike's Information Criterion score for small sample sizes

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[3] Difference in Akaike's Information Criterion score from the top model.
[4] Akaike's model weights
[5] Mean trapping grid density for *Artemisia tridentata*
[6] Percent of each trapping grid with *Bromus tectorum* present
[7] Deer mouse mean trapping/grid density
[8] Pocket mouse mean trapping/grid density
[9] Count of juniper trees within 50 m of the center of the trapping grid
[10] Percent of each trapping grid visually classified as >30% native grass cover
[11] Continuous juniper cover, 100 m
[12] Mean height of big sagebrush shrubs
[13] Percent of each trapping grid with rocks present
[14] Study year
[15] Mean density for all shrub species

Table B10. Final rankings for models predicting Great Basin pocket mice (*Perognathus parvus*) home-range size (range) in southwestern Idaho from 2017-2019. We conducted spatial capture-recapture analyses for pocket mice (*n* =158) and deer mice (*n* =387) captured between May and August at a total of 14 trapping grids. We estimated density for deer mice and pocket mice using maximum likelihood estimation. We conducted mean density for each trapping grid using estimates from the top model for each species. We used mean density estimates and habitat covariates for conditional likelihood models testing the effects of habitat and species interactions on range. We ranked models using Akaike's Information Criterion adjusted for small sample size.

Model	[1]K	[2]**AICc**	[3]**ΔAICc**	[4]ω_i
[5]Rock + [6]Intra + [7]Inter	5	4274.21	0.00	0.65
[8]Year + Intra + Inter	6	4278.29	4.08	0.08
[9]Juniper cover + Intra + Inter	5	4278.48	4.27	0.08
Juniper 100 m + [10]AT Den + Intra + Inter	6	4279.33	5.13	0.05
Juniper 100 m + [11]Cheatgrass + Intra + Inter	6	4280.08	5.87	0.03
[12]AT Height + Intra + Inter	5	4283.98	9.77	0.00
[13]Juniper Den + Intra + Inter	5	4284.48	10.28	0.00
Juniper Den + Cheatgrass + Intra + Inter	6	4285.71	11.51	0.00
Juniper Density + AT Den + Intra + Inter	6	4286.28	12.07	0.00
Cheatgrass + Intra + Inter	5	4286.43	12.22	0.00
[14]Native Grass + Intra + Inter	5	4286.95	12.74	0.00
AT Den + Intra + Inter	5	4287.08	12.88	0.00
[15]Shrub Den + Intra + Inter	5	4287.16	12.95	0.00
AT Den*AT Height + Intra + Inter	7	4288.13	13.92	0.00
Native Grass + Cheatgrass + Intra + Inter	6	4288.54	14.33	0.00
AT Den + Cheatgrass + Intra + Inter	6	4288.55	14.34	0.00
Juniper Den + Intra	4	4290.87	16.66	0.00
Juniper phase + Intra	4	4291.06	16.85	0.00

Juniper Den + Cheatgrass + Intra	5	4292.44	18.23	0.00
Juniper Den + AT Den + Intra	5	4292.86	18.65	0.00
AT Den*AT Height + Intra	6	4296.19	21.99	0.00
Juniper 100 m + Intra	4	4297.52	23.31	0.00
AT Height + Intra	4	4297.84	23.63	0.00
Year + Intra	5	4299.16	24.95	0.00
Juniper 100 m + AT Den + Intra	5	4299.45	25.24	0.00
Juniper 100 m + Cheatgrass + Intra	5	4299.59	25.39	0.00
Shrub density + Intra	4	4300.31	26.10	0.00
Rock + Intra	4	4301.98	27.77	0.00
Intra	3	4304.51	30.30	0.00
AT Den + Intra	4	4306.33	32.12	0.00
Cheatgrass + Intra	4	4306.50	32.29	0.00
AT Den + Cheatgrass + Intra	5	4308.25	34.04	0.00
Native Grass + Cheatgrass + Intra	5	4308.46	34.25	0.00
Rock + Inter	4	4311.01	36.80	0.00
Rock	3	4329.75	55.54	0.00
AT Den + Cheatgrass + Inter	5	4341.66	67.45	0.00
Native Grass + Cheatgrass + Inter	5	4342.29	68.08	0.00
Juniper 100 m + Cheatgrass + Inter	5	4344.63	70.42	0.00
Cheatgrass + Inter	4	4345.04	70.84	0.00
Juniper Den + Cheatgrass + Inter	5	4346.79	72.59	0.00
Cheatgrass	3	4349.34	75.13	0.00

Year	4	4355.10	80.89	0.00
Inter	3	4356.12	81.91	0.00
Year + Inter	5	4356.32	82.11	0.00
AT Den * AT Height	5	4358.84	84.63	0.00
AT Den	3	4362.07	87.86	0.00
AT Height + Inter	4	4363.61	89.40	0.00
AT Den + Inter	4	4364.55	90.34	0.00
Native Grass	3	4364.90	90.69	0.00
AT Height	3	4364.91	90.70	0.00
Shrub density	3	4366.30	92.09	0.00
Null	2	4366.31	92.10	0.00
Juniper 100 m + AT Den + Inter	5	4366.62	92.41	0.00
Juniper Den + AT Den + Inter	5	4366.66	92.45	0.00
Native Grass + Inter	4	4366.87	92.66	0.00
Juniper 100 m	3	4367.19	92.99	0.00
Shrub density + Inter	4	4368.18	93.97	0.00
Juniper Den	3	4368.30	94.09	0.00
Juniper 100 m + Inter	4	4369.22	95.01	0.00
Juniper Den + Inter	4	4369.91	95.70	0.00

[1] Number of model parameters
[2] Akaike's Information Criterion score for small sample sizes
[3] Difference in Akaike's Information Criterion score from the top model.
[4] Akaike's model weights
[5] Percent of each trapping grid with rocks present
[6] Pocket mouse mean trapping/grid density
[7] Deer mouse mean trapping/grid density
[8] Study year

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[9] Continuous juniper cover, 100 m
[10] Mean trapping grid density for *Artemisia tridentata*
[11] Percent of each trapping grid with *Bromus tectorum* present
[12] Mean height of big sagebrush shrubs
[13] Count of juniper trees within 50 m of the center of the trapping grid
[14] Percent of each trapping grid visually classified as >30% native grass cover
[15] Mean trapping grid density for all shrub species

Table B11. Final model rankings for deer mouse (*Peromyscus maniculatus*) juniper (*Juniperus occidentalis*) scale models in southwestern Idaho from 2017-2019. We conducted Cormack-Jolly-Seber survival analyses for deer mice (*n* =387) captured between May and August at a total of 14 trapping grids. We counted all juniper trees and snags within 50 m of the center of the trapping grid to estimate stem density. We estimated juniper cover within a 50, 100, 150, and 200 m radius of the center of the trapping grid.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
[5]JSD	6	1594.46	0.00	0.27
100 m	6	1595.86	1.40	0.13
50 m	6	1596.17	1.72	0.11
JSD*JSD	7	1596.41	1.95	0.10
Null	5	1596.73	2.27	0.09
150 m	6	1597.38	2.92	0.06
200 m	6	1597.53	3.07	0.06
100 m*100 m	7	1597.77	3.31	0.05
50 m*50 m	7	1598.10	3.65	0.04
200 m*200 m	7	1598.16	3.70	0.04
150 m*150 m	7	1598.28	3.82	0.04

[1] number of model parameters
[2] Akaike's Information Criterion score for small sample sizes
[3] Difference in Akaike's Information Criterion score from the top model
[4] Akaike's model weights
[5] Stem density of *Juniperus occidentalis* trees within 50 m of the center of the trapping grid

Table B12. Final model rankings for Great Basin pocket mice (*Perognathus parvus*) juniper (*Juniperus occidentalis*) scale models in southwestern Idaho from 2017-2019. We conducted Cormack-Jolly-Seber survival analyses for deer mice (*n* =387) captured between May and August at a total of 14 trapping grids. We counted all juniper trees and snags within 50 m of the center of the trapping grid to estimate stem density. We estimated juniper cover within a 50, 100, 150, and 200 m radius of the center of the trapping grid.

Model	[1]K	[2]AICc	[3]ΔAICc	[4]ω_i
[5]JSD*JSD	6	693.16	0.00	0.54
JSD	5	695.75	2.59	0.15
100 m*100 m	6	696.82	3.66	0.09
150 m*150 m	6	698.07	4.91	0.05
100 m	5	698.21	5.05	0.04
50 m	5	698.73	5.57	0.03
50 m*50 m	6	698.85	5.69	0.03
150 m	5	699.32	6.16	0.02
200 m*200 m	6	699.57	6.41	0.02
200 m	5	699.86	6.70	0.02
Null	4	701.72	8.56	0.01

[1] number of model parameters

[2] Akaike's Information Criterion score for small sample sizes

[3] Difference in Akaike's Information Criterion score from the top model

[4] Akaike's model weights

[5] Stem density of *Juniperus occidentalis* trees within 50 m of the center of the trapping grid

Table B13. We used a two-stage modelling process to assess effects of habitat covariates on small mammal density in southwest Idaho from 2017-2019. During stage one, we tested factors that may affect capture probability for small mammals and carried covariates from the top detection model into stage two. During stage two, we included habitat covariates from the National Land Cover Database and a juniper cover classification. We compared models using Akaike's Information Criterion adjusted for small sample size.

Stage 1: Detection	[1]Stage 2: Habitat Covariates
Null	[3]AT PC
Study year	[4]AT Height
Time within year	[5]Cheatgrass PC
[2] Learned behavior	[6]Litter PC
	[7]Sagebrush FC
	[8]Shrub height
	[9]Herbaceous FC
	[10]Shrub FC
	Juniper PC, 10, 20, 50, 100 m
	AT PC*AT PC
	AT Height*AT Height
	Cheatgrass PC*Cheatgrass PC
	Litter*Litter
	Sagebrush FC*Sagebrush FC
	Shrub Height*Shrub Height
	Herbaceous FC*Herbaceous FC
	Juniper PC*Juniper PC, 10, 20, 50, 100 m

[1] We estimated juniper cover and assigned values to 1 m resolution pixel cells. We then aggregated cells to 10 m resolution with mean

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juniper cover values at each scale. We obtained all other habitat covariates from 30 m resolution spatial layers from the National Land Cover Database.

[2] A change in capture probability following the initial capture event

[3] Percent cover of *Artemisia tridentata*

[4] Mean height of *Artemisia tridentata*

[5] Percent cover of *Bromus tectorum*

[6] Percent litter cover

[7] Fraction of habitat classified as sagebrush

[8] Mean height of all shrub species

[9] Fraction of habitat classified as herbaceous cover

[10] Fraction of habitat classified as shrub cover

Table B14. We used a three-stage modelling process to test the effects of habitat covariates on small mammal survival in southwest Id from 2017-2019. During stage one, we tested factors that may affect capture probability for small mammals. We included covariates from the top detection model in stages two and three. During stage two, we compared different scales and measurements of juniper. During the final stage, we included the juniper measurement which received the most support in a model set with other habitat features. We compared models using Akaike's Information Criterion adjusted for small sample size.

