Integrating Wildlife Count Models With State-and-Transition Models to Enhance Rangeland Management for Multiple Objectives

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A B S T R A C T

State-and-transition models (STMs) are tools used in rangeland management to describe linear and nonlinear vegetation dynamics as conceptual models. STMs can be improved by including additional ecosystem services, such as wildlife habitat, so that managers can predict how local populations might respond to state changes and to illustrate the tradeoffs in managing for different ecosystem services. Our objective was to incorporate songbird density into an STM developed for sagebrush rangelands in northwest Colorado to guide local management of sagebrush birds. The STM included two shrub-dominated community phases, a native grassland state, and a shrubland and grassland phase within an exotic-dominated state. We surveyed plots for songbirds, collected a suite of vegetation indicators at each plot, and quantified songbird habitat relationships with count-based regression models. We then used the estimated models to predict songbird density based on average vegetation conditions per state or community phase. Moderate or increasing shrub cover were important predictors for shrubland-associated species, and responses to understory components varied by species. In the STM, we predicted higher densities of shrubland-associated bird species in the shrub-dominated phases and higher densities of grassland-associated bird species in the state and phase lacking shrub cover. No single state or phase captured the highest density for all songbirds, illustrating the value of alternative states. Our results also demonstrate the utility of displaying traditional wildlife count models against the range of vegetation conditions associated with each state or phase to understand how wildlife density can vary within states and phases. Our approach can assist land managers to gauge the potential impacts of land-use decisions and natural vegetation variability on wildlife, especially for species of conservation concern.

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Introduction

The sagebrush biome of western North America once encompassed > 60 million ha but now occupies approximately half of its former distribution (Knick et al. 2003; Miller et al. 2011). The invasion of exotic grasses, such as cheatgrass (Bromus tectorum), and changing fire regimes have contributed to the loss of diverse sagebrush rangelands, in addition to increasing energy development, conifer expansion, and climate change (Miller et al. 2011). Given the fragmentation and deterioration of sagebrush rangelands, populations of many avian species in this ecosystem have declined (Knick and Rotenberry 2002). Some species rely entirely on sagebrush ecosystems for activities such as nesting and foraging (e.g., sagebrush sparrow [Artemisiospiza nevadensis], Brewer’s sparrow [Spizella breweri], and sage thrasher [Oreoscoptes montanus]), whereas others rely on shrub cover in general (e.g., green-tailed towhee [Pipilo chlorurus]; Braun et al. 1976). Several songbird species that rely on sagebrush during the breeding season have declined in all or part of their range (Knick and Rotenberry 2002).

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State-and-transition models (STMs) are among the tools currently used for rangeland management as a way to organize and communicate information about rangeland dynamics (Bestelmeyer et al. 2017). STMs are conceptual models that describe ecosystem change, allowing both alternative stable states and linear successional dynamics (Westoby et al. 1989). STMs are typically composed of a reference state (based on historical or “healthy” ecosystem conditions) and often several alternative states (US Department of Agriculture Natural Resources Conservation Service [USDA NRCS] 1997; Bestelmeyer et al. 2017). A state is a persistent vegetation community that is determined by both soil properties and vegetation structure (Stringham et al. 2003). Transitions are the trajectories or drivers of change between states (Bestelmeyer et al. 2017). Within a state, plant composition can shift among phases and along reversible pathways in response to weather or disturbance events, reflecting the natural dynamics of different plant communities; these community phases are transient plant communities (Stringham et al. 2003).

States were historically described in terms of productivity for livestock forage, but describing a state in terms of multiple properties like plant species richness, composition, structure, and ecological function could allow a broader inclusion of the services a state provides, such as wildlife habitat (Twidwell et al. 2013; Bestelmeyer et al. 2017). Land managers could then use STMs to predict how wildlife habitat, and thus local populations, may change in response to changing vegetation conditions (Holmes and Miller 2010). Incorporating habitat relationships for multiple species of concern within an STM would also illustrate the different habitats provided by alternative states and phases, which are likely necessary to support wildlife diversity (Fuhlendorf et al. 2012, 2017). Recent studies have examined avian occurrence within ecological sites and STMs (Doherty et al. 2011) or evaluated the potential for ecological sites and STMs to incorporate measures that assess wildlife habitat (Williams et al. 2011). For instance, grasshopper sparrow (Ammodramus savannarum) abundance was greatest in a native perennial grassland community phase, and a shift to a sagebrush or annual grassland community phase reduced sparrow abundance (Holmes and Miller 2010).

