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Effects of road presence and habitat covariates on sagebrush obligate bird density

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EFFECTS OF ROAD PRESENCE AND HABITAT COVARIATES ON SAGEBRUSH OBLIGATE BIRD DENSITIES

by

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Binghamton University (B.A.)

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Effects of road presence and habitat covariates on sagebrush obligate bird densities

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ABSTRACT Within the sagebrush steppe ecosystem in the intermountain west, sagebrush obligate birds occupy a variety of specialized niches. The purpose of our research was to identify the effect of road presence and habitat covariates on the density of sagebrush obligate birds during their breeding season. Roads through sagebrush threaten local bird abundance through anthropogenic disturbance and habitat fragmentation (Knick et al. 2012). However, research in the sagebrush steppe has historically focused on Sage-grouse; in our study area specifically, Gunnison Sage-grouse (*Centrocerus* minimus) (Young et al. 2020). Sagebrush obligate and near-obligate songbirds include the Brewer's sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), green-tailed towhee (*Pipilo chlorusus*), and vesper sparrow (*Pooecetes gramineus*). We assessed avian density in response to road presence and four habitat covariates at an approximate individual bird territory scale (3.14 ha or the area of a 100 m buffer around a survey point). We found that the effect of road presence varied between our study species but overall it was not a significant relationship. Additionally, we found that increased vegetation heights over 2 m were consistently associated with declines in our study species' densities and that increased shrub cover consistently increases study species densities. These findings indicate the importance of species specific monitoring in relation to habitat fragmentation and territory patch scale habitat conditions in sagebrush steppe ecosystems.

KEY WORDS Brewer's sparrow, Colorado, distance sampling, green-tailed towhee, Gunnison Basin, *Oreoscoptes montanus, Pipilo chlorusus, Pooecetes gramineus*, road presence, sage thrasher, sagebrush, *Spizella breweri*, vesper sparrow

The Gunnison Basin, located in southwestern Colorado within the intermountain west, contains over 500,000 acres (202,343 ha) of montane sagebrush (Rondeau et al. 2017), and is home to several sagebrush obligate bird species, most notably the federally threatened Gunnison sage-grouse (*Centrocercus minimus*). Conservation of sagebrush habitat is vital for this species and is the primary driver of wildlife program funding within the basin (K. Brodhead, Bureau of Land Management, personal communication). Sage-grouse require a mosaic of sagebrush to survive and raise their young (Phillips et al. 2020). For the last fifty years many bird populations have been declining across North America (Sauer et al. 2017), but some of the sharpest declines have occurred in shrubland obligate birds. Gunnison sage-grouse populations have continued to decline, with only 2,736 individuals estimated in 2020, 2,361 of which are within the Gunnison Basin (Colorado Parks and Wildlife, unpublished report). This could indicate that other sagebrush obligate bird species are also facing serious population declines. However, literature shows that using sage-grouse as an umbrella species is flawed because sagebrush obligate species are affected by sagebrush habitat fragmentation differently and to varying extents (Rowland et al. 2006). This work aims to address the lack of information surrounding sagebrush obligate bird populations and how road presence and habitat fragmentation impact them.

It may be necessary to collect information about all species to accurately monitor populations and to monitor conservation efficacy for sagebrush obligate species (Knick et al. 2003). There is little literature focusing on sagebrush obligate passerine birds across their ranges and there is even less about these birds that occupy the same range as the Gunnison sage-grouse. The Gunnison Basin sagebrush ecosystem is home to three other sagebrush obligate bird species during the breeding season: Brewer’s sparrow (*Spizella breweri*), sagebrush sparrow (*Artemisiospiza nevadensis*), and sage thrasher (*Oreoscoptes montanus*) (Boyle and Reeder

2005). Additionally, the green-tailed towhee (*Pipilo chlorusus*) and vesper sparrow (*Pooecetes gramineus*) are considered near obligates because when these species breed in the Gunnison Basin they primarily use sagebrush habitat (Wickerman 2016) . Within the Gunnison Basin, the population trends of these 5 sagebrush bird species (excluding Gunnison sage-grouse) have not been quantified reliably. Brewer's sparrow, sagebrush sparrow, sage thrasher, vesper sparrow, and green-tailed towhee are all listed as "Species of Concern" in by Colorado Parks and Wildlife (Boyle and Reeder 2005). With shrubland obligate birds facing widespread population declines it is important to monitor these sagebrush obligate species' population trends locally.

Population Trends

Brewer's sparrow global populations have decreased by over 50% since 1980 (Sauer et al. 2017) and in Colorado alone they decreased by 1.5% annually between 1993 and 2019 (Sauer et al. 2020). The Brewer's sparrow is the most abundant bird in the sagebrush ecosystem and has been designated a "common species in steep decline" by the Partners in Flight Tri-National Vision (Berlanga et al. 2010). About 7% the of sage thrasher global population breeds within Bird Conservation Region (BCR) 16, known as the Southern Rockies and Colorado Plateau, and sage thrashers have been identified as a species of regional concern by Partners in Flight (Population Estimates Database, version 3.1 2020). Green-tailed towhees have undergone a 1% annual population decline within Colorado between 1966 and 2003 (Sauer et al. 2020) and 52% of their global population breeds within BCR 16 (Population Estimates Database, version 3.1 2020). While only 5% of the global Vesper sparrow population breeds within BCR 16, it has been listed as a species of regional concern (Population Estimates Database, version 3.1 2020).

About 10% of the Sagebrush Sparrow global population breeds within BCR 16 and the species has a "regional concern" designation by Partners in Flight (Population Estimates Database, version 3.1 2020). Sagebrush sparrows are relatively rare in the Gunnison Basin, which has a lowest elevation point of 2,280 m, and throughout our study sagebrush sparrows had too few detections for robust statistical analyses, only 55 total detections from 2018-2020.

Breeding Habitat Selection

Sagebrush birds interact with their habitat at broad geographical scales. Habitat selection is hierarchical (Johnson 1980) and is variable even among ecologically similar species, and can be influenced by a variety of extrinsic factors and adaptive behavior (Jones 2001). The selection process begins with suitable geographical range, then a home range followed by a territory and finally, during the breeding season, a nesting site (Kristan et al. 2007). For the sagebrush obligate birds in the Gunnison Basin their geographical ranges during breeding are varied throughout the intermountain west (Dobbs et al. 2020, Jones and Cornely 2020, Reynolds et al. 2020, Rotenberry et al. 2020). Because home ranges vary by individual or individual social groups of birds, this scale is difficult to quantify (Johnson 1980) but for our study we can safely assume our study species' breeding home ranges at least fall within the Gunnison Basin.

Territory size varies among the 5 sagebrush obligate bird species. Brewer's sparrows occupy territories ranging from 0.6 -2.4 ha and males typically forage within 50 m of their nest site (Rotenberry et al. 2020). Sagebrush Sparrow territory size data are lacking in Colorado, but for the estimate from one study in Utah territory size averaged 1.5 ± 0.23 ha (Martin and Carlson 2020). Sage thrashers in Idaho (the closest study to our site) defended territories that averaged 0.96 ± 12 ha (Reynolds et al. 2020). Green-tailed towhees in shrub-steppe habitats in Utah average 0.9 ha territories (Dobbs et al. 2020). Vesper sparrow territory size ranges from 0.3 - 8.2 ha, with larger territories more common when food is scarce or widely dispersed (Jones and Cornely 2020). Among sagebrush birds habitat structure, specifically herbaceous structure, within 0.2 ha of a point count survey site is known to strongly influence relative abundance (Paczek 2002). Since territory sizes across all of our study species have been shown to exhibit elasticity in relation to extrinsic factors such as resource availability, this scale (3.14 ha or 100 m radius surrounding a survey point) is the focus of our study. Within each territory, each sagebrush obligate bird species uses varying nesting microhabitats.

