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Research Article

Managing for Multiple Species: Greater Sage-Grouse and Sagebrush Songbirds

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ABSTRACT Human activity has altered 33–50% of Earth's surface, including temperate grasslands and sagebrush rangelands, resulting in a loss of biodiversity. By promoting habitat for sensitive or wide-ranging species, less exigent species may be protected in an umbrella effect. The greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) has been proposed as an umbrella for other sagebrush-obligate species because it has an extensive range that overlaps with many other species, it is sensitive to anthropogenic activity, it requires resources over large landscapes, and its habitat needs are known. The efficacy of the umbrella concept, however, is often assumed and rarely tested. Therefore, we surveyed sage-grouse pellet occurrence and sagebrush-associated songbird abundance in northwest Colorado, USA, to determine the amount of habitat overlap between sage-grouse and 4 songbirds (Brewer's sparrow [*Spizella breweri*], sage thrasher [*Oreoscoptes montanus*], sagebrush sparrow [*Artemisiospiza nevadensis*]), and green-tailed towhee [*Pipilo chlorurus*]). During May and June 2013–2015, we conducted standard point count breeding surveys for songbirds and counted sage-grouse pellets within 300 10-m radius plots. We modeled songbird abundance and sage-grouse pellet occurrence with multi-scaled environmental features, such as sagebrush cover and bare ground. To evaluate sage-grouse as an umbrella for sagebrush-associated passerines, we determined the correlation between probability of sage-grouse pellet occurrence and model-predicted songbird densities per sampling plot. We then classified the sage-grouse probability of occurrence as high (probability >0.5) and low (probability ≤0.5) and mapped model-predicted surfaces for each species in our study area. We determined average songbird density in areas of high and low probability of sage-grouse occurrence. Sagebrush cover at intermediate scales was an important predictor for all species, and ground cover was important for all species except sage thrashers. Areas with a higher probability of sage-grouse occurrence also contained higher densities of Brewer's sparrows, green-tailed towhees, and sage thrashers, but predicted sagebrush sparrow densities were lower in these areas. In northwest Colorado, sage-grouse may be an effective umbrella for Brewer's sparrows, green-tailed towhees, and sage thrashers, but sage-grouse habitat does not appear to capture areas that support high sagebrush sparrow densities. A multi-species focus may be the best management and conservation strategy for several species of concern, especially those with conflicting habitat requirements.

KEY WORDS biodiversity, Brewer's sparrow, correlation, count-based regression, greater sage-grouse, green-tailed towhee, sage thrasher, sagebrush sparrow, umbrella.

Human activity, such as resource use and extraction and land-use conversion, has altered 33–50% of Earth's surface, which has consequences on regional climates, global carbon fluctuations, hydrological cycles, and biodiversity (Vitousek et al. 1997, Foley et al. 2005). The sagebrush ecosystem of western North America has been altered to promote agriculture, urban development, energy extraction, and herbaceous forage for livestock, and it occupies about half its historical distribution (Knick et al. 2003). With the current and projected alteration of native habitat in grassland, sagebrush, and other ecosystems, extinction rates for wildlife populations and species are unprecedented (Vitousek et al. 1997).

Managing for entire ecosystems may be more effective to conserve populations and species and promote ecosystem services, but biologists often monitor and manage with a single-species focus (Vitousek et al. 1997, Boyd et al. 2014). Many biologists manage for single species to generate support and awareness for the conservation of ecosystems that support charismatic species, such as Florida panthers (*Puma concolor coryi*; Simberloff 1998). Some biologists, however, are mandated via regulation (e.g., the Endangered Species

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Act) to manage for specific ecosystems that support protected species, such as old-growth forest and northern spotted owls (*Strix occidentalis caurina*; Simberloff 1998). Protecting habitats for wide-ranging or sensitive species could promote habitat for less exigent species in an umbrella effect and thus, promote biodiversity (Roberge and Angelstam 2004). However, the effectiveness of umbrella species for conservation and management of multiple species is often assumed and rarely tested (Simberloff 1998). Bifolchi and Lodé (2005) tested the umbrella concept with European otters (*Lutra lutra*) and found no difference in species richness for several taxa between paired sites with and without otters. Generalist species may serve as better umbrella species compared to specialists, such as otters, but potential beneficiary species should share similar habitat requirements (Bifolchi and Lodé 2005).

The greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) has been proposed as an umbrella for other sagebrush-obligate species (Rowland et al. 2006, Hanser and Knick 2011). Sage-grouse should be an effective umbrella because they have a large annual home range that overlaps with many other species (Braun et al. 1976), they are fairly sensitive to anthropogenic activity (Naugle et al. 2011), their biology is known (Patterson 1952), and many habitat recommendations have been evaluated and published for sage-grouse (Connelly et al. 2000). Further, sage-grouse use different areas throughout the year, reflecting their seasonal habitat needs. In winter, sage-grouse feed almost exclusively on sagebrush shrubs (Patterson 1952) and are often in areas with dense shrub cover (Carpenter et al. 2010). During summer, sage-grouse raise broods in mesic areas containing low shrub canopy cover and high plant diversity for abundant arthropods and succulent forbs (Connelly et al. 2000, Hagen et al. 2007). Therefore, environments that meet the differing seasonal needs of sage-grouse should also meet the needs of a variety of sagebrush-dependent species.