We sought to improve upon previous efforts by integrating habitat relationships for multiple songbird species of conservation concern within an STM as an additional ecosystem service. The STM we used was generalized across multiple ecological sites (Tipton 2015) to make it more likely to be used by landowners and managers (Bestelmeyer et al. 2016). An STM usually corresponds to one ecological site, which has distinctive soil, climatic, and topographical properties that determine a site’s characteristic plant community (Bestelmeyer et al. 2003). However, landowners may prefer to manage by vegetation types or ecosystems rather than at finer scales of ecological sites and soil map units (Knapp and Fernandez-Gimenez 2009). We also used an STM developed in collaboration with multiple stakeholders (e.g., ranchers, state wildlife biologists, range ecologists; Bruegger et al. 2016) so that the results would be more relevant to local land managers (Knapp et al. 2011; Kachergis et al. 2013).

Our first objective was to incorporate habitat relationships for several songbird species into an STM to predict how songbird density might respond to state or community phase changes and illustrate the tradeoff in managing for alternative states. Our second objective was to display the habitat relationships against the range of vegetation conditions associated with each state or phase to illustrate how this range affects songbird densities. We collected vegetation and songbird count data in three study areas dominated by sagebrush in northwest Colorado and used the vegetation data from STM development to model songbird counts. We then used the models to predict songbird density for states and community phases in an STM developed for one of the study areas and displayed the models for a shrubland and grassland-associated songbird against the variability in vegetation conditions for each state and phase.

Methods

Study Area

We collected vegetation and songbird data at three sagebrush-dominated study areas in northwest Colorado from 2013 to 2015 (Fig. 1). The western Moffat County study area (≈13 420 ha in size) was characterized by low sagebrush (Artemisia arbuscula) and Wyoming big sagebrush (A. tridentata wyomingensis) communities on sandier soils and salt shrub (Atriplex spp.) communities on clayey soils; however, soils were highly intermingled relative to the other study areas (USDA NRCS 2013). Wyoming big sagebrush communities and loamy or sandy soils dominated the eastern Moffat County study area (≈38 200 ha in size; USDA NRCS 2013). The study area in Routt County (≈1 700 ha in size) was dominated by mountain big sagebrush (A. t. vaseyana) on loamy soils and low sagebrush on clayey soils (USDA NRCS 2013). A bunchgrass (e.g., Sandberg bluegrass [Poa secunda]) or western wheatgrass (Pascopyrum smithii) dominated the understory in each study area. Annual precipitation during the study varied from ≈10 to 20 cm for western Moffat, 20 to 30 cm for eastern Moffat, and 30 to 50 cm for Routt (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu 2015). Three wildfires occurred before the study in eastern Moffat County: a 2010 wildfire (3 185 ha), a 2008 wildfire (10 243 ha), and a smaller 2008 fire (1 505 ha; Tipton 2015). Past mechanical treatments to reduce shrub density in eastern Moffat included mow, brush beat, and drag treatments, each < 200 ha in size and 13–19 years old as of 2015 (Tipton 2015).

In each study area, STM development was collaborative in that local stakeholders critiqued drafts of STMs and provided input after data collection and analyses (Tipton 2015; Bruegger et al. 2016). We used a stratified random sampling design across all three study areas and focused the sampling effort in each study area based on local stakeholder questions and interest and availability of existing ecological site descriptions. Although we used songbird and vegetation data collected at all three study areas to model habitat relationships, we only include STM development details for eastern Moffat because we only predicted songbird densities within the STM developed for the eastern Moffat study area.

In the eastern Moffat study area, stakeholders were most interested in sandy and loamy ecological sites as they were the predominant sites in the study area. Stakeholders also wanted to know about the effects of mechanical shrub treatments and wildfire on birds and plants. Therefore, we randomly allocated sampling plots within past treatments (i.e., burned and mechanically treated areas) and areas with no known treatments on Sandyland (R034AY330CO) and Rolling Loam (R034AY298CO) ecological sites (USDA NRCS 2013). Although an STM typically corresponds to one ecological site (Bestelmeyer et al. 2003), Tipton (2015) developed one STM across the two ecological sites. Because she found little difference in plant response to disturbance based on ecological site, and landowners also observed little difference in plant response to management actions across ecological sites, one generalized STM was sufficient. The STM (Fig. 2A) included a shrub-dominated state with two community phases (diverse shrubland and needle-and-thread [Hesperostipa comata] shrubland), a native grassland (predominantly western wheatgrass and Sandberg bluegrass) state with < 5% shrub cover, and a grass-dominated and shrub-dominated phase within a crested wheatgrass (Agropyron cristatum)–dominated state. In this STM, plant communities were most strongly associated with fire and seeding
Figure 1. Locations of songbird, vegetation, and soil surveys, 2013–2015, in northwest Colorado with three study areas labeled (western Moffat, eastern Moffat, and Routt). We collected vegetation, soil, and songbird data in all three areas to quantify songbird habitat relationships but predicted songbird densities in just the state-and-transition model developed for eastern Moffat (Tipton 2015).