Habitat Fragmentation Due to Road Presence

Suitable habitat for Gunnison sage-grouse is negatively correlated with high volume paved roads and presence of residential developments (Aldridge et al. 2012). Intact, contiguous sagebrush landscapes are critical for sage-grouse (Knick et al. 2003) and may be important for other sagebrush obligate birds (Holmes et al. 2005). Therefore, sagebrush habitat fragmentation is detrimental to sagebrush obligates (Knick et al. 2003). For example, within 100 m of a road, Brewer's sparrow and Bell's sparrow density decreased between 39% and 60% (Ingelfinger and Anderson 2004). In other habitats, breeding bird territory establishment has been shown to be negatively impacted by human recreation (Bötsch et al. 2017) and that noise from car traffic can reduce bird abundance within 250 m of a road (Reijnen et al. 1995). These studies focused on how the combined effects of habitat disturbances impact sagebrush obligates but there is little information about how road presence with low traffic volume impacts sagebrush obligate bird densities. Low traffic volume is defined as fewer than 400 cars per day, a designation which includes the majority of roads through public lands in Colorado (Colorado Department of Transportation 2018).

In sagebrush communities the presence of secondary roads, unpaved roads with low traffic volumes, creates fragmented habitat which reduces continuity of shrub canopy cover, increases openings and bare ground, and facilitates the spread of invasive plant species which further degrade sagebrush habitats (Knick et al. 2012). Sagebrush habitat alteration, specifically removal of sagebrush (i.e. when establishing new roads), decreases Brewer's sparrow and Sage thrasher abundance (Braun et al. 2002). A study out of Switzerland showed that trail presence alone in forested areas does not impact bird abundance but human use does (Bötsch et al. 2018). Because the roads through our study sites have low daily use, our study focuses on the presence of roads as a vector of habitat fragmentation and their potential effect on sagebrush obligate bird density. Given that road use and habitat fragmentation have an impact on multiple breeding bird species, that the use of roads on public lands has doubled over the past 30 years (Off-Highway Vehicle Management On Public Lands, U.S. Department of the Interior 2008), that 70% of remaining sagebrush habitat is publically owned (Knick et al. 2003), and that bird species associated with sagebrush ecosystems are experiencing widespread declines (Holmes et al. 2005), the objectives of this project were to evaluate whether the presence of roads have an effect on breeding bird density and to determine which habitat factors are most influential on bird density.

STUDY AREA

The study took place in the Upper Gunnison River Basin (Figure 1) where the elevation ranges from 2,280 to 2,900 m and encompasses roughly 2,025 km^2; 80% of which was public land (Rondeau et al. 2017). The Gunnison Basin is one of three expansive and relatively intact sagebrush-dominated ecosystems left in Colorado (Boyle and Reeder 2005). The average annual precipitation was 26.2 cm, temperatures ranged from -13 ˚C to -6.9 ˚C over the year (Cooperative Climatological Data Summaries 2021). The dominant vegetation was sagebrush (*Artemisia* spp.), which varied in taxonomy and structure depending on elevation, slope and moisture. Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) occupied lower elevations in drier landscapes, whereas mountain big sagebrush (*Artemisia tridentat*a *vaseyana)* dominated higher and wetter elevations (Rondeau et al. 2017). Black sagebrush (*Artemisia nova*) is a low growing sagebrush common in the Gunnison Basin and occurs on drier sites with shallow soil (Johnston 2001). Upland regions consisted of rolling hills varying in slope from moderate to steep. Drainages divided these areas, some of which contained permanent streams whereas others had intermittent flows. Mesas are common with steep slopes and flat, broad tops (Candidate Conservation Agreement For the Gunnison sage-grouse, *Centrocercus minimus* Gunnison Basin Population 1997). Throughout the area there were small patches of montane grasslands, high elevation meadows, conifer and aspen patches, wet meadows and wetlands (Rondeau et al. 2017). Significant portions of the Gunnison Basin had been classified as Gunnison sage-grouse Priority Areas for Conservation (Candidate Conservation Agreement For the Gunnison sage-grouse, *Centrocercus minimus* Gunnison Basin Population 1997), to help conserve the threatened sage-grouse that is native to the Gunnison River Basin (Figure 1).

METHODS

This study uses three years of avian survey data (2018 – 2020) collected in sagebrush ecosystems in the Gunnison Basin. Surveys were selected using overlay sampling within the Integrated Monitoring in Bird Conservation Regions (IMBCR) program (Latif and Pavlacky 2020). Surveys were located in sagebrush habitat within lands managed by the BLM Gunnison Field Office and within the Gunnison Sage-grouse Priority Area for Conservation (GUSG PAC) (Stiver et al. 2016). All potential lands for survey were overlaid with the IMBCR 1 km^2 grids. The road presence overlay was created using all designated roads and trails within the Bureau of Land Management (BLM) Gunnison Field Office. Grids were classified as "roaded" or "unroaded" based on the presence or absence of roads within the 1 km^2 grids.

Sampling scale

Sampling for bird density and habitat covariates was estimated within a 100 m radius of each survey point (3.14 ha), an approximated territory size surrounding each plot. Survey points were organized in 1 km^2 grids with 16 survey points per grid, spaced 250 m apart and arranged in a 4 x 4 pattern according to IMBCR protocols (McLaren et al. 2019) (Figure 1).

Avian Point Counts

Following the IMBCR protocol, most of our surveys occurred from 1-25 June 2018, 2019 and 2020, with some grids being surveyed twice in 2018. This time period allowed non-breeding migrants to pass through the study area and spotlighted only breeding birds within the Gunnison Basin at elevations ranging from 1,981 – 2,438 m in Colorado according to IMBCR protocol (Hanni et al. 2014).

Surveys began 30 minutes before sunrise and ended no later than 5 hours after sunrise to ensure most consistent singing of breeding birds (Hanni et al. 2014). Bird surveys were conducted according to the IMBCR distance sampling protocols outlined in the 2018 and 2019 Field Protocol for Spatially Balanced Sampling of Landbird Populations (Hanni et al. 2014, McLaren et al. 2019).

In 2020, one grid (I “South Beaver Creek”) was not surveyed because several points were located on private land that was developed in 2019. We replaced this grid with the next randomly sampled grid from our original roaded grid sampling framework (D “Kezar Basin”).

At each point within each grid, qualitative vegetation assessments were conducted prior to avian point count surveys. Qualitative vegetation assessments consisted of the observer estimating dominant vegetation type, tree layer percent cover and mean height, shrub layer percent cover and mean height, relative composition of tree and shrub layers by species and ground cover composition within a 50 m radius of each point. Six-minute point counts were completed by observers at each point, every bird observed was recorded within one-minute bins and no birds were recounted during subsequent one-minute intervals. Bird species were identified by sight or sound and gender was determined if possible. For bird detections that included more than one individual, cluster size was recorded. The radial distance at which the bird was first observed was measured using a rangefinder. Detections were truncated during field data collection at 500 m. Additional information about survey protocols is available at the Rocky Mountain Avian Data Center website (Rocky Mountain Avian Data Center 2021).