Sage-grouse populations have declined range-wide because of various factors that have fragmented and degraded sagebrush rangelands (Garton et al. 2011). Thus, large- and small-scale conservation efforts (e.g., Sage Grouse Initiative) are underway to promote sage-grouse habitat and prevent further declines in sage-grouse populations (U.S. Fish and Wildlife Service [USFWS] 2015). Many avifauna species dependent on this ecosystem have also experienced population declines and are of conservation concern (Braun et al. 1976, Knick et al. 2003). Over the last 50 years, Brewer's sparrow (*Spizella breweri*), sagebrush sparrow (*Artemisiospiza nevadensis*), sage thrasher (*Oreoscoptes montanus*), and green-tailed towhee (*Pipilo chlorurus*) populations have declined in all or specific regions of the western United States according to annual Breeding Bird Survey data (Dobkin and Sauder 2004). It is unclear how efforts to promote sage-grouse habitat will affect passerine species that are also completely or partially dependent on sagebrush (*Artemisia* spp.). Sagebrush rangelands are not homogenous and habitat features relevant to sage-grouse may not be relevant to species with smaller home ranges (Hanser and Knick 2011). For example, in areas actively managed for sage-grouse in Wyoming, USA, the relationship between sage-grouse and sagebrush-obligate songbirds is not always positive at fine scales, such as nest sites (Carlisle 2017, Carlisle et al. 2018). Previous efforts to evaluate sage-grouse as an umbrella examined overlap in broad land-cover types within species' ranges (Rowland et al. 2006), but several studies have reported that sagebrush avifauna respond to habitat features and disturbance at multiple scales (Wiens et al. 1987, Chalfoun and Martin 2007, Doherty et al. 2008, Carpenter et al. 2010, Aldridge et al. 2011). Thus, umbrella relationships should be evaluated in a multi-scaled framework (Hanser and Knick 2011).

Given the reduction in sagebrush rangelands and associated avifauna populations, understanding niche conditions that affect avifauna distribution and abundance could help inform conservation of this ecosystem and its associated species. These relationships could inform land-use planning and management decisions, which are needed for species of conservation concern, such as sage-grouse and Brewer's sparrow. Further, the decline in sage-grouse populations and the impetus to manage for sage-grouse habitat begs the question of how managing for 1 species could affect other species with potentially similar habitat requirements. To address these concerns, we tested the hypothesis that sage-grouse are an effective umbrella for sagebrush-associated songbirds (Brewer's and sagebrush sparrow, green-tailed towhee, and sage thrasher) in northwest Colorado, USA, because sage-grouse habitat should encompass habitat for these songbirds. On the basis of this hypothesis, we predicted that areas with a high probability of sage-grouse occurrence (based on pellet occurrence) should contain high densities of these 4 songbirds, with higher densities suggesting greater resource quality or quantity for songbirds (Boyce and McDonald 1999) compared to areas of low probability of sage-grouse occurrence. We also predicted that species richness for these songbirds should be higher in areas with a higher probability of sage-grouse occurrence (compared to areas with a low probability of sage-grouse occurrence) if sage-grouse habitat is capturing habitat for these songbirds.

STUDY AREA

We conducted sage-grouse pellet surveys and songbird point count surveys on privately and publicly owned lands in Moffatt County in northwest Colorado, USA (Fig. 1). In this region, migratory birds generally return to their breeding grounds mid-March to late April, court May through early July, nest mid-May through late July, fledge chicks June through August, and depart for fall migration in August or September (Wickersham 2016). Sage-grouse typically breed on leks mid-March through early June, nest from late April to late June, raise broods from mid-May through September, and winter November through February (Colorado Parks and Wildlife [CPW] 2008).

The 2 study sites, East and West Moffat, were characterized as sagebrush steppe and composed primarily