Figure 2. A, State-and-transition model developed for eastern Moffat County on Sandyland and Rolling Loam ecological sites in northwest Colorado, 2013–2015 (based on Tipton 2015) with states and transitions represented by solid borders and arrows and community phases and pathways represented by dashed borders and arrows. Photo credits: Jennifer Timmer, CSU. B, Average and minimum-maximum values for vegetation attributes in each state and community phase. Production estimates include grasses and forbs. See Tipton (2015) for full description of possible transition drivers and determination of states and phases.
history. Tipton (2015) classified plant communities associated with crested wheatgrass (average 41% cover) as one state, but due to functional and structural differences, we divided this state into two community phases: shrubland and grassland dominated (Bestelmeyer et al. 2003). Both phases resulted from past crested wheatgrass seeding (Tipton 2015), and the grassland-dominated phase had experienced a wildfire in 2010.

Field Surveys

We surveyed 144 plots for songbirds across the study areas (73 in eastern Moffat, 52 in western Moffat, and 19 in Routt; see Fig. 1) mid-May to late June 2013–2015. To estimate songbird abundance, we conducted standard point count surveys at the center of each plot following a distance sampling protocol (Buckland et al. 2001). The protocol included focusing on detections at and surrounding the plot and measuring radial distance with rangefinders to the point where each bird was first detected (Buckland et al. 2001). We identified birds both aurally and visually within a 6-min interval at each point and recorded detected individuals only once. We conducted surveys during the breeding season from sunrise to approximately 4 h after sunrise, depending on weather. We did not conduct surveys during inclement weather, such as rain or windy conditions when activity of the birds or detectability of the birds was hindered. We also conducted surveys beginning at lower-elevation plots earlier in the breeding season and moved up in elevation as the season progressed to capture the phenology of the birds’ breeding activity (Hanni et al. 2013). We surveyed each plot for songbirds once a field season.

We measured a suite of ecological site metrics (e.g., vegetation and soils characteristics; Herrick et al. 2005) at all survey plots late June through mid-August 2013–2015. We collected the vegetation measurements during this period rather than concurrently with bird count surveys because STMs typically describe the vegetation at peak biomass, and our intent was to link states and phases to avian habitat relationships. Thus, the vegetation metrics described what the birds’ habitat would look like in mid to late summer when they are nesting or raising young as opposed to attracting mates (Billerman et al. 2020). For predictors in the songbird count models, we primarily used foliar cover by species, litter, rock, dung, and bare ground as measured with the line-point intercept (LPI) method (Bonham 1989; Herrick et al. 2005) on five parallel 50-m transects at 1-m intervals. We summed foliar cover by species to determine cover by functional group (e.g., shrub cover). For further details on the ecological site metrics, see Tipton (2015). We collected several additional metrics to further characterize songbird habitat. We assessed visual obstruction (VO) with a modified Robel pole (Robel et al. 1970). We recorded VO at five evenly spaced points along two transects per plot, with VO viewed from each ordinal direction per point. We also measured grass height of the nearest plant to each VO reading and averaged the 10 heights per plot. We measured height of the tallest shrub (excluding inflorescences) intercepting the transect when taking LPI measurements.

Data Analyses

Songbird Detection Probabilities

We restricted analyses to the more commonly detected songbirds in the study areas, both shrubland-associated (Brewer’s sparrow, green-tailed towhee, sage thrasher, and sagebrush sparrow) and grassland-associated (horned lark [Eremophila alpestris], vesper sparrow [Pooecetes gramineus], and western meadowlark [Sturnella neglecta]) species (Wiens and Rotenberry 1981). To estimate songbird density and examine potential variables affecting detectability, we used program Distance 6.0 (Thomas et al. 2010). We excluded outlier detections on the basis of visual inspection of detection histograms and binned distances accordingly (Buckland et al. 2001). Detectability variables included start time; Julian date; observer; how the bird was detected (i.e., calling, singing, or visual); temperature; cloud cover; and wind speed (Hanni et al. 2013). We selected the best detection model for each species using Akaike's
information criterion (AIC; Burnham and Anderson 2002) and used
the best model to predict density estimates for each plot. We also
compared density estimates for the most common songbirds across
plots surveyed in multiple years to determine if we could pool
data from multiple field seasons (eq. 3.102 in Buckland et al. 2001).
Most of the plots (105 out of 144) were surveyed only once dur-
during the three field seasons. We did not compare vegetation metrics
across years because all plots with vegetation data were surveyed
only once over the three field seasons.