For analysis, we used bird detections to estimate densities at each point as well as percent of shrub cover and mean shrub height from the qualitative vegetation assessments from these surveys to inform our habitat models. Over the 3 year’s survey, means for both shrub cover and shrub height within a 50 m radius of the survey point were calculated. These habitat measurements were used in addition to remotely sensed habitat covariates for habitat modelling.

Sagebrush obligate bird density was calculated for each species using R 3.6.2 (The R Foundation for Statistical Computing Platform, 2019) and the Distance package version 1.0.2 (Miller et al. 2020). Species detections were truncated to 100 m to coincide with the territory scale for habitat modelling; radial distances were left as continuous variables and not binned. To adjust for inconsistent surveying across the points, each point was assigned an 'Effort' score which reflected the number of times each point was surveyed from 2018-2020 (minimum = 1, maximum = 4).

First, we fit multiple detection functions to estimate actual bird abundance from observed bird detections. Half-normal and hazard rate detection functions with 'observer' and/or 'year' as covariates were then fitted to each species individually therefore we did not need to determine detection probability for each species. All detection functions that attempted to fit both 'observer' and 'year' as covariates failed. The detection function for each species was selected based on Akaike's Information Criterion (AIC) (Bozdogan 1987), Cramér-von Mises test (LaRiccia and Mason 1986) and visual inspection of plotted models, avoiding those that showed skew (Figure 2).

After detection functions were selected, abundance and density estimates for each survey point associated territory (100 m buffer around each point, 3.14 ha) were estimated using a stratified bootstrap function. Many of the density estimates by point, especially for Sage thrashers, were close to 0 or were 0 which would cause zero-inflation (Martin et al. 2005). To adjust for this we converted density estimates by point to estimates per 10 ha and then rounded to the nearest whole number, this will be referred to as the observer corrected counts hence forth.

Presence and Magnitude of Roads

From 849 possible roaded grids and 149 unroaded grids that were mapped by the Bird Conservancy of the Rockies, 10 of the unroaded grids and 10 roaded grids were randomly selected for avian sampling. After ground-truthing this selection, it became evident that the BLM-designated routes, which were used to classify the sampling grids as ‘roaded’ or ‘unroaded’, did not include a network of user-created routes that exist across the sampling area. Therefore, we used a post-hoc method to quantify road presence and area within each sampling grid and within the 100 m radius circle surrounding each sampling point. Using ArcMap 10.6.1 (Esri, Redlands, CA, USA) and Google Earth ([Gunnison, CO], Google Earth Pro, 2021), we identified and traced all visible roads and trails within each 1 km^2 survey grid. To calculate area covered by roads, we added a 1.5 m buffer to all visible roads on both sides from the road center to approximate road area; this criterion was based on the 3 m average width of unpaved roads (Mitigation Strategies For Design Exceptions: Federal Highway Administration n.d.). Our road inventory included all roads currently present on the landscape that were detected using Google Earth but may not have been on the BLM registered road maps.

The average total road length in roaded grids was 1.9 km and in unroaded grids it was 1.1 km. Total road length in roaded grids ranged from 0.54 km to 3.98 km, whereas total road length in unroaded grids ranged from 0 km to 1.85 km. Only one grid had no roads.

Due to the large variability in road presence within each grid, we removed the designation of roaded and unroaded grids based on BLM-designated routes, and grid identifiers were replaced with alphabetical letters starting from the northwest corner of our study area to the southwest corner. We then conducted a point-scale inventory of roads labeling each point as roaded or unroaded (Figure 1). A point was labeled as roaded if one of the traced roads crossed into a 100 m buffer zone around the point. Out of 336 points (16 points per grid, 21 total grids), 113 were labeled as roaded (34%). The area (m^2) covered by roads within each point buffer zone was used as a covariate in the bird density models. Because of low traffic volumes on roads within our grids, the presence and magnitude of roads in our analyses represent the amount of habitat fragmentation but here we do not address roads in the context of anthropogenic use and potential disturbance.

Remote Sensing for Vegetation Cover

We used a combination of LiDAR (Light Detection and Ranging, resolution-14 points per 30 cm^2 or better) and NAIP (National Agriculture Imagery Program, resolution-1 m ground sample distance) to calculate habitat variables.

To quantify vegetation height, we used LiDAR tiles that were collected across Gunnison County in summer 2019, 67 of which covered 19 of our grids. Two of the grids, T and S, occur in Saguache County and did not have LiDAR data sets available. The LiDAR tiles were normalized by interpolating ground surface from lowest pulse points and then subtracting the ground surface from vegetation pulses (pulses that were higher than ground pulses) (Streutker and Glenn 2006). Percent of vegetation pulses above 2 m tall within each 1 m^2 pixel were calculated and are referred to as canopy density. These data were transformed into a raster data set using ArcMap 10.6.1 (Esri, Redlands, CA, USA) and the mean canopy density values within each point territory (3.14 ha) were calculated to create a vegetation height variable that accounts for all vegetation that is most likely not sagebrush cover as the average height of sagebrush, *Atremisia tridentata* spp., ranges from 0.8-1.0 m (Frandsen 1983).

NAIP imagery was from September 2019 and covered all 21 grids. From these images the normalized vegetation difference index (NDVI) was calculated, and used to estimate sagebrush cover. Sagebrush has some of the lowest NDVI signatures of all sagebrush ecotone plants and in September, when the imagery was collected, sagebrush NDVI signatures average 0.1 (Kremer and Running 1993). Therefore, the lower NDVI scores represent areas with lower vegetative production (i.e. bare ground), the median NDVI scores represent areas with median vegetative production (i.e. sagebrush), and higher NDVI scores reflect "greener" sites with more vegetative production (i.e. hardwood forests). NDVI values were converted into a raster data set using ArcMap 10.6.1 (Esri, Redlands, CA, USA) and the mean value was calculated for each 3.14 ha point territory. This habitat factor delineated between sagebrush dominated communities and other plant communities like grasslands, other shrublands and tree communities.

Incorporating Habitat Covariates into Predictive Bird Density Modeling

We used general linear mixed models to investigate the effects of roads and the four habitat covariates on avian density. To model the effect of covariates on sagebrush obligate bird density, we used R 3.6.2 (The R Foundation for Statistical Computing Platform, 2019) with the rstanarm package (Gabry et al. 2020) to build Bayesian generalized linear mixed models with a negative binomial probability distribution for the response variable, accounting for the highly skewed nature of the corrected counts, which also included many zeros (Martin et al. 2005). First we modeled each bird species individually using grid as a random effect, with the species density corrected count as the dependent variable and one covariate as the independent variable. Then out of each species' potential models, the top candidate model was selected using functions in the loo package (Vehtari et al. 2017). We selected the model that had the highest expected log pointwise predictive density (elpd) for each bird species. Expected log pointwise predictive density (elpd) measures the accuracy of prediction for the data points with leave-out cross validation (loo):

$$epld_{loo} = \sum_{i=1}^{n} \log p\,(y_i|y - i)$$

Where *n* is the number of data points, *i* is the left out data point and *y* is the data point (Vehtari et al. 2017). Then we modeled each species individually using grid as a random effect, with the species density corrected count as the dependent variable and road area (ha) with combinations of the habitat covariates (mean NDVI value, mean canopy density, mean shrub cover and shrub height mean) as the independent variable(s). Again the top candidate model was selected for each species using functions in the loo package.