Stage 1: Detection Models	[1]Stage 2: Juniper	Stage 3: Habitat Covariates
Null	50 m	[4]AT Den
Study year	50 m*50 m	[5]AT Height
Time within year	100 m	[6]Rock
[2]Learned behavior	100 m*100 m	[7]Cheatgrass
Year + Learned behavior	150 m	[8]Native Grass
Year + Time within year	150 m*150 m	[9]Shrub Den
	200 m	JSD
	200 m*200 m	Juniper Den*Juniper Height
	[3]JSD	AT Den*AT Height
	JSD*JSD	Cheatgrass + Native Grass
		JSD + Shrub Den
		JSD + AT Den
		AT Den + Cheatgrass + Native Grass
		JSD + Cheatgrass
		JSD + Cheatgrass + Native Grass

JSD + Cheatgrass + Native Grass + AT Den

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[1] We estimated juniper cover and assigned values to 1 m resolution pixel cells. We then aggregated cells to 10 m resolution with mean juniper cover values at each scale. We obtained all other habitat covariates from 30 m resolution spatial layers from the National Land Cover Database.
[2] A change in capture probability following the initial capture event.
[3] Stem density of *Juniperus occidentalis* trees within 50 m of the center of the trapping grid
[4] *Artemisia tridentata* mean density/m^2.
[5] Mean height of *Artemisia tridentata*
[6] Percentage of the trapping grid classified as rock.
[7] Percentage of the trapping grid featuring *Bromus tectorum*.
[8] Percentage of the trapping grid featuring native grass cover > 30%
[9] Shrub density/m^2, all species

Chapter 4: Tree removal in sagebrush habitats: implications for the songbird community.

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Abstract

Declining populations of songbirds associated with the sagebrush-steppe ecosystem have been attributed to loss of habitat and degradation of remaining habitat. One factor that has contributed to habitat loss and degradation for shrub-associated songbirds is an increase in conifer woodlands within the sagebrush-steppe biome. Efforts to quantify the direct relationship between the presence of conifer trees, and subsequently the prospect for conifer removal as a conservation tool for sagebrush populations, have yielded inconsistent results. Shrub-nesting songbirds may not immediately respond to conifer removal alone because shrub structure is an important influencer of distributions for this group. We examined the response of two sagebrush-obligate species, Brewer's sparrow (*Spizella breweri*) and sage thrasher (*Oreoscoptes montanus*), and one sagebrush-ecotone species, green-tailed towhee (*Pipilo chlorurus*; hereafter shrub-nesting species), to variation in conifer and shrub structure. Further, we examined the short-term response of the songbird community to conifer removal in a ~ 15,000 ha conifer removal project area. We conducted point-count surveys for three years before and one year after treatment using a before-after control-impact study design. Shrub characteristics (volume, density, and height) were important predictors of density for Brewer's sparrow and green-tailed towhee, while conifer cover was an important predictor for all three shrub-nesting species. However, each species responded to conifer cover at different spatial scales. Following conifer removal, areas with more conifer removed exhibited lower increases in abundance of shrub-nesting songbirds, likely due to reduced shrub structure at these locations. Abundances of conifer-nesting songbirds remained steady or increased in remaining conifer woodlands in the year following conifer removal, suggesting that removal of habitat featuring conifer <20% may not impact overall landscape diversity, at least in the short term. Our study shows that considering shrub characteristics and the spatial scale of remaining conifer is an important factor for conifer removal projects for which the aim is to support songbird populations.

Introduction

Shrublands are one of the most imperiled biomes in the world, and expansion of native and invasive woody vegetation is a major cause of degradation and fragmentation in these systems (Reinhardt et al. 2020). The expansion of woody vegetation alters ecosystem processes such as nitrogen deposition and water availability, leading to changes in understory vegetation including reductions in shrub and grass cover and changes to plant community composition (Archer et al. 2017). These effects increase as woody expansion and infill intensify until a tipping point is reached and ecological processes come to be dominated by expanding and invading plant species (Briske et al. 2008, Bestelmeyer et al. 2017). As expansion advances toward a transition between two ecological states (e.g., shrubland to woodland), foundational ecosystem processes of the pre-invasion community are interrupted, making restoration of the previous ecological state unlikely (Williams et al. 2017).

Expansion of woody plants has occurred worldwide in rangelands (Archer et al. 2017). Shrublands in the Mediterranean, South Africa, and American west have experienced an expansion of native conifer trees (Venter et al. 2018, Andersen and Steidl 2019, Ben-David et al. 2019). In the arid and semi-arid sagebrush (*Artemesia* spp.) shrublands of western North America, conifer expansion has converted large swaths of land to forested habitat, reducing or eliminating the shrub and grass structure upon which sagebrush-associated wildlife rely (Miller et al. 2019). Conversion of sagebrush habitat to conifer savannahs and woodland has had negative consequences for sagebrush-associated wildlife (Knick et al. 2003, Coates et al. 2020).

The response of wildlife to woody-plant expansion varies, both within and among taxa (Blaum et al. 2007, Archer et al. 2017). However, major gaps exist in our understanding of wildlife responses along the gradient of woody-plant expansion (Bombaci and Pejchar 2016). For songbirds, woody-plant expansion in grasslands and shrublands may increase overall diversity and abundances at intermediate levels of expansion where rangeland species are not yet eliminated from the community and woody plants provide novel resources that allow new species to enter the community (Andersen and Steidl 2019). However, the addition of colonizing species to a community may impact species interactions (e.g., predator/prey) that may indirectly impact previously occurring species (Tylianakis et al.

2008). Improving our understanding of wildlife responses to conifer in rangelands is important for efforts to conserve declining wildlife populations.

The sagebrush steppe of the western United States, originally spanning > 62 million ha and home to ~350 plants and animals of conservation concern (Wisdom et al. 2005), has been reduced to 59% of its original extent (Davies et al. 2011). Concern over populations of sagebrush dependent species, including the greater sage-grouse (*Centrocercus urophasianus*; hereafter sage grouse), has led to the initiation of efforts to restore shrub-steppe communities through removal of conifer species including pinyon (*Pinus spp.*) and juniper (*Juniperus spp.*, hereafter conifer) which have expanded into areas previously dominated by sagebrush shrubs (BLM 2018, BLM 2020). Conversion of sagebrush habitat into conifer woodlands represents a direct loss of habitat for sage grouse and other sagebrush obligates, and evidence shows that even in early stages of expansion conifer establishment has deleterious demographic effects on sage grouse (Coates et al. 2017, Severson et al. 2017). Effects of early-stage conifer expansion on other populations of conservation concern associated with sagebrush, including several species of songbirds (Donnelly et al. 2017, Holmes et al. 2017) and pygmy rabbits (*Brachylagus idahoensis*; Woods et al. 2013) has begun to receive increased attention. However, our understanding of the relationships between wildlife and early-stage conifer expansion are incomplete, especially when it comes to understanding the effect of spatial scale and the importance of the structure of native shrubs that remain in the understory

Shrub-nesting songbirds, including Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee (*Pipilo chlorurus*) have experienced population declines over the past 30 years in the northern Great Basin, and are listed as species of management concern in multiple states across their range (Pardiek et al. 2019). Each of these species are dependent on shrubs for nesting, foraging, and singing, although nest site characteristics for these species vary (Dobbs et al. 2020, Reynolds et al. 2020, Rotenberry et al. 2020). The distribution for each of these species coincides geographically with the area affected by high rates of conifer cover, suggesting woody-plant expansion may play a role in population declines for each of these species. Research on the effects of conifer expansion, and of restoration of sagebrush habitat, on shrub-associated songbirds has yielded weak or unclear patterns, suggesting that individual species may respond to habitat characteristics other than conifer, or at spatiotemporal scales beyond those measured (Knick et al. 2017). However, individuals within the shrub-nesting group are unlikely to be homogenous in their response to both conifer expansion and habitat restoration. Songbirds may respond to novel structures such as trees in a formerly treeless landscape in context-dependent ways. For example, species may respond to tree cover because of changes in real or perceived-predation risk associated with altered habitat structure, or species may respond to a loss of understory shrubs and herbaceous vegetation caused by the establishment of trees (Herse et al. 2017, McNeil et al. 2020, Rees et al. 2020). Therefore, practical limits to previous research, including limited spatial scales, lack of before-after control designs, and thinning of conifer as opposed to complete removal, may limit the ability to make inference to the community as a whole.

Restoration efforts that alter habitat at large scales are likely to affect not only the target populations (i.e., sagebrush-associated wildlife), but also have implications for the community within the broader mosaic of conifer-sagebrush habitat, including species that are associated with conifer. Conifer is an historic component of the sagebrush steppe, and conifer woodlands support a high diversity of songbird species (Paulin et al. 1999, Bombaci and Pejchar 2016). However, as conifer expands and sagebrush habitat is converted by human development and conifer expansion, populations of sagebrush songbirds have declined while conifer-associated populations have generally remained level or increased (Pardieck et al. 2019). Responding to concerns over declining populations of sagebrush songbirds, research has focused on this group under the assumption that conifer associated populations are not habitat limited. Many sagebrush restoration efforts acknowledge the historic presence of conifer in the sagebrush landscape by removing only low-density, early-expansion conifer, leaving old-growth trees and juniper woodlands uncut (e.g., BLM 2018). Reductions in the total abundance of conifer songbirds following conifer removal are to be expected and have been demonstrated (Holmes et al. 2017). However, the value of remaining conifer cover, ranging from individual old-growth trees to contiguous conifer woodlands (> 20% cover), for landscape-level diversity remains unexplored. Therefore, minimizing impacts on conifer species diversity requires data to assess the short- and long-term effects of sagebrush ecosystem restoration on conifer songbirds.

We studied the relationship between the distribution of shrub-nesting songbirds along a gradient of conifer expansion and sagebrush characteristics in southwest Idaho. In addition, we tested the short-term response of both shrub-nesting and conifer-nesting songbirds to conifer removal and habitat characteristics using a before-after control-impact study design (BACI). We sought to establish the relationship between woody-plant expansion, and removal, and songbird communities. We address two questions: 1.) are expanding conifer trees the primary factor determining the distribution of songbird populations associated with an invaded ecosystem (shrub-nesting species), and 2.) what are the short-term effects of conifer removal on community abundance, including both shrub-nesting- and conifer-nesting species? Because songbirds often respond primarily to structural aspects of vegetation (Wiens 1969, Rotenberry and Wiens 1980), we focused on changes in vegetation structure as the primary mechanism affecting songbird habitat use.