**Songbird Count Model Development and Evaluation**

We evaluated count-based regression models (i.e., generalized
linear models) for songbird counts (i.e., response variables) with
the vegetation metrics (i.e., predictor variables) collected at each
plot. We first identified the appropriate distribution, Poisson or
negative binomial, for each species using an intercept-only model
and Vuong’s test (Hilbe 2011). For each songbird model, we ex-
cluded songbird counts beyond the truncation distance, as de-
termined by detection histograms, and included an offset term,
which accounted for plot-specific variability in detection and sur-
vey effort (eq. 2.2 in Buckland et al. 2009). This allowed us to
model observed songbird counts while incorporating differences in
detectability across plots as determined from distance sampling.
We then used the data in an exploratory approach to determine
the appropriate model structure for each species and predictor
variable. We examined scatterplots of raw counts and predictor
variables to check for nonlinear relationships, outliers, and pre-
dictor variables with limited distributions in the study areas. If
plots showed evidence of nonlinearity, we evaluated a linear and
a quadratic regression model with Bayesian information criterion
(BIC) to determine which model structure to retain (i.e., retained
the model form with the lowest BIC score). We used BIC for eval-
uation of the models because BIC penalizes model complexity more
heavily than AIC (Burnham and Anderson 2002), and given many
predictor variables, we wanted to prevent models from becoming
overly complex (Johnson and Omland 2004). We used Pearson’s
correlation coefficient to test individually if any of the predictor
variables were correlated (i.e., \( r \geq 0.7 \); Zar 2010).

For each species, we determined the best shrub structure variable (i.e., sagebrush cover, shrub cover, or VO) to include in
all candidate models by evaluating univariable models with BIC.
We then evaluated all model combinations of predictor variables
to determine the best models explaining songbird counts and
retained only the highest-ranking model for each species. For all
species, we included the best shrub structure variable in each
model and also evaluated a shrub structure-only model. Most
species included in the analysis are shrub-obligate species, and
models without a shrub structure variable would not be as useful
for management of sagebrush rangelands. We tested all possible
combinations of uncorrelated variables, provided the model
included the best shrub structure variable. We only excluded
variables from a species’ candidate model set if they were corre-
related with the best shrub structure variable for that species.
We examined variance inflation factors (VIF) for each species’
top model that contained multiple variables (Menard 1995) and
excluded models with mean VIF scores > 2 (Chatterjee et al. 2000)
to further reduce multicollinearity. We also excluded models when
coefficients of predictor variables were unstable (i.e., reversed their
relationship to the response variable across models; Arnold 2010).

To assess the amount of variation explained by our fitted mod-
els over an intercept-only model, we calculated a McFadden’s
pseudo-\( R^2 \) value (Zar 2010). We also used a chi-square likelihood
test with the lrtest function in package “lmtest” (Hothorn et al. 2019)
to determine goodness-of-fit for the top model over an intercept-only (null) model. We evaluated predictive ability for
each model by measuring the root mean squared error using five-
fold cross validation (Hastie et al. 2009) with the cvFit function in
package “cVTools” (Alfons et al. 2015). We performed all analyses in Pro-
gram R 3.3.2 (R Core Team 2015).

**Songbird Density by State or Community Phase**

To incorporate songbird density into the STM, we used our best
count model for each species to predict the number of individ-
ual songbirds per hectare for each state or community phase. For
each state or phase, we calculated average vegetation conditions
for predictor variables (e.g., shrub cover and bare ground) and av-
erage offset terms for songbird detectability. We then used the av-
erage vegetation conditions and offset terms per state and phase
to predict songbird density per state and phase using each species’
best count model. We calculated variability around each predicted
density estimate using 95% confidence intervals for the vegetation
variables associated with each state or phase because we wanted
density estimates to reflect the variability in vegetation conditions.
We used a T distribution rather than a normal distribution to cal-
culate the confidence intervals because the population standard
deviations were unknown and vegetation sample sizes used to
build the STM were small (\( n < 33 \) plots for each state and phase).
Finally, we displayed the variation in predicted songbird density as
a function of vegetation variables in the top model for a shrubland
and grassland-associated species. We used violin plots to show the
distribution of a given vegetation variable within each of the states
and community phases from the STM where each violin is plot-
ted at mean predicted density for the songbirds for each state or
phase.

**Results**

**Songbird Detection Probabilities**

We detected a total of 367 Brewer’s sparrows on 109 plots, 97
green-tailed towhees on 45 plots, 129 sagebrush sparrows on 49
plots, 103 sage thrashers on 56 plots, 353 horned larks on 93 plots.
166 vesper sparrows on 64 plots, and 230 western meadowlarks on
77 plots. On the basis of 39 plots surveyed in consecutive field sea-
sons, we did not find a difference among years in density estimates
for the most common songbirds and, therefore, pooled data across
years. We grouped songbird counts into six or seven bins of dis-
ance from the point count and truncated distances > 200–250 m.