A final hierarchical model was built using observer corrected counts for all species as the dependent variable. This model included all habitat covariates that were selected more than once across individual-species models: Mean NDVI, mean canopy density and mean shrub cover. Each selected habitat covariate and road area were included as a fixed effect for each individual bird species and again grid was added as a random intercept. The model included mean intercepts and slopes (habitat effects) across all species, as well as zero-centered deviations from these effects that varied by species, assuming that these species-specific effects were drawn from a normal distribution. We defined strong relationships as covariates with both a posterior probability greater than 95% that the slope is different from zero and estimated percent change in bird density across the range of the covariate greater than 50%. We defined noteworthy relationships with both a posterior probability greater than 90% that the slope is different from zero and estimated percent change greater than 20%.

RESULTS

Over the 3-year study period, 21 grids were surveyed a total of 67 times with 336 total points accumulating 998 surveys by point. In 2018, 10 grids were surveyed twice for a total of 30 surveys. In 2019 only 17 grids were surveyed and in 2020 all accessible grids were surveyed for a total of 20 surveys. In total, 7,681 bird detections were made and of those detections 62% (n = 4,792) were of our selected study species. Green-tailed towhee was the most commonly encountered, and accounted for 42% (n = 2,006) of sagebrush obligate bird detections. Brewer's sparrows comprised 28% (n = 1,363) of sagebrush obligate bird detections, Vesper sparrows comprised 18% (n = 873) and Sage thrashers comprised 13% (n = 605).

Brewer's sparrow and Vesper sparrow detection functions were fit to 100 m truncated data. Detection functions fit to 100 m truncated data did not pass the Cramér-von Mises test for GTTO and SATH. For these species their truncation was extended to 125 m and detection functions were fit again. Green-tailed Towhees required an additional left truncation of 10 m in order for the detection functions to pass the Cramér-von Mises test (Table 1, Figure 2).

Brewer's sparrow point territory density estimates ranged from 0 – 1.81 birds per 3.14 ha with a mean ± standard deviation of 0.65 ± 0.45 birds. Green-tailed towhee point territory density estimates ranged from 0 – 3.02 birds per 3.14 ha with a mean of 0.65 ± 0.04 birds. Sage thrasher point territory density estimates ranged from 0 – 0.40 birds per 3.14 ha with a mean of 0.07 ± 0.01 birds. Vesper sparrow point territory density estimates ranged from 0 – 3.02 birds per 3.14 ha with a mean of 0.53 ± 0.07 birds.

Total road area across point territories ranged from 0 – 662.1 m^2 with a mean ± standard deviation of 80.04 ± 136.57 m^2. Mean NDVI across point territories ranged from -0.14 to 0.27 with a mean ± standard error of -0.03 ± 0.0018. Mean canopy density across point territories ranged from 0% to 28.73% with a mean ± standard error of 0.74% ± 0.077%. Mean shrub cover across point territories ranged from 2.33% to 50.00% with a mean ± standard error of 20.15% ± 0.24% standard error. Shrub height mean across point territories ranged from 0 – 3.25 m with a mean ± standard error of 0.66 ± 0.01 m. No covariates had correlations with each other that were likely to impact our analysis (all correlation coefficients were below 0.8) (Figure 3).

Canopy density was the top candidate model for all species for models that contained only one covariate (Table 2). The mean canopy density covariates was included in all species selected models, NDVI and mean shrub cover were included in 3 out of 4 species selected models and shrub height mean was only included in 1 species selected model (Table 3).

Mean road area and bird observer corrected counts did not have a significant slope for any of our study species (Figure 4). Mean NDVI and bird observer corrected counts had a positive slope for Green-tailed towhee and Vesper sparrow and had a negative slope for Brewer’s sparrow and Sage thrasher (Figure 4). Mean canopy density and bird observer corrected counts had negative slopes for all four species (Figure 4). Mean shrub cover and bird observer corrected counts had positive slopes for all four species (Figure 4).

DISCUSSION

Our findings did not strongly support road presence as the primary driver in territory scale density variation among sagebrush obligate birds. None of the species relationships to road presence within our models met the criteria for strong or noteworthy relationships. This indicates that in our study, habitat covariates were more influential on bird density than road presence. Other research has shown that Vesper sparrows are negatively impacted by trails in grassland ecosystems (Svedarsky et al. 2000). Brewer's sparrow abundance has been reported to decrease with increased habitat fragmentation caused by roads within sagebrush habitat (Holmes et al. 2005). Reports for Green-tailed towhee and Sage thrasher suggest that road presence does not directly affect abundance of these species but likely contributes to fragmented habitat which does directly impact abundance (Buseck et al. 2004, Congdon et al. 2006). Roads may affect birds in two distinct ways. The presence of the road directly reduces vegetation cover and causes increased habitat fragmentation. The amount of roads present in our study area did not appear to cause enough habitat alteration to impact bird densities. The other road effect is associated with human use of roads. A study in Switzerland showed that human presence on trails negatively impacted bird abundance in forests while trail presence with low human use did not produce a statistically significant impact (Bötsch et al. 2018). More work centered on road use within our study sites would be needed in order to determine if roads with higher use produced an effect on bird density and what threshold of human activity and types of activities would trigger a change in density.

NDVI had a mixed effect on sagebrush bird density within our study sites. The low overall mean NDVI (-0.03) across all points reflects the presence of bare ground and sagebrush which has a low NDVI signature. Green-tailed towhees' positive correlation with NDVI was defined as a strong relationship in our models which is likely due to their relatively high use of non-sagebrush shrub species particularly when selecting nest sites (Dobbs et al. 2020). Non-sagebrush shrub species have higher NDVI signatures than sagebrush shrubs (Kremer and Running 1993). Brewer's sparrows had noteworthy negative correlations with NDVI which supports other research indicating that the species is a true sagebrush obligate and the presence of sagebrush dominated habitat is critical to its territory selection process (Holmes et al. 2005). While Sage thrashers are also true sagebrush obligates their relationship with NDVI was not considered noteworthy within our models although it was a negative correlation. In a study done in Wyoming, Sage thrashers had negative correlations with NDVI values (Buseck et al. 2004). The weak relationship between sage thrashers and NDVI that we found in this study may have been a result of the relatively small sample of detections of sage thrashers with 605 total detections, all other study species had greater than 800 detections. Vesper sparrows had a positive correlation with NDVI but this relationship was not defined as noteworthy and as NDVI increased the variability in Vesper sparrow density also increased. This could be accounted for by Vesper sparrows' preference for specific types of herbaceous cover (Paczek 2002). With increased herbaceous cover, the NDVI increased and the variability in Vesper sparrow density also increased. Overall the effect of NDVI is negative, indicating intermixed bare ground with sagebrush cover are important factors in territory selection for sagebrush obligate birds.