Methods

We surveyed songbirds in southwest Idaho in 2017-2020 across ~ 115,000 ha of sagebrush steppe with varying degrees of juniper expansion (Figure 4.1). The study site is in the Northern Basin and Range ecoregion (McGrath et al. 2002) and western juniper is the only conifer species within the boundaries of our sampled area. Cottonwood trees (*Populus trichocarpa*) are found in shallow, rocky canyons containing streams. Curl-leaf mountain mahogany (*Cerocarpus ledifolius*) achieves heights of up to four m and is found in dense stands in the southwest portion of the study site. Elevation ranges 1,250 − 1,920 m and topography is varied with low lying riparian areas interspersed with open sagebrush tablelands and rocky ridgelines. Areas of dense juniper are found along ridgetops and in drainages, and juniper has expanded into sagebrush habitat, forming a gradient of tree cover across the landscape that varies as a function of elevation, topography and fire history, and hydrology. Where juniper is well established, areal coverage of juniper trees may reach 60% with individual trees achieving heights of 12 m, average tree heights of 3.65 m ± SD 2.26, and an average density of 198 trees/ha ± SD 193. Where juniper has more recently expanded into sagebrush-dominated habitat, trees are sparsely distributed, with an average height of 2.79 m ± SD 2.06 and an average density of 19 trees/ha ± SD 25.

The Bruneau-Owyhee Sage Habitat (BOSH) project began removing juniper in 2019 (BLM 2018) and will eventually remove phase 1 and 2 juniper from habitat formerly dominated by sagebrush across a 676,000-ha landscape to support sage-grouse and other sagebrush-obligate species (BLM 2018). Our study site was ~30, 000 ha, and in the fall of 2019 ~15,000 ha of juniper was hand-cut within our study site. Juniper was cut using chainsaws and scattered so that no debris was higher than one meter. We conducted surveys for three years before and one year after juniper removal began.

Survey design

We conducted repeated-visit surveys over four years to assess effects of habitat structure on the density of songbird populations within our study site. We selected point-count locations using random points generated in a GIS stratified by established categories of juniper cover. Expansion of conifer in sagebrush ecosystems is categorized into three phases defined by the degree to which juniper affects ecosystem processes (Miller and Rose 1999). Phase 1 is habitat that is still dominated by sagebrush shrubs, but conifer is present (1-10% conifer canopy cover). Phase 2 is habitat where sagebrush and juniper co-dominate, but reductions in shrub and grass layers have occurred (10%-20% conifer canopy cover). Phase 3 is habitat where juniper dominates, and extensive reductions or elimination of shrub and grass components have occurred (>20% juniper canopy cover). We surveyed 87 points for four consecutive years and an additional 24 points in the final three years of the study (n = 111 survey points). We randomly distributed point-count locations among conifer phases but ensured that each phase was represented proportionally to its occurrence on the landscape (Table 4.1).

Point count surveys

We conducted point-count surveys from the first week of May to the second week of July each year. We visited each point-count location three times per year with at least two weeks between visits. Point counts consisted of ten-minute surveys during which we limited observations to 100 m to minimize double counting of individuals (Petit et al 1995). Observers waited one minute after arriving at the point-count location to begin a survey, and we did not conduct surveys in winds > 10 kph or steady rain. We conducted surveys between 6:00 am and 10:00 am local time to coincide with the time of day that birds are most active at our site. Over the course of the study, four observers conducted surveys, and the lead author conducted 83% of the surveys.

Vegetation measurement

To address our goal of testing effects of vegetation structure on the songbird community we assessed shrub structure and conifer cover at each of our point-count locations. To measure shrub characteristics, we established an 80 m^2 sampling area in the center of each point-count location. Within this sampling area we measured the height, greatest width, and the width perpendicular to the greatest width for every big sagebrush shrub in the plot. From these measurements we calculated mean height, mean volume (cm^3), and the density of big sagebrush within each point-count location. To address our goal of testing the effect of conifer cover on the songbird community we created a 1-m supervised classification in ArcGIS (Esri, Redding CA, 2019). For each of our point-count locations we then manually corrected any misclassifications using visual inspection and ground truthing to minimize bias in estimates of conifer cover. Four point-count locations contained curl leaf-mountain mahogany in addition to juniper, but we did not attempt to differentiate between mahogany and juniper because we assumed that vegetation structure is more important than species composition. Cover of curl-leaf mahogany was very low (<5%) at these points, and we assume that songbirds respond similarly to juniper and curl-leaf mahogany trees since they both provide an additional structural layer above the shrub canopy. Following our classification, we calculated juniper cover in a radius around each point-count location at six different spatial scales; 50, 100, 150, 200, 500, and 1,000 m. We also classified 30 m^2 pixels by conifer expansion phase to test for an effect of distance to phases on community change.

Statistical analysis

To test if juniper is an important ecological gradient influencing songbird density, we used N-mixture models to estimate density at each point-count location in relation to habitat characteristics. N-mixture models account for imperfect detectability using a hierarchical modeling approach to provide density estimates (Royle 2004). N-mixture models link two generalized linear models, a binomial model and a poisson model, to estimate abundance (N) and detection (p). Because our point-count surveys were fixed radius (100 m), we converted abundance to density/ha. We estimated density for each of the three most common shrub-nesting species at our site: Brewer's sparrow, sage thrasher, and green-tailed towhee. We built our set of candidate models in four stages. In the first stage we tested models with no covariates using Poisson, zero-inflated Poisson (ZIP), and negative binomial distributions to identify the distribution that best fit the data for each species. Second, we tested for an effect of observer on detection. If a model using observer as a covariate was ranked higher using Akaike's Information Criterion adjusted for small sample size (AIC_c) then we included observer as a detection covariate in all subsequent models. Third, we ranked models that tested the effect of percent juniper cover at multiple scales on density estimates. We then carried the juniper model which best fit the data forward into our last stage of modeling in which we tested models that contained combinations of sagebrush structure and juniper cover (Table 4.2). We ranked the final model set using AIC_c and considered models within two AIC_c of the top model to be competitive.

To examine the change in the songbird community following removal of juniper, we used non-metric multidimensional scaling (NMDS) and linear regressions (McCune and Grace 2002). First, we conducted an NMDS ordination of point-count locations before and after juniper removal using abundance data for individual species from our two groups, shrub-nest species and conifer-nesting species. We conducted an ordination for each year, and for the first three years we averaged scores for the two axes of each point-count location to represent the pre-removal community space for each point. The ordination for the fourth year represented the community space for each point-count location following juniper removal. We set the maximum number of runs at 50 and constrained the final solution to two axes. Each run of an ordination begins from a random starting point, and stability is assumed when the program arrives at two similar solutions. We then used the 'env.fit' function in package vegan in program R to describe the relationship between juniper and shrub characteristics in community space (Oksanen et al. 2011). The function visualizes an arrow in the direction of increasing variability between the environmental gradient and the community ordination. The length of the arrow corresponds to the strength of the correlation between the environmental variable and the ordination.

To quantify the change in community space for each point-count location following juniper removal, we calculated centroids by averaging axis scores for each species in the shrub-nesting and conifer-nesting groups (*sensu* Knick et al. 2017). For example, the ordination scores for each member of the shrub-nesting group was averaged to obtain a single ordination score, which was the centroid of the shrub-nesting group. We calculated an average the three centroid values for the first three years to represent the pre-removal centroid. We then calculated the centroids for the fourth year (post-removal) and calculated the change in Euclidean distance from each centroid for each point-count location following juniper removal. We then used the change in Euclidean distance as the response variable in a set of linear models that tested treatment variables including remaining juniper cover, change in juniper cover, distance to phases one, two, and three, and shrub characteristics. We ranked this model set using AIC_c. We created two model sets, one for the shrub-nesting group and one for the conifer-nesting group. The conifer-nesting group included chipping sparrow (*Spizella passerina*), Cassin’s finch (*Haemorhous cassinii*), dark-eyed junco (*Junco hyemalis*), mountain chickadee (*Poecile gambeli*), hermit thrush (*Catharus guttatus*), black-throated grey warbler (*Setophaga nigrescens*), and western tanager (*Piranga ludoviciana*). The model set for the shrub-nesting group included both shrub and conifer variables, whereas the model set for the conifer-nesting group included only conifer related variables because we *a priori* assumed that shrub structure is not important for conifer-nesting species.

Results

We conducted 1,269 point-count surveys for songbirds and recorded 8,327 individuals of 74 species. Prior to juniper removal, average juniper cover for all point-count locations was 7% (SD ± 9%) and the average juniper cover for point-count locations that were scheduled for juniper removal was 5% (SD ± 5%). Following removal of juniper in the fall of 2019, average juniper cover for all point-count locations was 5% (SD ± 9%) and the average juniper cover for point-count locations where juniper was removed was 0% (SD ± 2%).

Habitat characteristics

Brewer’s sparrow - The negative effect of juniper cover on Brewer’s sparrow density was mediated somewhat by sagebrush density (Table 4.3, Figure 4.2). Brewer’s sparrow density increased with big sagebrush density ($\beta = 0.22 \pm$ SE 0.02; Figure 3A) and declined as juniper cover within 500 m increased (β = -0.42 ± SE 0.05). Brewer’s sparrows also responded positively to sagebrush height (β = 0.08 ± SE 0.03; Figure 4.3B).

Sage thrasher - For sage thrasher, juniper had a strong negative effect on density. (Table 4.3). Sage thrasher density declined in response to juniper within 100 m, and estimated density of sage thrashers approached zero at < 5% juniper cover (β = -2.36 ± SE 0.58; Figure 4.4).

Green-tailed towhee - The positive effect of juniper on green-tailed towhee density was strongly mediated by sagebrush volume (Figure 4.5). Green-tailed towhee density increased with sagebrush volume (β = 0.22 ± SE 0.06, Figure 4.5), sagebrush height (β = 0.20 ± SE 0.06; Figure 4.5A), and sagebrush density (β = 0.11 ± SE 0.05; Figure 4.5B, Table 4.3) and juniper cover (β = 0.24 ± SE 0.06 Figure 6),.

Effect of juniper removal

Ordinations of pre-removal density and post-removal density yielded a two-dimension solution with final stress levels below 0.20 for all years (stress = 0.15-0.19, R^2 = 0.96-0.97). Stress levels below 0.20 are considered reliable (Oksanen et al. 2011). Before conifer removal, conifer-nesting songbirds, juniper cover and big sagebrush volume were strongly associated with the first axis, whereas shrub-nesting songbirds, sagebrush height and density were associated with the second axis (Table 4.4). The centroid for the shrub-nesting group was associated with increased variability along the environmental gradient of sagebrush density and decreased variability in sagebrush height. The centroid for the conifer-nesting group was associated with more variability along the environmental gradient of sagebrush height and tended toward more variability in juniper cover (Figure 4.7).

In the fall of 2019 juniper was manually cut from ~ 15,000 ha leaving behind scattered course woody debris that was less than 1-m high. As a result, estimates from 2020 represent the short-term response of songbirds to juniper removal. An ordination of post-removal data showed conifer-nesting songbirds were most strongly associated with the first axis, as were sagebrush volume and density. Shrub-nesting songbirds were most strongly associated with the second axis, as were juniper cover and sagebrush height (Table 4.4). The shrub-nesting group was centered on the axis for sagebrush density and volume. Conifer-nesting songbirds were strongly associated with the juniper-cover axis, in the direction of low variability on the environmental gradient. (Figure 4.8). The average density (across all survey points) of Brewer's sparrows and green-tailed towhees was significantly higher in 2020 following juniper removal, while sage thrasher detections were too sparse to estimate a year effect (Table 4.5).