**Songbird Count Model Development and Evaluation**

Detectability offset values, represented as constants in each species’
model, were 0.25 for Brewer’s sparrows, 1.29 for green-
tailed towhees, 1.27 for sagebrush sparrows, 1.42 for sage thras-
chers, 0.66 for horned larks, 0.71 for vesper sparrows, and 1.79 for
western meadowlarks. We detected one horned lark and no sage-
brush sparrows or sage thrashers in the Routt study area; there-
fore, we restricted model development for these species to data
collected only in the eastern and western Moffat study areas.

Of the 11 predictor variables considered (Table 1), sagebrush
cover, total shrub cover, and VO were correlated, so we retained
only the best variable for each species. Shrub height and VO, as
well as grass and herbaceous cover, were positively correlated, and
bare ground was negatively correlated with litter, grass cover, and
herbaceous cover. For species’ models that were restricted to the
eastern and western Moffat study areas, shrub height was also cor-
related with sagebrush and shrub cover, and litter and grass were
correlated. Therefore, we did not include these variables in the
same model. For species’ models that were restricted to the east-
ern and western Moffat study areas (i.e., horned lark, sage thrasher,
Table 1: Definitions of vegetation predictors used in count-based regression models for sagebrush-associated songbirds in northwest Colorado, 2013–2015.

<table>
<thead>
<tr>
<th>Predictor^1</th>
<th>Predictor description</th>
</tr>
</thead>
<tbody>
<tr>
<td>sb</td>
<td>Absolute sagebrush foliar cover as measured via line-point intercept (LPI)^2</td>
</tr>
<tr>
<td>shrub</td>
<td>Absolute shrub foliar cover as measured via line-point intercept</td>
</tr>
<tr>
<td>VO</td>
<td>Visual obstruction as measured via a modified Robel pole^3</td>
</tr>
<tr>
<td>shrubHT</td>
<td>Height (cm) recorded for the tallest part of a shrub (excluding inflorescences) intercepting the transect line via line-point intercept</td>
</tr>
<tr>
<td>grassHT</td>
<td>Height (cm) of nearest grass measured while recording VO</td>
</tr>
<tr>
<td>bg</td>
<td>Absolute grass foliar cover as measured via line-point intercept</td>
</tr>
<tr>
<td>litter</td>
<td>Absolute litter and woody litter cover as measured via line-point intercept</td>
</tr>
<tr>
<td>herb</td>
<td>Total herbaceous foliar cover as measured via line-point intercept</td>
</tr>
<tr>
<td>exotic</td>
<td>Absolute exotic plant foliar cover as measured via line-point intercept</td>
</tr>
<tr>
<td>forb</td>
<td>Absolute forb foliar cover as measured via line-point intercept</td>
</tr>
</tbody>
</table>

^1 All predictors were collected in 50 × 50 m or 20 × 50 m plots.
^2 Bonham 1989. Absolute cover was measured based on the proportion of any LPI hits out of the total hits, and total cover was measured on the basis of the proportion of top hits out of the total hits (Tipton 2015).
^3 Robel et al. 1970. See text for further description.

Table 2: Count-based regression models for sagebrush-associated songbirds in northwest Colorado, 2013–2015. We report log-likelihood (LL), number of parameters (K), Bayesian information criterion (BIC), difference in BIC compared with lowest BIC of the model set (∆BIC), BIC weight (w), pseudo-R² value, root mean squared error (error) from 5-fold cross validation, and P value from likelihood ratio test for models with ∆BIC < 2 and intercept-only models.