Mean canopy density, defined as the percent of pixels within each territory containing vegetation greater than 2 m in height, had a negative correlation with density for all study species and was selected as the covariate for all species' single covariate models. Both sage thrasher and vesper sparrow had strong negative relationships with canopy density, whereas Brewer's sparrow and green-tailed towhee had noteworthy negative relationships. Researchers in Utah and Nevada reported decreased abundance of sagebrush obligate and near-obligate birds in sagebrush steppe with woodland encroachment (Pierson et al. 2010). This effect likely outweighed shrub height when selecting species models. Shrub height was only selected as a significant covariate for vesper sparrow whereas all species selected models included canopy density, therefore shrub height was not included in the overall species model since it was unlikely to improve model predictions. This indicates that the four sagebrush obligate songbirds may be intolerant of trees across sagebrush steppe ecosystems.

Within our study area vegetation over 2 m is due to aspen (*Populus tremuloides*) and mixed conifer species rather pinyon (*Pinus* spp.) or juniper (*Juniperus spp.*) which has been shown to negatively impact sagebrush obligate birds (Pierson et al. 2010, Knick et al. 2012, Coates et al. 2017). Out of our 336 survey points, primary habitat was identified as Aspen for 7 points, Mixed Conifer for 5 points and 0 were identified as Pinon-Juniper/Juniper (McLaren et al. 2019). Across the intermountain west sudden aspen decline has been increasing (Singer et al. 2019) with aspen stands being replaced by mixed conifer stands (Crawford et al. 1998). This habitat turnover also has potentially negative impacts for local bird communities (Richardson and Heath 2004). The trade-offs between sagebrush bird community and forest edge bird community benefits will need to be carefully considered and monitored if sagebrush habitats experience more forest edge encroachment.

Shrub cover was positively correlated with density for most study species. The Brewer's sparrow density relationship with shrub cover was strong, which is supported by reports of increased abundance and nest success of Brewer's sparrows with increased shrub cover (Chalfoun and Martin 2007). Green-tailed towhee and sage thrasher both had noteworthy positive relationships which is supported by reports for shrub coverage selection within both species breeding ranges

(Dobbs et al. 2020, Reynolds et al. 2020). Vesper sparrows slight positive correlation to shrub cover was not considered noteworthy in our models which is supported by reports that herbaceous cover and plant species drive territory selection for vesper sparrow (Paczek 2002, Jones and Cornely 2020).

Our study indicates that road presence is less influential over bird density than other habitat covariates. The consistent negative correlations of all four species to vegetation heights over 2 m and positive correlations to shrub cover among all of our study species indicate the need for continued management practices focused on reducing woodland encroachment and habitat fragmentation. As the potential of increased recreation, habitat fragmentation and woodland encroachment threatens the sagebrush steppe (Duchardt et al. 2018), sagebrush obligate bird densities need to be continuously monitored to understand impacts and determine effective mitigation strategies for management.

MANAGEMENT IMPLICATIONS

Our study highlights the variable relationship of sagebrush songbirds to habitat conditions at the territory scale. Whereas all four birds are sagebrush obligate or near obligate species, they uniquely select habitats during the breeding season and therefore potentially benefit from individual management scenarios. While roads with low traffic volumes did not affect sagebrush obligate species' density in our study, road use and its effect on bird densities should be monitored. The negative effect of vegetation heights over 2 m indicates the need for encroachment monitoring and mitigation throughout the Gunnison Basin as all of our study species are vulnerable to even low increases of vegetation heights over 2 m according to our models.

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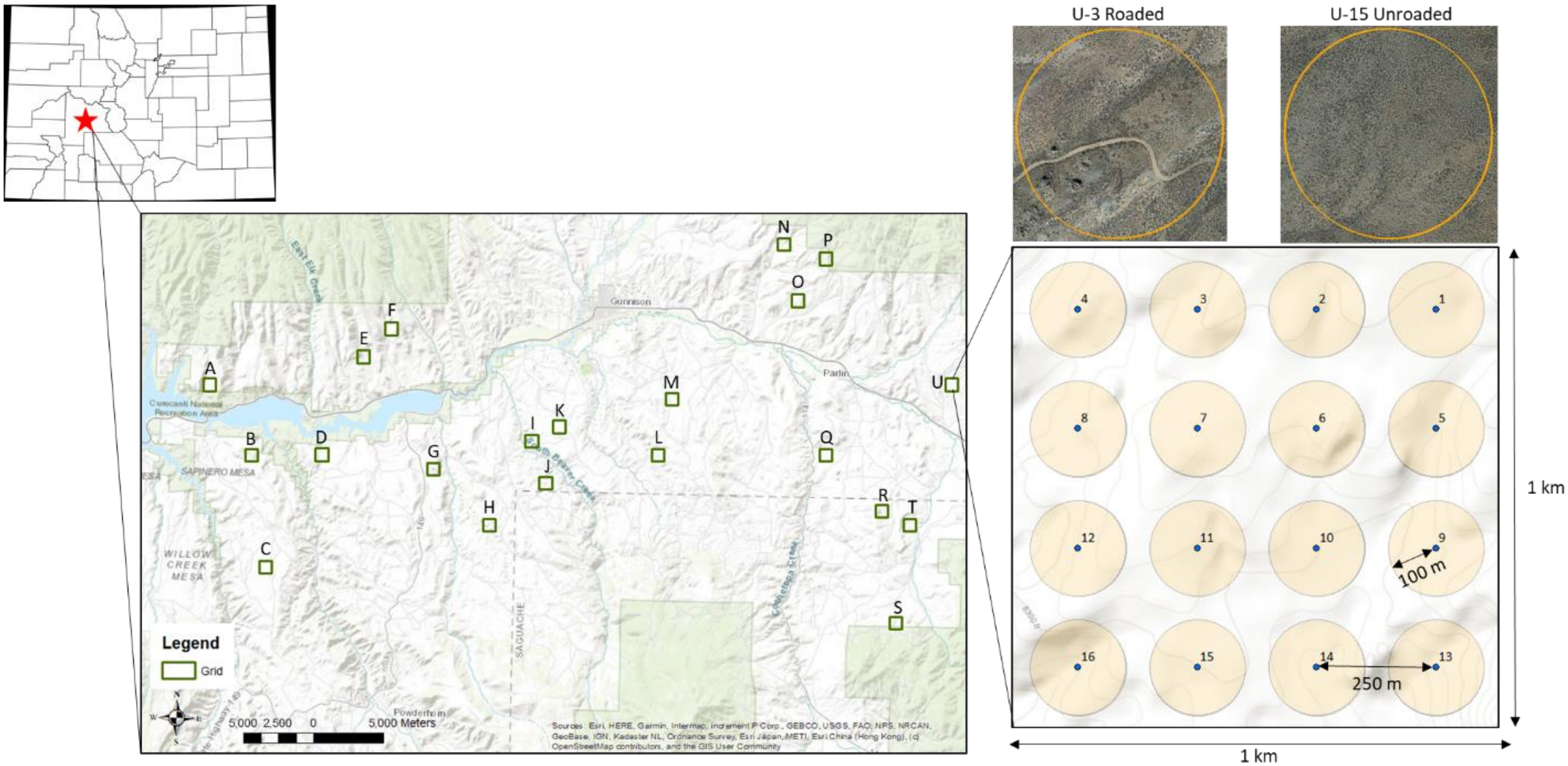
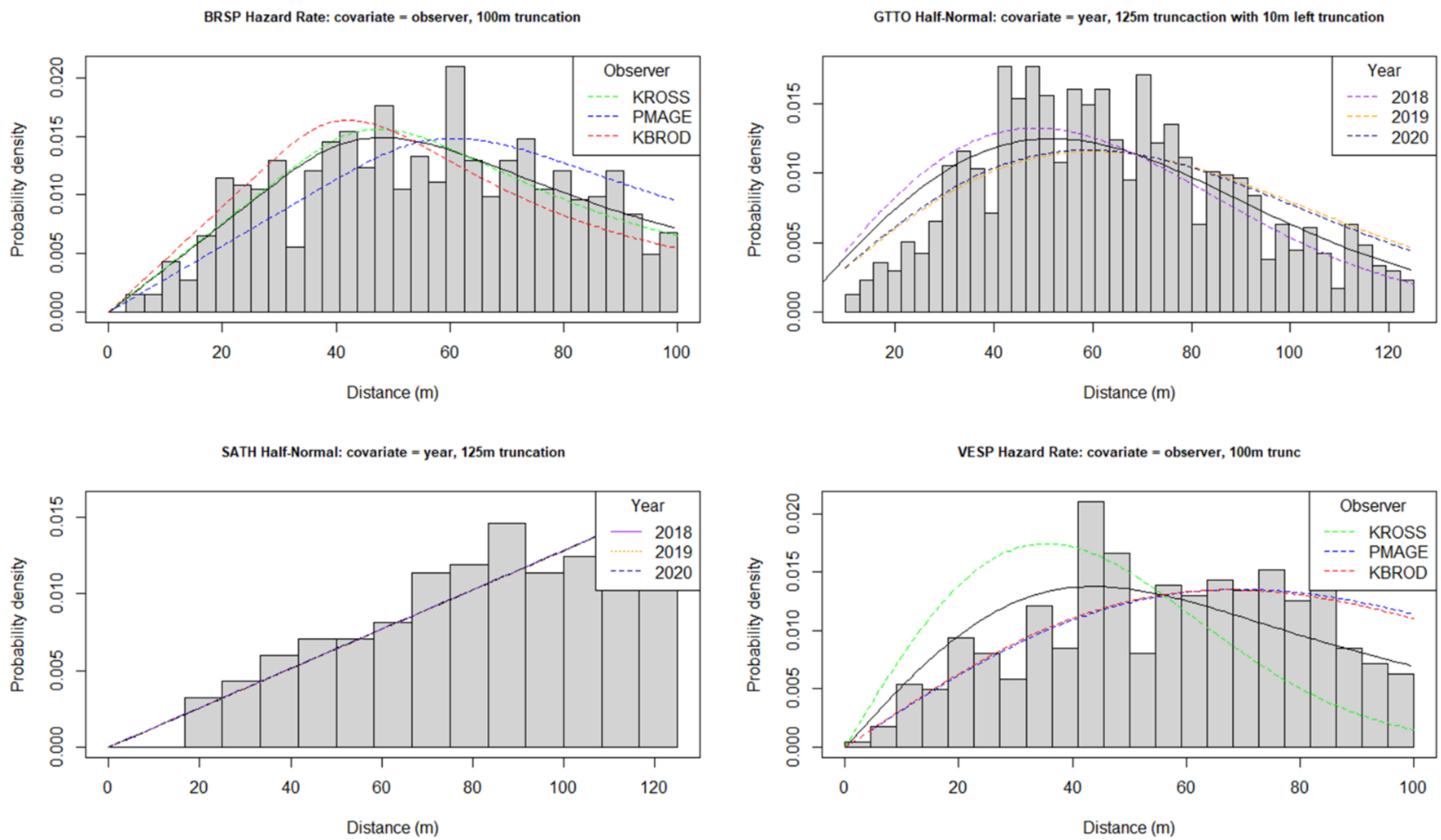