We observed increased dominance of shrub-nesting species within the community at 23 point-count locations in cut areas and 23 point-count locations in uncut areas (41% of point-count locations; Figure 4.9). Conifer-nesting species dominance of the community increased at six untreated survey points. All the survey points that moved toward the conifer-nesting group occurred in phase 3 (> 20% juniper cover). For shrub-nesting songbirds, the amount of juniper removed from within 50 m of the point-count location ($\beta = -0.34 \pm$ SE 0.08) most strongly influenced the degree of community change. Point-count locations with the greatest change in juniper cover moved the least toward shrub-nesting songbird dominance. Given that point-count locations with the greatest change in juniper cover tended to have a lower total volume and mean densities of sagebrush, this pattern reinforces the importance of the condition of the shrub understory in affecting responses of the shrub-nesting group to juniper removal. For conifer-nesting songbirds, the distance to phase 3 juniper habitat most strongly influenced the degree of community change, with point-count locations closer to phase 3 juniper cover retaining or increasing the dominance of conifer-nesting species within the community ($\beta = -0.44 \pm$ SE 0.08).

Discussion

Our study highlights the potential for immediate increases in density of shrub-nesting songbirds following removal of juniper from a sagebrush ecosystem. However, increases in density following juniper removal are dependent on remaining shrub structure, and shrub-nesting songbirds displayed species-specific associations with juniper cover. For conifer-nesting songbirds, a strong relationship with juniper cover > 20% limited impacts on the overall songbird community because only areas of juniper cover < 20% were cut. Managers interested in restoration projects that benefit songbirds as well as other vertebrate species such as greater sage-grouse should consider remaining shrub structure in the understory when selecting sites that would be best-suited to juniper removal.

Habitat gradients

Our results provide further evidence that sagebrush structure is important for sagebrush songbirds, but also highlight how individual species respond to juniper in sagebrush habitat. For all three of the shrub-nesting species we examined, juniper cover had a stronger effect on density than other habitat variables, suggesting that the habitat gradient of juniper cover has the greatest influence on densities of shrub-nesting songbirds. Brewer's sparrows at our site responded to juniper at relatively large spatial scales and were more tolerant of juniper cover if adequate shrub structure was present. Sage thrashers were sensitive to small amounts of juniper at fine spatial scales and densities for this species approached zero at < 5% conifer cover. For sage thrasher, the effect of conifer expansion was stronger than any association with shrub structure, which was surprising given this species nests in shrubs. In contrast, green-tailed towhee, which responded to juniper at the largest spatial scale, responded positively to juniper cover. However, shrub structure was also an important aspect of green-tailed towhee distributions. Shrub structure has long been established as an important influencer of local densities of sagebrush songbirds (Wiens and Rotenberry 1981). However, recent studies of the effects of sagebrush degradation on sagebrush-obligate songbirds have examined effects of conifer removal and thinning on smaller scales (e.g., 40-1300 ha, Knick et al. 2014, 2017), have used a chronosequence design to indirectly test the effects of juniper removal with minimal consideration of shrub structure (e.g., Holmes et al. 2017), or have simulated conifer removal while accounting for shrub structure using broad-scale geospatial classifications with course resolution (Zeller et al. 2021). Our results therefore represent new and important direct information about how juniper removal may benefit sagebrush songbirds while explicitly accounting for the importance of remaining shrub structure at fine scales.

Community change

The increase in density of shrub-nesting songbirds following juniper removal suggests that either the individuals using our study area shifted from nearby spots in response to juniper removal or immigrating individuals selected habitat based on cues at the landscape scale. Given that juniper removal occurred during autumn when many sagebrush songbirds had already left for wintering grounds, birds returning in the spring would have encountered a new landscape physiognomy, and at finer scales would have fewer concessions to make when selecting habitat featuring appropriate shrub structure that may have in previous seasons also included juniper. Previous research conducted at smaller spatial scales or using a chronosequence study design assumed that there is a time lag for increases in sagebrush songbird density following juniper removal because increases in density were either negligible or increased linearly in subsequent years (Holmes et al. 2017, Knick et al. 2017). Although it may be that density of shrub-nesting songbirds at our site will continue to increase in subsequent years, our results suggest that when juniper removal occurs at larger scales and shrub structure is adequate, increases in density the following season can be significant. Determining whether these increases are a product of shifts in the distribution of the local population or a result of an influx of additional individuals dispersing from different regions is beyond the scope of this project. However, given that habitat selection by songbirds is influenced by habitat features at multiple scales (Herse et al. 2017), both the local population and dispersing individuals from other populations may have settled at our site after juniper removal.

Songbird species associated with conifer receive little attention when the benefits of sagebrush habitat restoration are considered (but see Bombaci and Pejchar 2016). The assumption most often made is that as conifer habitat expands, populations of conifer songbirds will take advantage of new habitat. Our results suggest a strong relationship between the conifer songbird group and habitat classified as phase 3 because this habitat retained or increased conifer songbird dominance following juniper removal. Eliminating phase 3 conifer habitat from the sagebrush ecosystem would likely provide little direct benefit to sage grouse or sagebrush songbirds because shrub cover is very low or already eliminated in much phase 3 habitat (Williams et al. 2017). However, indirect benefits of removing phase 3, such as reductions in predators, remain largely untested. Although removing phases 1 and 2 juniper habitat from the landscape will reduce density of some conifer songbirds, allowing phase 3 habitat to remain intact would likely provide a refuge. We did not examine the relationships between phase 3 patch size or landscape configuration and conifer songbird community composition, and future analyses examining these questions would be valuable to informing specific juniper removal prescriptions.

Continuing concern over sage-grouse population trends has prompted habitat restoration projects across the Great Basin focused on providing habitat suitable for breeding sage-grouse (Reinhardt et al. 2020). At broad spatial scales, there is a high percentage of overlap between sage grouse and sagebrush songbird distributions (Donnelly et al. 2017, Zeller et al. 2021). However, comparatively less attention has been paid to sagebrush songbird population declines and understanding the potential for habitat restoration to benefit this group. Our study represents one of the first large scale (~ 15,000 ha) BACI study designs to test the effect of juniper removal on sagebrush songbirds. Because populations of sagebrush songbirds are declining and habitat requirements for sagebrush songbirds and breeding sage grouse are similar at course spatial scales (Carlisle et al. 2018a), targeting restoration in sagebrush habitat to support both sage grouse and songbird populations gives managers a proverbial “two birds with one stone” opportunity. However, some management practices undertaken to support sage grouse (e.g., mowing) can be detrimental for sagebrush songbirds, and not all species that use sagebrush habitat select areas suitable for sage-grouse (Carlisle et al. 2018a, Carlisle et al. 2018b). To support both sage grouse and songbirds, managers should assess shrub structure at fine spatial scales as well as considering the composition of the local sagebrush songbird community and the spatial response of individuals to remaining conifer. For example, Brewer’s sparrow is more tolerant of juniper than sage thrasher but requires a high density of medium-volume sagebrush shrubs (~ 30 – 200 cm^3) for nesting (Chalfoun and Martin 2007). Sage thrashers are sensitive to juniper at small spatial scales, whereas green-tailed towhees may prefer the presence of juniper, but conversely are associated with tall, dense shrubs of large volume. Therefore, targeting sagebrush habitat for restoration that features a mosaic of shrub structure (e.g. areas of small dense shrubs interspersed with larger tall shrubs) would be more likely to successfully support populations of shrub-nesting songbirds (Fuhlendorf et al. 2017).

Plant invasions and woody-plant expansion are likely to continue to alter sagebrush habitat (Polley et al. 2017). Although some localized reductions in conifer forest area have naturally occurred due to drought, recent research estimates that conifer woodlands continue to expand across the Great Basin at a rate of 0.46% per year (Filippelli et al. 2020). Changes to sagebrush ecosystem function caused by conifer expansion, including hydrology and nitrogen sequestration, can lead to lower biomass or species richness for native plants (Archer et al. 2017). Changes to vegetation and increased fire risk in conifer woodlands can lower system resilience and facilitate invasions by non-native plant species, further altering the sagebrush steppe (Weltz et al. 2014). Combined with losses of sagebrush habitat to human development and more frequent, intense, and larger fires, conifer expansion contributes to habitat degradation for shrub nesting songbirds. Our study highlights how habitat selection operates at different scales for species that are considered to have similar habitat associations and lifestyles. Our study also suggests that sagebrush songbirds may respond quickly to habitat restoration if the scale of conifer removal and the characteristics of shrub cover are considered. However, because we only have one year of post-treatment data, further research is warranted. Given the fact that conifer expansion is likely to continue, targeted restoration should be considered an important part of conserving sagebrush songbird populations.

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Table 4.1. Number of points surveyed for songbirds by year and associated conifer cover category in southwest Idaho, 2017-2020. Conifer was removed from ~ 15,000 ha in fall of 2019, affecting 55 of our survey points.

		Juniper Cover			
Year	**Survey Points**	**0%**	**1-10%**	**10-20%**	**>20%**
2017	87	21	40	18	8
2018	111	21	60	19	11
2019	111	22	59	19	11
2020	111	58	32	10	11

Table 4.2. Habitat variables used to test the effects of shrub characteristics and juniper cover for Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee (*Pipilo chlorurus*) in southwest Idaho, 2017-2020.

Model
[1]Density
[2]Height
[3]Volume
Juniper % Cover
Density + Juniper % Cover
Height + Juniper % Cover
Volume + Juniper % Cover
Density*Juniper % Cover
Height*Juniper % Cover
Volume*Juniper % Cover
Density + Height
Density*Height
Density + Volume
Density*Volume
Density + Height + Juniper % Cover
Density*Juniper % Cover + Height
Density + Height*Juniper % Cover
Density + Volume + Juniper % Cover
Density*Juniper % Cover + Volume
Density + Volume*Juniper % Cover
Density + Volume + Height + Juniper % Cover
Null

[1] Density (m^2) of *Artemisia tridentata*
[2] Mean height (cm) of *Artemisia tridentata*
[3] Mean volume (cm^3) *Artemisia tridentata*

Table 4.3. Top models predicting density for Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee (*Pipilo chlorurus*) in southwest Idaho, 2017-2020. We used N-mixture models to test the effect of shrub characteristics and juniper cover on densities of sagebrush songbirds. We ranked models using Akaike's Information Criterion. This table includes only models with a ΔAIC of less than two for each species.