<table>
<thead>
<tr>
<th>Model^2</th>
<th>LL</th>
<th>K</th>
<th>BIC</th>
<th>Delta</th>
<th>w</th>
<th>R²</th>
<th>Error</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brewer’s</td>
<td>Shrub + shrubHT</td>
<td>277.19</td>
<td>4</td>
<td>574.26</td>
<td>0.00</td>
<td>0.45</td>
<td>0.06</td>
<td>2.78</td>
</tr>
<tr>
<td>sparrow:</td>
<td>Shrub + shrubHT + herb + herb^2</td>
<td>272.42</td>
<td>5</td>
<td>574.65</td>
<td>0.39</td>
<td>0.37</td>
<td>0.08</td>
<td>2.78</td>
</tr>
<tr>
<td>Sage</td>
<td>Shrub + shrub^3</td>
<td>137.11</td>
<td>4</td>
<td>293.53</td>
<td>0.00</td>
<td>0.38</td>
<td>0.04</td>
<td>1.66</td>
</tr>
<tr>
<td>thrasher:</td>
<td>Intercept only</td>
<td>142.26</td>
<td>2</td>
<td>294.18</td>
<td>0.65</td>
<td>0.28</td>
<td>0.00</td>
<td>1.47</td>
</tr>
<tr>
<td>Sagebrush</td>
<td>Shrub + shrub^3 + L</td>
<td>135.28</td>
<td>5</td>
<td>294.71</td>
<td>1.18</td>
<td>0.21</td>
<td>0.05</td>
<td>1.64</td>
</tr>
<tr>
<td>sparrow:</td>
<td>Shrub + shrub^3 + grass + exotic</td>
<td>139.52</td>
<td>6</td>
<td>308.01</td>
<td>0.00</td>
<td>0.36</td>
<td>0.21</td>
<td>2.89</td>
</tr>
<tr>
<td>Green-tailed towhee:</td>
<td>Shrub + shrubHT + bg</td>
<td>131.83</td>
<td>5</td>
<td>288.51</td>
<td>0.00</td>
<td>0.57</td>
<td>0.19</td>
<td>2.29</td>
</tr>
<tr>
<td>Horned lark:</td>
<td>Shrub + L</td>
<td>239.95</td>
<td>4</td>
<td>499.22</td>
<td>0.00</td>
<td>0.55</td>
<td>0.12</td>
<td>3.22</td>
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<tr>
<td>Vesper</td>
<td>Shrub + bg</td>
<td>179.76</td>
<td>4</td>
<td>379.39</td>
<td>0.00</td>
<td>0.57</td>
<td>0.15</td>
<td>2.07</td>
</tr>
<tr>
<td>Vesper</td>
<td>Shrub + shrubHT + bg</td>
<td>177.56</td>
<td>5</td>
<td>379.98</td>
<td>0.58</td>
<td>0.43</td>
<td>0.16</td>
<td>2.11</td>
</tr>
<tr>
<td>Western meadowlark:</td>
<td>Intercept only</td>
<td>212.45</td>
<td>2</td>
<td>434.84</td>
<td>55.45</td>
<td>0.00</td>
<td>0.00</td>
<td>1.98</td>
</tr>
</tbody>
</table>

^1 Predictor variables described in Table 1.
^2 Did not run the likelihood ratio test to compare a null (intercept only) model against a null model.

and sagebrush sparrow, we included forb and exotic cover as they had an even distribution across these two areas; the variables had limited distribution across all three study areas, so they were excluded from the other species’ models.

We determined the negative binomial distribution was the best model structure for all songbird species. Abundances of all shrubland-associated songbirds were better explained by variation in total shrub cover rather than just sagebrush cover (Table 2). For both Brewer’s sparrow and sage thrasher, the best model was based on shrub attributes with no additional improvement in the model from herbaceous or ground layer attributes (Table 3). For green-tailed towhees, abundance was inversely associated with the amount of bare ground (see Table 3). For sagebrush sparrows, abundance was inversely associated with total cover of grasses and exotic plant cover (see Table 3).

For the grassland-associated birds, the best models were based on shrub cover and bare ground, with density consistently declining with increasing shrub cover across all three species (horned lark, vesper sparrow, western meadowlark; see Tables 2 and 3). Horned larks increased with decreasing litter cover (see Table 3), which was inversely correlated with bare ground exposure; thus, horned lark abundance increased with more bare ground (see Table 3). In contrast, vesper sparrows and western meadowlarks declined with increasing bare ground exposure (see Table 3).

All species’ top models explained more variation than a null model with the exception of sage thrasher. Green-tailed towhee, sagebrush and vesper sparrow, horned lark, and western meadowlark models explained the most variation and had good to excellent fit (see Table 2; McFadden 1979). All top models had low root mean squared errors from fivefold cross validation (see Table 2).