Figure 1: Upper left; county map of Colorado with town of Gunnison marked by red star. Lower left; study area map within Upper Gunnison Basin, marking the locations of 21 sampling grids (labeled A-U). Lower right; Grid "U" illustrating all 16 survey points buffered by a 100-m radius to show extent of sampled area. Upper right; Google Earth satellite imagery of points "U-3" and "U-15" indicated by orange outlines and labeled according to road presence. Maps were created using 10.6.1 ArcGIS® software (Esri, Redlands, CA, USA).



BRSP = Brewer's sparrow, GTTO = green-tailed towhee, SATH = sage thrasher, VESP = vesper sparrow

Figure 2. Selected detection functions for each species: model is indicated by solid black line, colored lines represent covariates used within the model. Gray bars indicated number of detections within each distance bin.

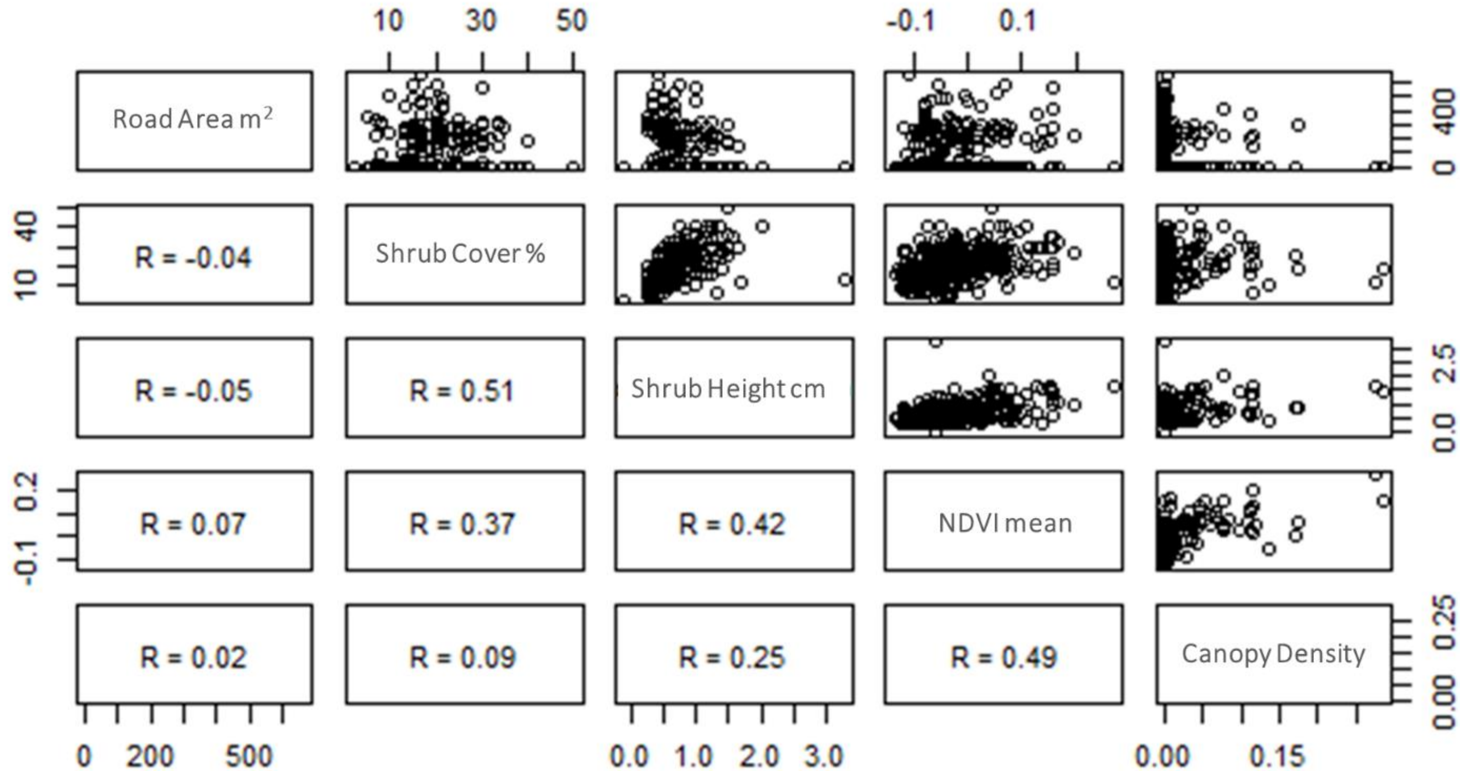


Figure 3: Covariate relationships comparison with correlation coefficients indicated below scatterplots. Any value over 0.8 were considered significant.