Model	**K**[1]	**AIC**[2]	**ΔAIC**[3]	**Wt**[4]
Brewer's Sparrow				
TR Den[5]*Juoc 500 m[6] + Avg. TR Height[7]	10	3494.79	0.00	0.62
Sage Thrasher				
Juoc [8]100 m	7	514.99	0.00	0.30
[9]Avg. TR Vol. + Juoc 100 m	8	516.57	1.59	0.43
TR Den. + Juoc 100 m	8	516.88	1.89	0.55
Avg. TR Height + Juoc 100 m	8	516.96	1.97	0.66
Green-tailed Towhee				
TR Den. + Avg. TR Vol.*[10]Juoc 1000 m	10	1904.60	0.00	0.21
TR Den. + Avg. TR Vol. + Juoc 1000 m	9	1904.69	0.08	0.41
TR Den. + Avg. TR Height + Juoc 1000 m	9	1905.37	0.76	0.55
TR Den.*Juoc 1000 m + Avg. TR Vol.	10	1905.93	1.32	0.66
TR Den. + Avg. TR Height*Juoc 1000 m	10	1905.98	1.38	0.77
TR Den.*Juoc 1000 m + Avg. TR Height	10	1906.14	1.54	0.86

[1] # of model parameters, [2] Akaike's Information Criteron score, [3] Difference between the top score, [4] Cumulative model weight, [5] Density/m^2 of *Artemisia tridentata*, [6] *Juniperus occidentalis* % cover within 500 m, [7] Average height of *Artemisia tridentata*, [8] *Juniperus occidentalis* % cover within 100 m, [9] Average volume of *Artemisia tridentata*, [10] *Juniperus occidentalis* % cover within 1000 m

Table 4.4. Correlation of variables with axes from a non-metric dimensional scaling ordination of songbird density (*n* = 111 survey points) in southwest Idaho, 2017-2020. The sagebrush songbird variable is the mean axis values for Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee (*Pipilo chlorurus*). The conifer songbird is the mean axis values for chipping sparrow (*Spizella passerina*), Cassin's finch (*Haemorhous cassinii*), dark-eyed junco (*Junco hyemalis*), mountain chickadee (*Poecile gambeli*), hermit thrush (*Catharus guttatus*), black-throated grey warbler (*Setophaga nigrescens*), and western tanager (*Piranga ludoviciana*). Pre-juniper removal coefficients represents the average scores from 2017-2019. The Post-juniper removal coefficients represent scores from 2020 after juniper was removed from ~15,000 ha of our study site.

Variable	**Correlation coefficient**	
	Axis 1	Axis 2
Pre-juniper removal		
Sagebrush songbirds	0.07	0.56
Conifer songbirds	0.28	-0.39
Big sagebrush volume	0.95	-0.30
Big sagebrush density	0.74	0.66
Juniper cover	0.99	-0.04
Big sagebrush height	0.76	-0.63
Post-juniper removal		
Sagebrush songbirds	-0.03	-0.44
Conifer songbirds	0.98	0.47
Big sagebrush volume	0.98	-0.16
Big sagebrush density	0.99	-0.10
Juniper cover	0.43	-0.90
Big sagebrush height	-0.21	0.97

Table 4.5. Yearly estimates of sagebrush-associated songbirds (individuals/ha) in southwest Idaho, 2017-2020. We used N-mixture models with year as a covariate to estimate density at 111 point-count locations. Sage thrasher (*Oreoscoptes montanus*) detections were too sparse to allow estimation of density.

Species	**2017**	**2018**	**2019**	**2020**
Brewer’s Sparrow	2.45 ± SE 0.35	3.70 ± SE 0.39	3.38 ± SE 0.34	5.05 ± SE 0.45
Green-Tailed Towhee	1.10 ± SE 0.32	0.97 ± SE 0.23	1.48 ± SE 0.30	2.01 ± SE 0.39

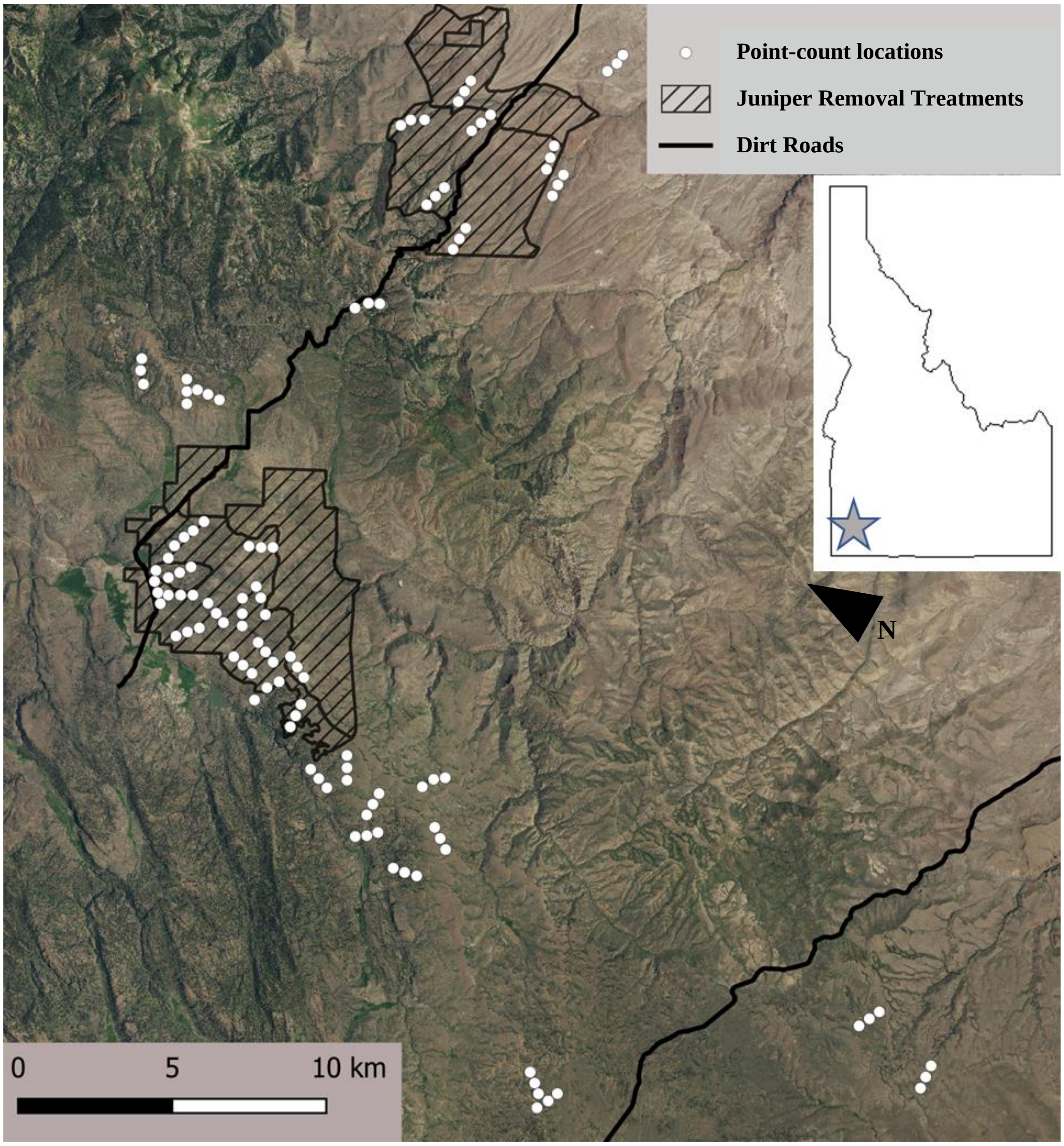

Figure 4.1. Our study occurred in the Owyhee Mountains of southwestern Idaho. Surveys took place 2017-2020 at 100-m radius survey points (*n* = 111) inside and outside areas of juniper removal which occurred in the fall of 2019.

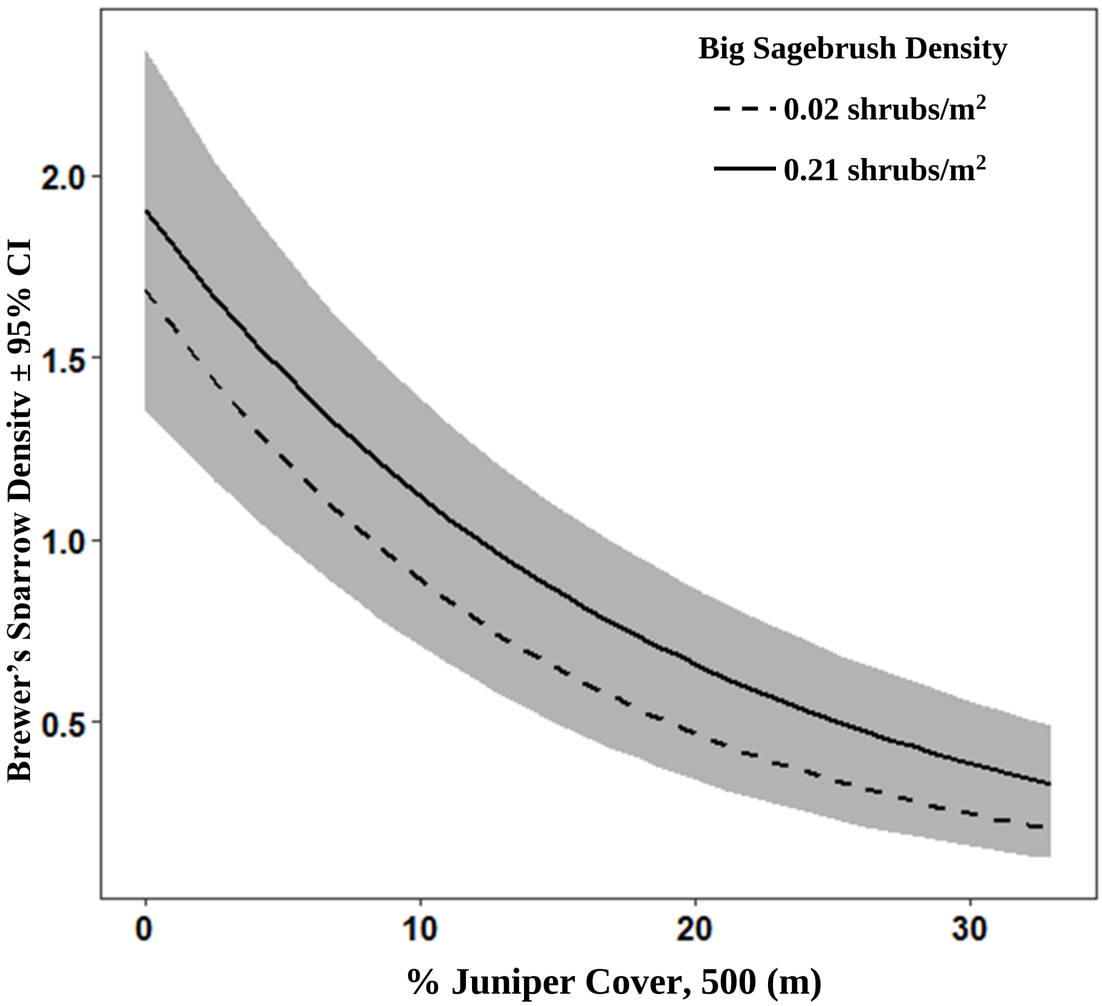

Figure 4.2. Predicted effect of percent cover of western juniper (*Juniperus occidentalis*) and big sagebrush (*Artemisia tridentata*) on Brewer's sparrow (*Spizella breweri*) density in southwest Idaho, 2017-2020 where juniper removal occurred in fall 2019. We conducted point counts at 111 survey points and used N-mixture models to test the effect of habitat characteristics on songbird density. We then ranked models using Akaike's Information Criterion.