Songbird Density by State or Community Phase

In general, we predicted higher densities for shrubland-associated songbirds in the shrub-dominated community phases and higher densities for grassland-associated songbirds in the native grassland state and crested wheatgrass–grassland phase (Table 4). For example, we predicted approximately 3.3 Brewer’s sparrows/ha in the diverse shrubland phase compared with 0.8 Brewer’s sparrows/ha in the crested wheatgrass–grassland phase; for western meadowlarks, we predicted approximately 4.4 birds/ha in the native grassland state compared with 1.1 birds/ha in the crested wheatgrass–shrubland phase (see Table 4). Predicted songbird densities reflected relationships between songbird species and ground and shrub cover variables associated with the states and phases. Shrubland-associated species that preferred more shrub cover and taller shrubs (i.e., Brewer’s sparrow and green-tailed towhee) had higher predicted densities in the diverse...
Table 3
Beta coefficient estimates ($\beta$), standard errors (SE), and 95% confidence intervals for model parameters in the highest-ranked count-based regression model for sagebrush-associated songbirds in northwest Colorado, 2013–2015.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\beta$</th>
<th>SE</th>
<th>95% Lower</th>
<th>95% Upper</th>
</tr>
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<td>Brewer's sparrow:</td>
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<td>$-0.39$</td>
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<td>$0.01$</td>
<td>$0.02$</td>
</tr>
<tr>
<td></td>
<td>ShrubHT</td>
<td>$0.02$</td>
<td>$0.01$</td>
<td>$0.01$</td>
</tr>
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<td>$0.01$</td>
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<tr>
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<td>$0.01$</td>
<td>$0.01$</td>
</tr>
<tr>
<td></td>
<td>bg</td>
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<td>$0.02$</td>
<td>$-0.10$</td>
</tr>
<tr>
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<td>$0.04$</td>
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<tr>
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<td>Sagebrush sparrow:</td>
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<tr>
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<td>Exotic</td>
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<td>$-0.06$</td>
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<tr>
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<td>bg</td>
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<tr>
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<tr>
<td></td>
<td>bg</td>
<td>$-0.08$</td>
<td>$0.01$</td>
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<tr>
<td></td>
<td>Dispersion</td>
<td>$1.08$</td>
<td>$0.26$</td>
<td>$0.57$</td>
</tr>
</tbody>
</table>

$^1$ Predictor variables described in Table 1.

The results indicate that sagebrush-associated songbird densities are positively correlated with the percentage of shrub cover. This suggests that habitat characteristics such as shrub cover and ground cover are important for the abundance and species richness of these birds. The models also show that the presence of grassland and meadow habitats can influence the distribution of these songbirds. The use of multiple regression models allows for a more comprehensive understanding of the factors affecting the distribution of sagebrush-associated songbirds in the study area.

Discussion

The results of this study serve as a foundation for future research on the ecology of sagebrush-associated songbirds. The models developed in this study can be used to inform conservation efforts and restoration projects. For example, increasing shrub cover and ground cover can potentially benefit the songbird community, as suggested by the positive relationships observed in the models. Further studies could focus on the role of different successional stages in influencing songbird communities, as well as the effects of land use changes on the distribution and abundance of these species. Understanding these relationships is crucial for developing effective management strategies that support the conservation of sagebrush-associated songbirds.
and a diversity of taller shrubs for nesting (Aldridge et al. 2011; Dobbs et al. 2020). Thus, green-tailed towhee predicted densities were highest for the diverse shrubland community phase, which contained the greatest shrub cover, the tallest shrubs, and less bare ground on average than the other shrubland phases (see Fig. 2B).

Within grassland-associated songbirds, differences in peak predicted densities among the grassland phase and state also reflected different life history traits. Horned larks typically forage on the ground and place their nests in the open on bare ground (Beason 1995). Thus, horned lark predicted density was greatest for the crested wheatgrass-grassland phase, which was associated with more bare ground on average (see Fig. 2B). In contrast, vesper sparrows usually conceal their nests with grasses and forbs or other vegetation (Jones and Connelly 2020). Vesper sparrow abundance increased with less bare ground, so predicted vesper sparrow density was highest in the native grassland state, which had less bare ground on average than the crested wheatgrass-grassland phase.

These results reflect the value of alternative states within sagebrush ecosystems to support a diverse avian community. Although it is a shrub-dominated system, disturbances, management actions, and abiotic factors promote structural diversity within the sagebrush landscape. This structural diversity is represented by shrub- and grass-dominated states and community phases and supports both shrubland- and grassland-associated species (Rotenberry and Wiens 1980; Wiens and Rotenberry 1981). We likely would not have observed as many grassland species, such as horned larks, if fires had not created grassland patches in the study area. Even shrubland-associated songbirds have different habitat needs within sagebrush rangelands, from green-tailed towhees that prefer more sagebrush and herbaceous cover (i.e., the diverse shrubland phase) to sagebrush sparrows that prefer less shrub and ground cover (i.e., the needle-and-thread shrubland phase; Timmer et al. 2019). Indeed, no single state or phase in the STM captured the highest density for all species. By incorporating habitat relationships for shrubland and grassland-associated species in an STM, we can see the value of different states and phases for supporting bird diversity (Fuhlendorf et al. 2012). Our approach also allows managers to evaluate the tradeoff in ecosystem services from a state or community phase change. Shrubland-associated songbird densities may decline in response to a fire that transitions a native shrubland state to a native grassland state, but grassland bird densities and forage production for livestock would likely increase (see Fig. 2B).

Although our approach illustrates the value of alternative states and community phases in the sagebrush steppe, our models for songbird abundance did not incorporate landscape-level effects of the size or juxtaposition of different vegetation patches on songbird abundance. Such spatially explicit information may be especially important in predicting habitat quality or abundance for species, such as greater sage-grouse (Centrocercus urophasianus), that use multiple patch types across different seasons (Connelly et al. 2011). However, the bird species that we modeled all have relatively small breeding season home ranges that typically encompass a single vegetation patch type (at least at the scale at which we measured different states and phases) and then migrate out of the region during the nonbreeding season (Billerman et al. 2020).