Table 1. Detection functions for each species with covariate, truncation distance (m), AIC and Cramér-von Mises (CvM) test statistics (p-values >0.05 indicate acceptable goodness-of-fit).

Species	**Detection Function**	**Covariate**	**Left Truncation**	**Right Truncation**	**AIC**	**CVM p-value**
BRSP	Half-normal	Observer		100	9325.09	0.45**
		Year		100	9340.482	0.57**
		Observer + Year		100	NA	
	Hazard Rate*	Observer*		100	9322.083	0.86**
		Year		100	9342.616	0.72**
		Observer + Year		100	NA	
GTTO	Half-normal	Observer		100	13650.15	6.41E-06
		Year		100	13645.33	4.41E-06
		Observer + Year		100	NA	
	Hazard Rate	Observer		100	13594.27	0.02
		Year		100	13588.55	0.016
		Observer + Year		100	NA	
	Half-normal	Observer		125	15788.86	5.43E-07
		Year		125	15765.84	4.71E-07
		Observer + Year		125	NA	
	Hazard Rate	Observer		125	15713.85	0.088**
		Year		125	15691.75	0.075**
		Observer + Year		125	NA	
	Half-normal	Observer	10	125	15653	6.29E-06
		Year	10	125	15629.34	4.17E-06
		Observer + Year	10	125	NA	

GTTO	Hazard Rate*	Observer	10	125	15591.84	0.20**
		Year*	10	125	15569.6	0.17**
		Observer + Year	10	125	NA	
SATH	Half-normal	Observer		100	1370.731	0.044
		Year		100	1370.731	0.044
		Observer + Year		100	NA	
	Hazard Rate	Observer		100	NA	
		Year		100	NA	
		Observer + Year		100	NA	
	Half-normal*	Observer		125	2044.663	0.047
		Year*		125	2045.564	0.078**
		Observer + Year		125	NA	
	Hazard Rate	Observer		125	NA	
		Year		125	2046.992	0.41**
		Observer + Year		125	NA	
VESP	Half-normal*	Observer*		100	4381.247	0.16**
		Year		100	4370.958	0.13**
		Observer + Year		100	NA	
	Hazard Rate	Observer		100	4356.06	0.17**
		Year		100	4347.235	0.12**
		Observer + Year		100	NA	

* Indicates selected detection function and covariate

** Indicates acceptable CvM p-value

BRSP = Brewer's sparrow, GTTO = green-tailed towhee, SATH = sage thrasher, VESP = vesper sparrow

Table 2: Habitat models for each species, x indicates that the covariate was included in model. Models with expected log pointwise predictive density difference (elpd Δ) of 0 indicate models of best fit and therefore the selected model for each species.

Species	**Road Area**	**Mean NDVI**	**Mean canopy density**	**Mean shrub cover**	**Shrub Height Mean**	**elpd Δ**	**Standard Error Δ**
BRSP			x			0	0
				x		-0.3698	3.0536
					x	-2.1737	2.5811
		x				-3.0516	2.1141
	x					-3.3281	2.4212
GTTO			x			0	0
				x		-1.9098	1.7985
					x	-2.1881	1.5416
	x					-2.2491	1.1277
		x				-2.9007	2.0303
SATH			x			0	0
				x		-1.6256	1.9965
					x	-2.9237	1.5497
		x				-3.0446	1.2387
	x					-3.4895	1.3909
VESP			x			0	0
				x		-0.1929	4.1237
	x					-0.2266	4.3078
		x				-0.8163	3.8048
					x	-1.1141	3.9158

BRSP = Brewer's sparrow, GTTO = green-tailed towhee, SATH = sage thrasher, VESP = vesper sparrow

Table 3: Habitat models with combined covariates for each species, x indicates that the covariate was included in model. Models with expected log pointwise predictive density difference (elpd Δ) of 0 indicate models of best fit and therefore the selected model for each species.

Species	**Road Area**	**Mean NDVI**	**Mean canopy density**	**Mean shrub cover**	**Shrub Height Mean**	**elpd Δ**	**Standard Error Δ**
BRSP	x	x	x	x		0	0
	x	x	x	x	x	-1.689	0.9991
	x		x	x	x	-2.0036	1.5106
	x			x		-3.2249	2.5619
	x	x	x			-3.4327	2.2095
	x	x		x		-4.1332	2.9888
	x				x	-5.2302	3.1097
	x					-5.6906	3.227
	x			x	x	-5.9253	3.3678
	x	x				-6.1024	3.1551
GTTO	x	x	x			0	0
	x	x	x	x		-0.8686	0.5949
	x		x	x	x	-1.4171	1.7063
	x	x	x	x	x	-1.5934	0.6809
	x					-2.1985	1.9878
	x			x		-2.725	1.8778
	x				x	-2.9848	1.9959
	x			x	x	-3.5574	1.8965
	x	x				-3.9281	1.9353
	x	x		x		-4.3369	1.974
SATH	x	x	x	x		0	0
	x		x	x	x	-0.0708	0.6756
	x	x	x	x	x	-0.8233	0.3961
	x	x	x			-0.8422	1.5829
	x			x		-2.1999	1.5512
	x					-3.0153	2.009
	x			x	x	-3.1196	1.5301
	x				x	-3.3774	2.0407
	x	x				-3.4952	1.9277
	x	x		x		-4.1693	2.0371
VESP	x		x	x	x	0	0
	x					-0.2544	3.8559
	x			x		-0.385	3.823

	x	x	x			-0.4946	1.2197
	x	x				-0.7291	3.8305
	x			x	x	-0.9029	3.7561
	x	x	x	x		-1.0454	1.0576
	x				x	-1.2662	3.8584
	x	x	x	x	x	-1.2929	0.2724
	x	x		x		-1.8295	3.8414

BRSP = Brewer's sparrow, GTTO = green-tailed towhee, SATH = sage thrasher, VESP = vesper sparrow

Table 4. Estimated slope of covariates to bird species observer corrected counts with 50% and 90% credible intervals. Overall indicates the effect on all species observer corrected counts. Slopes indicate unit change of bird observer corrected counts per unit change of covariates. Covariate units differ and therefore slopes of different covariates cannot be compared relative to one another. Percent change calculated from posteriorly predicted changes in bird density.