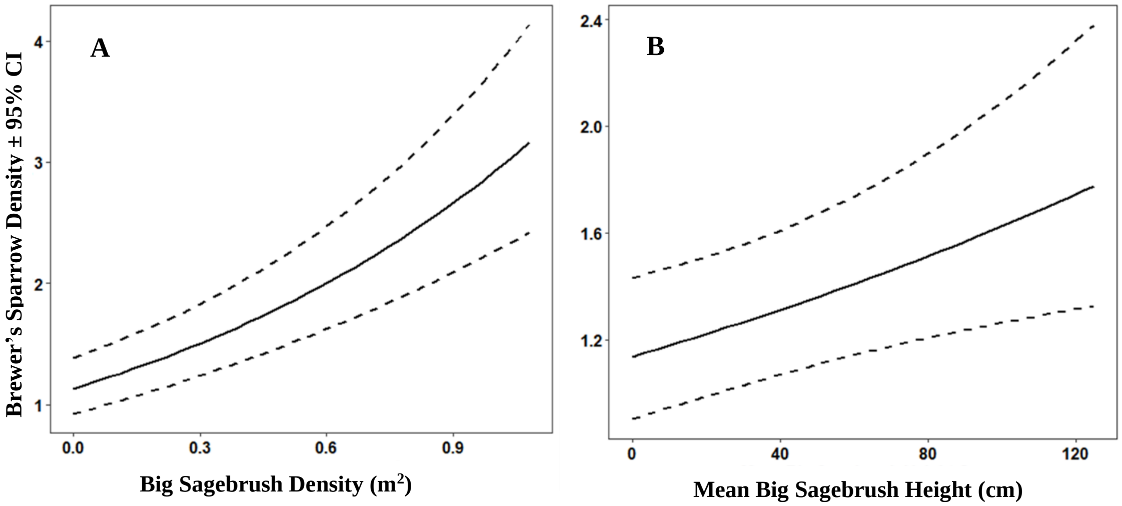

Figure 4.3. Predicted effects of (A) big sagebrush (*Artemisia tridentata*) density and (B) mean height on Brewer's sparrow (*Spizella breweri*) density/ha in southwest Idaho, 2017-2020. We conducted point counts at 111 survey points and used N-mixture models to test the effect of habitat characteristics on songbird density. We then ranked models using Akaike's Information Criterion.

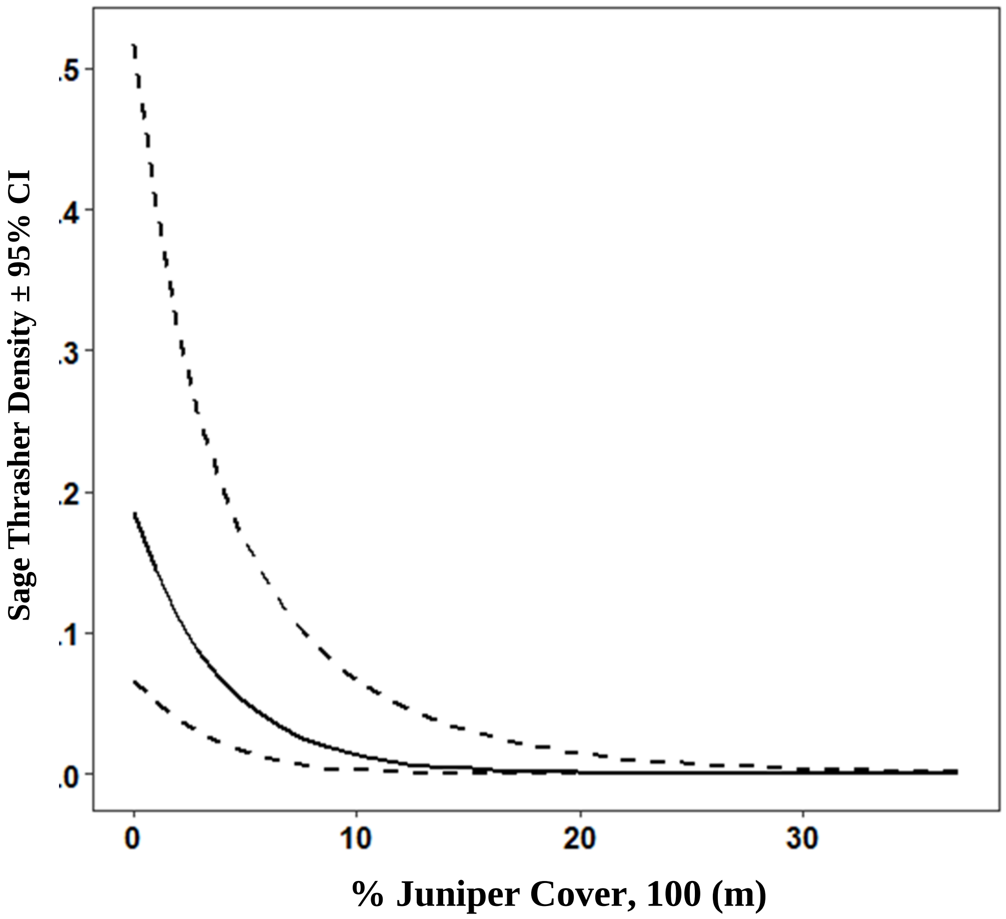

Figure 4.4. Predicted effect of percent cover of western juniper (*Juniperus occidentalis*) on sage thrasher (*Oreoscoptes montanus*) individuals/ha in southwest Idaho, 2017-2020. We conducted point counts at 111 survey points and used N-mixture models to test the effect of habitat characteristics on songbird density. We then ranked models using Akaike's Information Criterion.

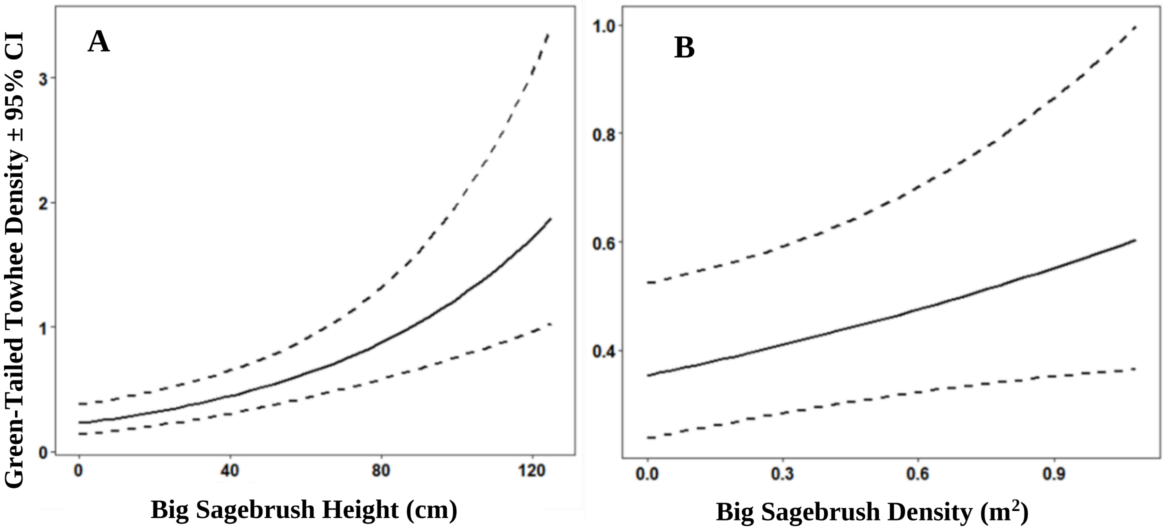

Figure 4.5. Predicted effect of big sagebrush (*Artemisia tridentata*) (A.) mean height and (B.) density on green-tailed towhee (*Pipilo chlorurus*) density/ha in southwest Idaho, 2017-2020. We conducted point counts at 111 survey points and used N-mixture models to test the effect of habitat characteristics on songbird density. We then ranked models using Akaike's Information Criterion.

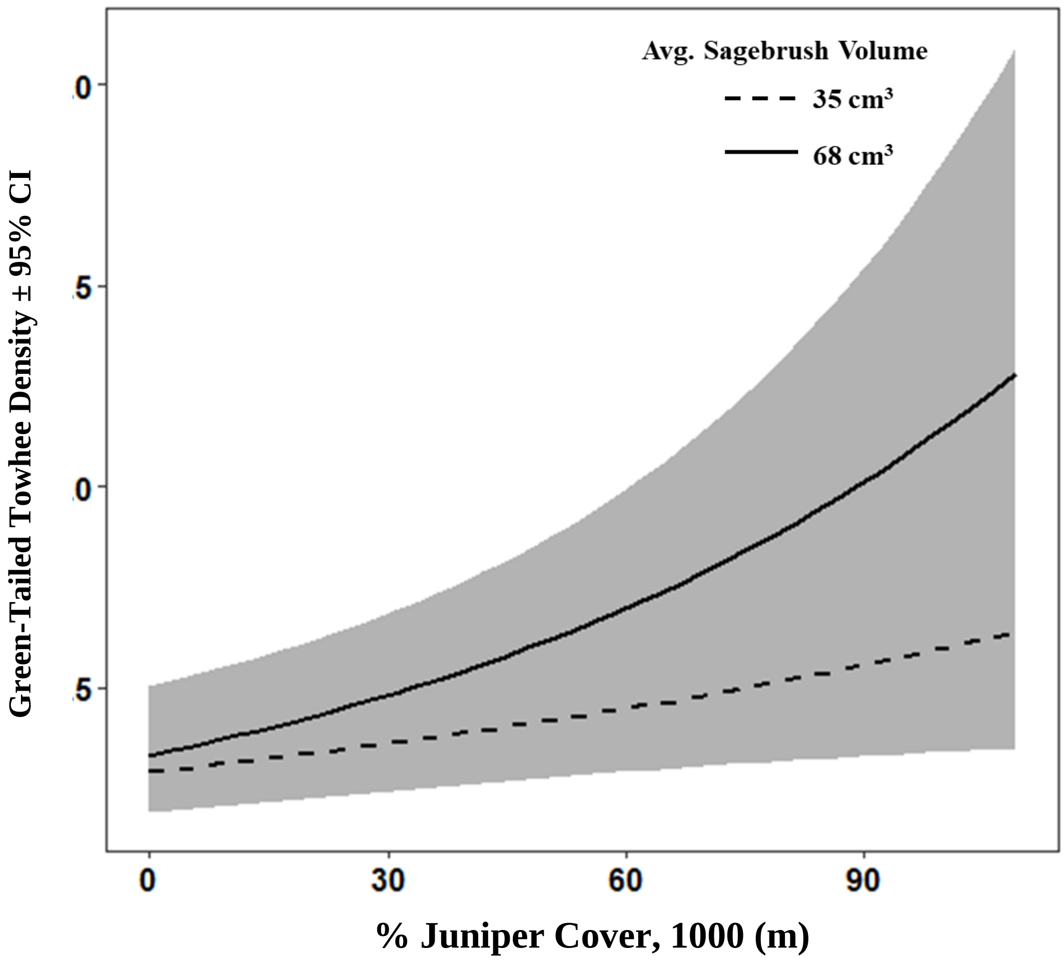

Figure 4.6. Predicted effect of percent cover of western juniper (*Juniperus occidentalis*) and mean volume of big sagebrush (*Artemisia tridentata*) on green-tailed towhee (*Pipilo chlorurus*) density/ha in southwest Idaho, 2017-2020. We conducted point counts at 111 survey points and used N-mixture models to test the effect of habitat characteristics on songbird density. We then ranked models using Akaike's Information Criterion.