Our approach of predicting how abundance varies across states and community phases within an STM is especially suited for these types of wildlife species. We also acknowledge that our study area consisted of large expanses of the diverse shrubland and needle-and-thread shrubland phases, interspersed with smaller patches of the native grassland and crested wheatgrass states (Tipton 2015). As a result, we cannot assess the degree to which our model predictions would apply to landscapes with extensive grasslands interspersed with smaller shrubland patches.

Managing for Variability in Vegetation Conditions Within States and Community Phases

One limitation of predicting songbird densities into states and community phases based on average vegetation conditions is that it obscures the influence of variability in vegetation conditions within a state or phase. Simply identifying the diverse shrubland community phase as the optimal phase for green-tailed towhees masks the influence of bare ground on their abundance because bare ground exposure varies from 0% to 37% within the diverse shrubland phase. Our count model predicts that towhee density can vary from ≈0.2 birds/ha at 37% bare ground to ≈1.1 birds/ha at 0% bare ground (see Fig. 3A). Similarly, vesper sparrow density was greatest in the native grassland state (see Table 4), and managing for average bare ground exposure in this state (6%) is predicted to result in ≈1.6 vesper sparrows/ha. However, vesper sparrow density varies from ≈3.2 vesper sparrows/ha at 0% bare ground exposure to < 1 vesper sparrow/ha at 18% bare ground exposure (see Fig. 3B).
For both of these species, it is easy to visualize the benefit of managing for less bare ground, which is often a land management objective (Morgan 2005). However, this approach could be especially useful for visualizing how species with different habitat needs, such as a shrubland- and grassland-associated songbird, respond to variation in vegetation conditions from management actions, like shrub removal. There could be a threshold of treatment that minimizes negative impacts to both species or maximizes benefit to the species of greatest conservation concern. Understanding the effect of vegetation variability on wildlife populations within a state or phase could therefore increase management options and promote progress toward wildlife population goals (Hiers et al. 2016).

**Conclusion**

By incorporating songbird count models into an STM developed for the sagebrush steppe in northwestern Colorado, we can predict songbird response to vegetation change among states and community phases in a way that can be clearly communicated to land and wildlife managers. Managers can also see how alternative states and community phases within an STM benefit songbird species of concern within and across habitat associations. Further, understanding how songbird density varies with the natural range of vegetation conditions rather than just average conditions provides greater flexibility when managing multiple species of concern with different habitat needs (Hiers et al. 2016). Because rangeland systems are complex and dynamic, we argue that STMs should communicate ecosystem change both among and within states and phases, as well as how these changes impact ecosystem services in order to be useful tools for rangeland managers.

**Management Implications**

If managers or landowners within the sagebrush steppe of northwestern Colorado manipulate understory or ground vegetation, then our approach provides them with a tool to gauge how songbird densities may change in response. For example, if a manager promotes vegetation characteristics associated with the diverse shrubland state, such as greater shrub and herbaceous cover and taller shrubs, then green-tailed towhees would likely benefit. Our approach also allows managers to evaluate the trade-offs in managing for one songbird species or one state or phase over another. We predicted the highest green-tailed towhee density for the diverse shrubland community phase and the highest sagebrush sparrow density for the needle-and-thread shrubland phase. If managers treated one of these shrubland phases as the management standard or reference condition and promoted it on the landscape above other states and phases (USDA NRCS 1997), this could have negative consequences for other songbirds (Derner et al. 2009; Fuhlendorf et al. 2012).

A manager may also want to understand the range of songbird densities within a state or phase based on the natural variability of understory and ground conditions. For example, shrub height within the diverse shrubland phase varied from 25 cm to 67 cm (see Fig. 2B). Therefore, a manager could expect green-tailed towhee density to vary across this phase on the basis of minimum (≈0.2 birds/ha) and maximum (≈0.7 birds/ha) shrub height and also predict the effect of managing for average shrub height conditions (≈0.4 birds/ha; see Fig. 3A). Finally, managers can estimate how other ecosystem services might respond to a landscape disturbance, such as fire. In our study area, a fire transitioning the needle-and-thread shrubland community phase to a native grassland state is predicted to reduce Brewer’s sparrow density by ≈2 birds/ha (see Table 4) but increase forage for domestic or wild ungulates by roughly 350 kg/ha (see Fig. 2B). These tradeoffs can be empirically evaluated by using traditional wildlife count models to predict wildlife densities across ecological states and phases in an STM (Ritten et al. 2018).

**Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References