		5%	**25%**	**Mean**	**75%**	**95%**	**Probability of positive slope**	**Probability of negative slope**	**Estimated Percent Change**
Overall	Intercept	-1.751	-0.6851	-0.1561	0.3881	1.373	42%	58%	N/A
	Road Area	-6.832	-2.862	-0.8341	1.316	4.795	40%	60%	N/A
	Mean NDVI	-5.188	-2.081	-0.7837	0.5334	2.895	36%	64%	N/A
	Mean canopy density**	-20.76	-11.61	-9.217	-5.385	-1.54	3%	97%	N/A
	Mean shrub cover*	-0.00584	0.007083	0.0131	0.01888	0.03485	90%	10%	N/A
BRSP	Intercept	-0.04202	0.1291	0.2526	0.3765	0.5355	92%	8%	
	Road Area	-3.417	-0.6711	1.474	3.474	6.865	68%	32%	50%**

BRSP	NDVI *	-3.935	-2.766	-1.965	-1.162	-0.01411	5%	95%**	32%*
	Canopy density *	-15.52	-11.83	-9.42	-6.809	-3.95	0%	100%**	40%*
	Shrub Cover **	0.009343	0.01545	0.01998	0.02428	0.03078	100%**	0%	88%**
GTTO	Road Area	-4.926	-2.373	-0.5633	1.218	3.652	42%	58%	42%*
	NDVI **	0.2013	1.115	1.689	2.292	3.135	97%**	3%	58%**
	Canopy density *	-6.256	-4.586	-3.52	-2.399	-0.9402	1%	99%**	40%*
	Shrub Cover *	-0.001937	0.003528	0.007178	0.01094	0.01583	90%*	10%	53%**
SATH	Intercept	-2.964	-2.417	-2.16	-1.85	-1.509	0%	100%	
	Road Area	-9.883	-3.521	-0.8216	2.155	7.272	44%	56%	415%**
	NDVI	-9	-5.136	-3.188	-0.871	1.221	16%	84%	278%**
	Canopy density **	-42.33	-18.97	-15.28	-6.26	-1.872	2%	98%**	363%**
SATH	Shrub Cover **	-0.000707	0.01056	0.02137	0.0305	0.05165	94%*	6%	882%**

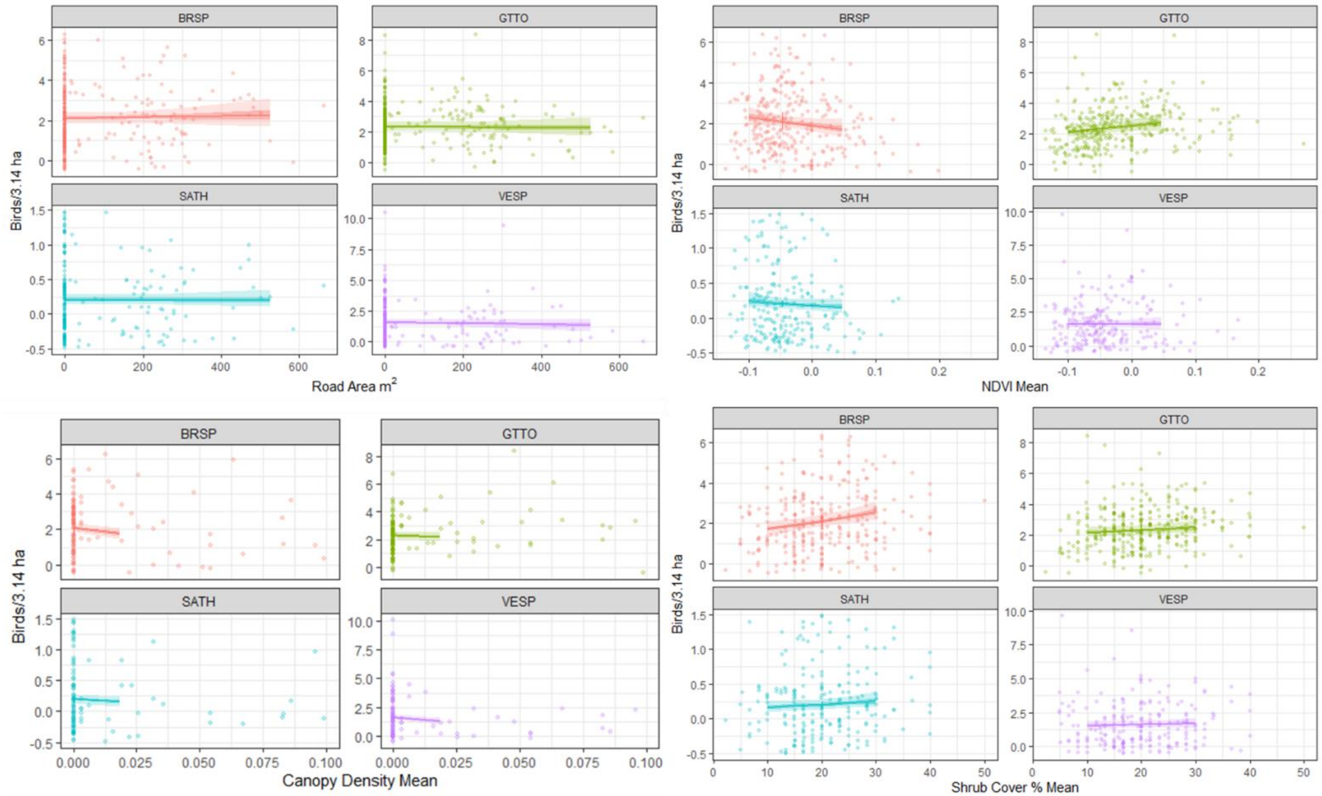
VESP	Intercept	0.07763	0.2555	0.3892	0.5233	0.713	98%	2%	
	Road Area	-11.05	-6.017	-3.49	-0.5489	2.36	20%	80%	55%**
	NDVI	-1.999	-0.8182	0.0397	0.879	2.146	51%	49%	61%**
	Canopy density **	-18.22	-12.62	-9.915	-6.523	-3.384	0%	100%**	51%**
	Shrub Cover	-0.007235	0.000266	0.005402	0.01075	0.0172	76%	24%	72%**

*indicates noteworthy relationship
**indicates strong relationship
BRSP = Brewer's sparrow, GTTO = green-tailed towhee, SATH = sage thrasher, VESP = vesper sparrow

Summary for online Table of Contents

We modelled the effects of road presence and four other habitats covariates on the estimated densities of sagebrush obligate birds. Overall vegetation heights over 2 m, percent shrub cover and the mean normalized difference vegetation index were found to have varying impacts on sagebrush bird obligate density while road presence did not. This work serves to improve management decisions throughout the sagebrush steppe by emphasizing the need for species specific modelling and the vulnerability of sagebrush obligate birds to habitat fragmentation and woodland encroachment.

SUPPORTING INFORMATION



BRSP = Brewer’s sparrow, GTTO = green-tailed towhee, SATH = sage thrasher, VESP = vesper sparrow

Figure 4: Fit habitat-density relationships for focal species when other habitat covariates are held constant. Center solid line represents mean, opaque region represents 50% credible intervals and more transparent region represents 90% credible intervals. Plotted points represent actual observer corrected counts for each species. Points beyond 0.1 in mean canopy density were not included in plots.