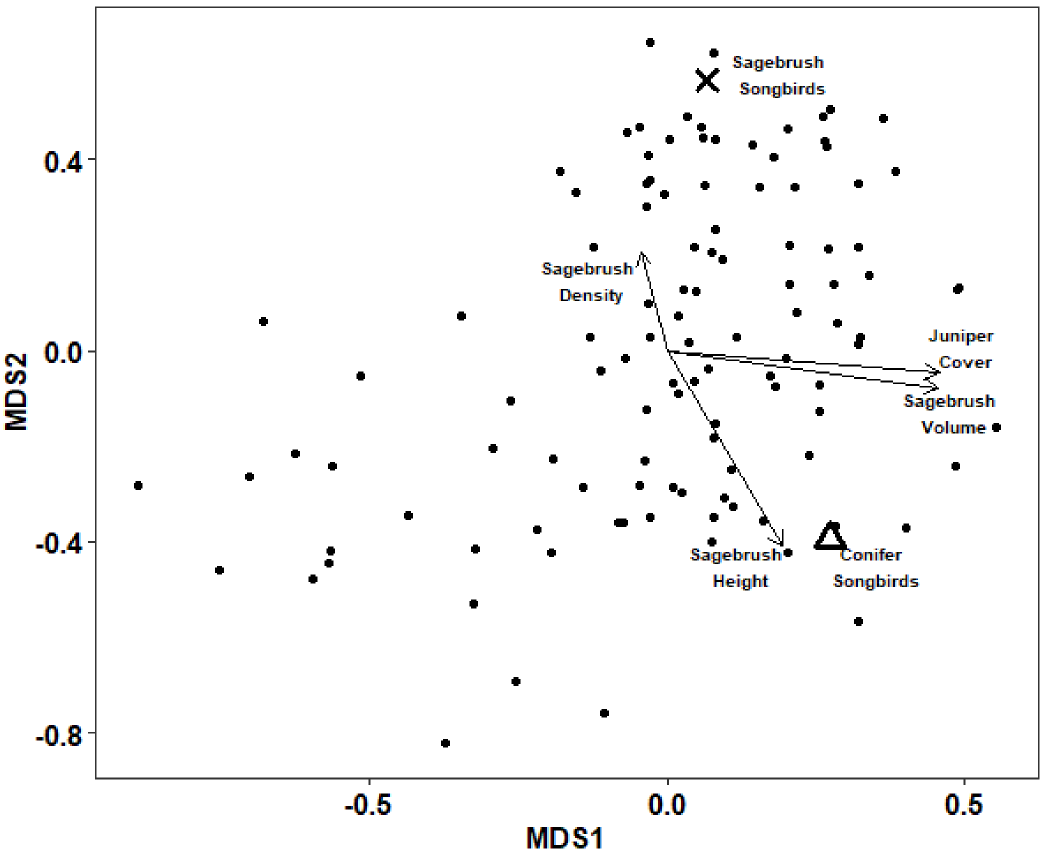

Figure 4.7. We used non-metric multidimensional scaling to elucidate relationships between songbird point count data collected prior to juniper removal in southwest Idaho 2017-2019 and habitat characteristics. Dots represent survey points ($n = 111$) in species space and arrows represent habitat characteristics overlaid onto the final ordination big sagebrush (*Artemisia tridentata*) density (m^2), mean volume (cm^3), and mean height (cm), and percent cover of western juniper (*Juniperus occidentalis*). The 'X' represents the mean species space for the group of sagebrush associated songbirds which includes Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee (*Pipilo chlorurus*). The triangle is the mean species space for the conifer associated community which includes chipping sparrow (*Spizella passerina*), Cassin's finch (*Haemorhous cassinii*), dark-eyed junco (*Junco hyemalis*), mountain chickadee (*Poecile gambeli*), hermit thrush (*Catharus guttatus*), black-throated grey warbler (*Setophaga nigrescens*), and western tanager (*Piranga ludoviciana*).

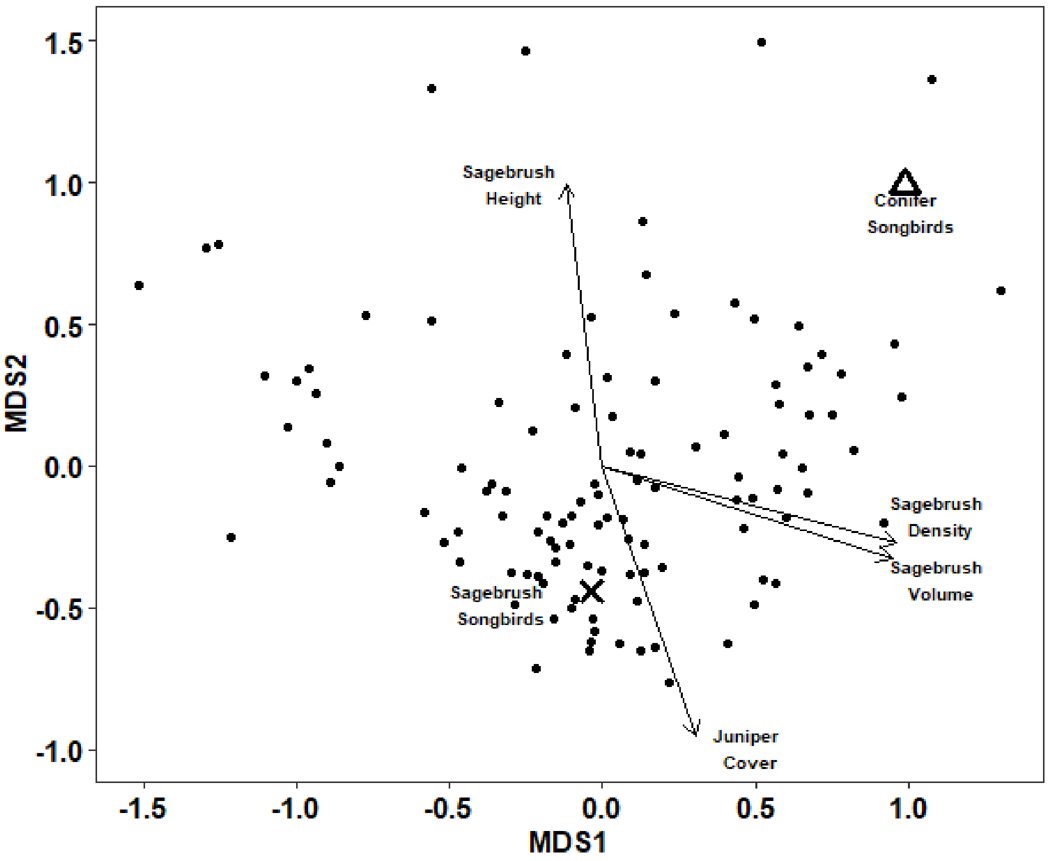

Figure 4.8. Ordination of songbird community composition in response to habitat characteristics after removal of western juniper in southwest Idaho during 2019. Dots represent survey points (*n* = 111) and arrows represent habitat gradients. We used count data and habitat characteristics to conduct a non-metric multidimensional scaling. We then fit environmental gradients for big sagebrush (*Artemisia tridentata*) density/m^2, mean volume cm^3, mean height cm, and percent cover of western juniper (*Juniperus occidentalis*). The 'X' represents the mean species space for the group of sagebrush associated songbirds which includes Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee (*Pipilo chlorurus*). The triangle is the mean species space for the conifer associated community which includes chipping sparrow (*Spizella passerina*), Cassin's finch (*Haemorhous cassinii*), dark-eyed junco (*Junco hyemalis*), mountain chickadee (*Poecile gambeli*), hermit thrush (*Catharus guttatus*), black-throated grey warbler (*Setophaga nigrescens*), and western tanager (*Piranga ludoviciana*).

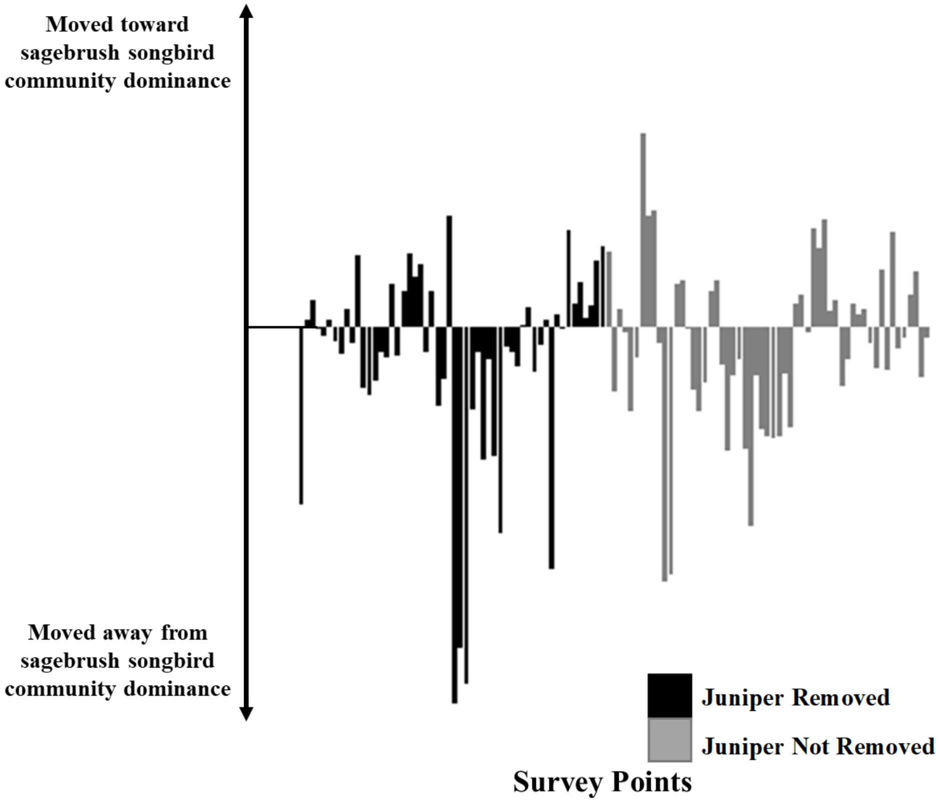

Figure 4.9. Changes in songbird community composition in 2020 after removal of juniper from sagebrush communities in southwest Idaho that occurred fall of 2019. We calculated the Euclidian distance of each survey location (*n* = 111) from the mean centroid of sagebrush songbirds in a two-axis non-metric dimensional scaling ordination space for the three years prior to juniper removal (2017-2019) as well as the year following juniper removal (2020). For each survey point (juniper removal = 54 points, no juniper removal = 57 points) we then calculated the change in Euclidian distance from the mean centroid of sagebrush songbirds between 2017-2019 and 2020. Negative values indicate that the proportion of the songbird community composed of sagebrush-associated songbirds declined or did not change after juniper removal. Positive values indicate that the proportion of the community composed of sagebrush-associated songbirds increased at a location after juniper removal.

Appendix C

Table C1. Ranking of models predicting density for Brewer's sparrow (*Spizella breweri*) in southwest Idaho, 2017-2020. We used N-mixture models to test the effect of shrub characteristics and juniper cover on sagebrush songbird densities. We ranked models using Akaike's Information Criterion.

Model	**K**[1]	**AIC**[2]	**ΔAIC**[3]	**Wt**[4]
TR Den[5]*Juoc 500 m[6] + Avg. TR Height[7]	10	3494.79	0.00	0.62
TR Den + Avg. TR Vol.[8]*Juoc 500 m	10	3496.87	2.08	0.84
TR Den*Juoc 500 m + Avg. TR Vol.	10	3498.06	3.26	0.96
TR Den*Juoc 500 m	9	3500.34	5.55	1.00
TR Den + Avg. TR Height*Juoc 500 m	10	3505.10	10.31	1.00
TR Den + Avg. TR Height + Juoc 500 m	9	3513.20	18.41	1.00
TR Den + Avg. TR Vol. + Avg. TR Height +Juoc 500 m	10	3514.15	19.36	1.00
TR Den + Avg. TR Vol. + Juoc 500 m	9	3516.96	22.17	1.00
TR Den + Juoc 500 m	8	3521.21	26.42	1.00
Avg. TR Vol.*Juoc 500 m	9	3537.91	43.12	1.00
Avg. TR Height*Juoc 500 m	9	3555.87	61.08	1.00
Avg. TR Vol. + Juoc 500 m	8	3563.97	69.17	1.00
Avg. TR Height + Juoc 500 m	8	3569.52	74.72	1.00
TR Den*Avg. TR Height	9	3572.30	77.50	1.00
TR Den*Avg. TR Vol.	9	3572.61	77.82	1.00
TR Den + Avg. TR Height	8	3576.91	82.12	1.00
TR Den + Avg. TR Vol.	8	3577.31	82.52	1.00
Juoc 500 m	7	3581.52	86.73	1.00
TR Den	7	3585.88	91.09	1.00
Avg. TR Vol.	7	3606.64	111.85	1.00
Avg. TR Height	7	3615.10	120.31	1.00
Null	6	3629.22	134.43	1.00

[1] # of model parameters, [2] Akaike's Information Criteron score, [3] Difference between the top score, [4] Cumulative model weight, [5] Density/m^2 of *Artemisia tridentata,* [6] *Juniperus occidentalis* % cover within 500 m, [7] Average height of *Artemisia tridentata,* [8] Average volume of *Artemisia tridentata*

Table C2. Ranking of models predicting density for sage thrasher (*Oreoscoptes montanus*) in southwest Idaho, 2017-2020. We used N-mixture models to test the effect of shrub characteristics and juniper cover on sagebrush songbird densities. We ranked models using Akaike's Information Criterion.

Model	[1]**K**	[2]**AIC**	[3]**ΔAIC**	[4]**Wt**
[5]Juoc 100 m	7	514.99	0.00	0.30
[6]Avg. TR Vol. + Juoc 100 m	8	516.57	1.59	0.43
[7]TR Den. + Juoc 100 m	8	516.88	1.89	0.55
[8]Avg. TR Height + Juoc 100 m	8	516.96	1.97	0.66
TR Den. + Avg. TR Vol. + Juoc 100 m	9	518.54	3.55	0.71
Avg. TR Vol.*Juoc 100 m	9	518.56	3.57	0.76
TR Den. *Juoc 100 m	9	518.63	3.64	0.81
Avg. TR Height*Juoc 100 m	9	518.73	3.74	0.85
TR Den. + Avg. TR Height + Juoc 100 m	9	518.86	3.87	0.90
TR Den. + Avg. TR Vol. + Avg. TR Height + Juoc 100 m	10	519.74	4.75	0.92
TR Den. *Juoc 100 m + Avg. TR Vol.	10	520.31	5.33	0.95
TR Den. + Avg. TR Vol.*Juoc 100 m	10	520.52	5.53	0.96
TR Den. *Juoc 100 m + Avg. TR Height	10	520.61	5.63	0.98
TR Den. + Avg. TR Height *Juoc 100 m	10	520.63	5.64	1.00
Null	6	552.72	37.73	1.00
Avg. TR Vol.	7	552.84	37.86	1.00
TR Den.	7	553.48	38.49	1.00
TR Den. *Avg. TR Vol.	9	554.10	39.11	1.00
Avg. TR Height	7	554.25	39.26	1.00
TR Den. + Avg. TR Vol.	8	554.36	39.37	1.00
TR Den. + Avg. TR Height	8	555.25	40.26	1.00
TR Den. *Avg. TR Height	9	557.12	42.14	1.00

[1] # of model parameters, [2] Akaike's Information Criteron score, [3] Difference between the top score, [4] Cumulative model weight, [5] *Juniperus occidentalis* % cover within 100 m, [6] Average volume of *Artemisia tridentata*, [7] Density/m^2 of *Artemisia tridentata*, [8] Average height of *Artemisia tridentata*

Table C3. Ranking of models predicting density for green-tailed towhee (*Pipilo chlorurus*) in southwest Idaho, 2017-2020. We used N-mixture models to test the effect of shrub characteristics and juniper cover on sagebrush songbird densities. We ranked models using Akaike's Information Criterion.

Model	[1]**K**	[2]**AIC**	[3]**ΔAIC**	[4]**Wt**
[5]TR Den. + [6]Avg. TR Vol.*[7]Juoc 1000 m	10	1904.60	0.00	0.21
TR Den. + Avg. TR Vol. + Juoc 1000 m	9	1904.69	0.08	0.41
TR Den. + [8]Avg. TR Height + Juoc 1000 m	9	1905.37	0.76	0.55
TR Den.*Juoc 1000 m + Avg. TR Vol.	10	1905.93	1.32	0.66
TR Den. + Avg. TR Height*Juoc 1000 m	10	1905.98	1.38	0.77
TR Den.*Juoc 1000 m + Avg. TR Height	10	1906.14	1.54	0.86
Avg. TR Vol.*Juoc 1000 m	9	1907.03	2.42	0.93
Avg. TR Vol. + Juoc 1000 m	8	1907.66	3.06	0.97
Avg. TR Height*Juoc 1000 m	9	1910.37	5.77	0.98
Avg. TR Height + Juoc 1000 m	8	1910.81	6.20	0.99
TR Den. + Juoc 1000 m	8	1912.90	8.30	1.00
TR Den.*Juoc 1000 m	9	1914.16	9.55	1.00
TR Den.*Avg. TR Height	9	1916.82	12.21	1.00
Juoc 1000 m	7	1918.60	13.99	1.00
TR Den.*Avg. TR Vol.	9	1918.79	14.18	1.00
TR Den. + Avg. TR Vol.	8	1920.33	15.72	1.00
TR Den. + Avg. TR Height	8	1920.69	16.09	1.00
Avg. TR Vol.	7	1924.08	19.48	1.00
Avg. TR Height	7	1927.62	23.02	1.00
TR Den.	7	1927.76	23.16	1.00
Null	6	1934.68	30.07	1.00

[1] # of model parameters, [2] Akaike's Information Criteron score, [3] Difference between the top score, [4] Cumulative model weight, [5] Density/m^2 of *Artemisia tridentata*, [6] Average volume of *Artemisia tridentata*, [7] *Juniperus occidentalis* % cover within 1000 m, [8] Average height of *Artemisia tridentata*

Closing Remarks

Conifer expansion is likely to continue, and the negative consequences of conifer expansion for sagebrush-associated species make conifer removal an important tool for wildlife managers. This dissertation highlights ways that three important groups may be affected by conifer removal. Increased occupancy of common ravens associated with juniper woodlands has implications for many prey groups, including small mammals, songbirds, and greater sage-grouse. The effectiveness of conifer removal for reducing habitat use by ravens requires further research because our data only examines occupancy rates for one year following juniper removal. Further research is also warranted concerning the relationship between ravens and juniper woodlands that remain on the landscape. Woodlands with cover >20% (phase 3) were not cut as part of the removal project at our site. Though this management decision is likely beneficial for species such as conifer-nesting songbirds that contribute to landscape diversity, the strong relationship that we observed with ravens and juniper woodlands suggests that remaining woodlands may influence use of treated sagebrush habita by ravens. Given the fact that conifer removal was justified as a conservation tool to support sage grouse populations, further research is needed to assess how ravens use a landscape with reduced, but not eliminated, conifer.

Increased densities of deer mice associated with habitat featuring 10% juniper cover suggest that the removal of juniper to <10% cover may lead to lower densities of this generalist omnivore and predator. Decreased densities of deer mice may be beneficial for sagebrush songbirds, a group that deer mice commonly prey on. Reduced densities of deer mice may also alter habitat use and densities of other species in the small mammal group, including the Great Basin pocket mouse. Our data demonstrate evidence for density-dependent interactions between these two species because pocket mouse home range decreases as deer mouse densities increase. Reduced home-range size for pocket mouse may limit access to resources including food and protection from predation, thereby lowering habitat quality. However, we were not able to directly test this possibility, and further research may shed light on how interspecific interactions may be mediated by habitat conditions.

Our study shows that conifer removal will likely contribute to increases in density for two sagebrush-obligate songbirds, Brewer’s sparrow and sage thrasher. However, the positive relationship between density of green-tailed towhee, a sagebrush/ecotone species, and juniper cover suggests that conifer removal may negatively impact this species. Again, further study is warranted in this case because the density of green-tailed towhees increased following conifer removal. Further, greater density, volume, and height of sagebrush shrubs was associated with increased densities of green-tailed towhee. Given the fact that shrub structure is likely to increase in size and density following juniper removal, any negative effects of conifer removal may be ameliorated for green-tailed towhee.