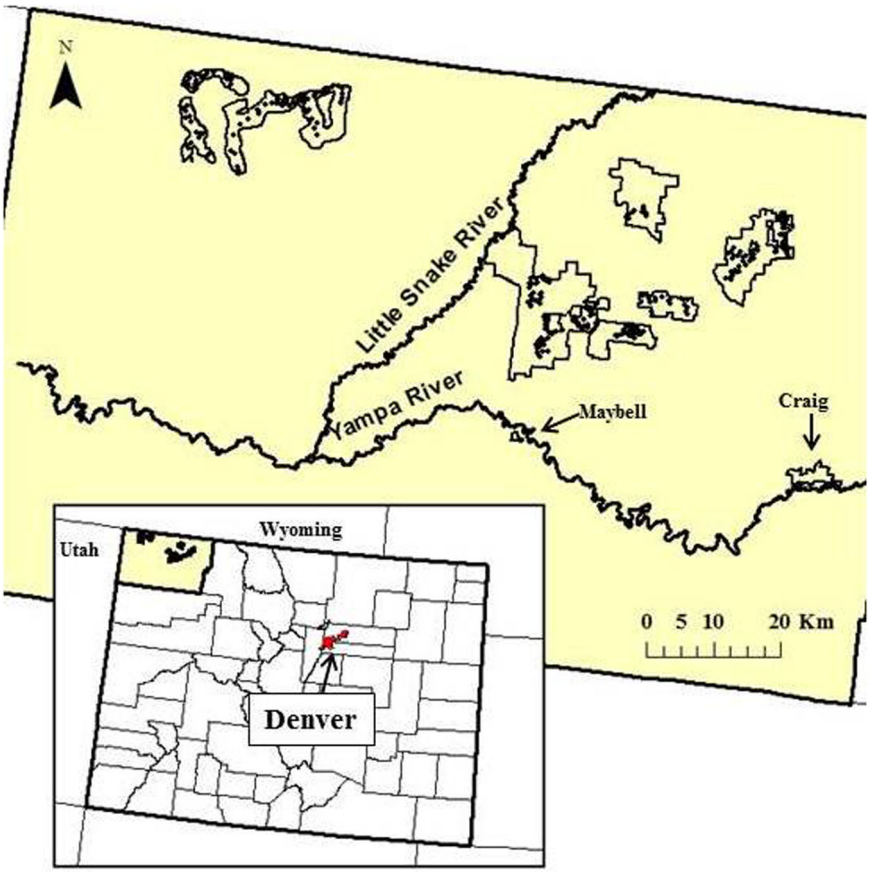

Figure 1. Study area for sagebrush-associated songbird and greater sage-grouse pellet surveys (shown as black dots), in Moffat County, northwest Colorado, USA, 2013–2015. The West Moffat study site is located west of Little Snake River and East Moffat study site is to the east of the river.

of various big sagebrush (*Artemisia tridentata* spp.) communities with either a bunchgrass (e.g., bluebunch wheatgrass [*Pseudoroegneria spicata*] or western wheatgrass [*Pascopyrum smithii*]) understory. Wyoming big sagebrush (*A. t. wyomingensis*) communities dominated the East Moffat site and low sagebrush (*A. arbuscula*)-salt shrub (*Atriplex* sp.)-Wyoming big sagebrush communities dominated the West Moffat site. Annual precipitation varied between 18 cm and 30 cm for East Moffat and 20–40 cm for West Moffat (Miller et al. 2011). Both sites included elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*) as the dominant fauna year-round (CPW 2019). The East Moffat site (~38,200 ha in size with average elevation of 2,020 m) was comprised mostly of sandy or loamy soils (Tipton 2015), whereas West Moffat (~13,420 ha and average elevation of 2,050 m) contained sandy, loamy, and clay soils (U.S. Department of Agriculture Natural Resources Conservation Service [USDA NRCS] 2013). Three wildfires occurred before surveys and overlapped portions of on the East Moffat study site: a 3,185-ha wildfire in 2010, a 10,243-ha wildfire in 2008, and a smaller 1,505-ha fire in 2008 (Monitoring Trends in Burn Severity 2012). The East Moffat site was grazed by cattle and sheep during spring and fall or summer, whereas the West Moffat site was grazed by cattle during fall, winter, and spring. Both sites were grazed at or below recommended guidelines intended to minimize negative long-term effects to forage species (Bureau of Land Management 2005). We collected data from mid-May to late June 2013–2015.

METHODS

To test our predictions in an observational study, we surveyed sage-grouse occurrence and sagebrush-associated songbird abundance (i.e., Brewer's and sagebrush sparrows, sage thrashers, and green-tailed towhees) in northwest Colorado, modeled sage-grouse occurrence and songbird counts with multi-scaled environmental features using logistic regression and count-based regression models, determined the correlation between probability of sage-grouse pellet occurrence and model-predicted songbird densities, and determined average songbird densities and species richness in areas with a higher probability of sage-grouse occurrence. We assumed that areas containing more sage-grouse pellets received more use by sage-grouse than areas with fewer pellets.

We selected sampling locations in a stratified random design based on the objectives of a larger collaborative project to build state-and-transition models in each study site with local input and field data (Bruegger et al. 2016). In East Moffat, we randomly allocated survey points spaced >200 m apart within past treatments or disturbances (e.g., fire) and areas with no treatments or disturbances on target ecological sites (e.g., Rolling Loam and Sandyland; Tipton 2015).

Thus, sampling locations were randomly distributed first among target ecological sites, and secondly in disturbed and undisturbed areas, so that we captured the variability in sagebrush cover across the dominant ecological sites in our study site. In West Moffat, we stratified survey points based on big sagebrush cover (Homer et al. 2012) and elevation to capture landscape variability because ecological sites were too finely intermingled to target sampling locations (USDA NRCS 2013). We allocated greater effort to strata containing higher sagebrush cover (i.e., ≥4%) because these areas represented a larger proportion of our study area. To estimate sage-grouse occurrence, we surveyed within a 10-m radius for sage-grouse pellets at each songbird plot. To survey plots, we attached a measuring tape to a piece of rebar in the center of each plot and searched within 2-m increments to reduce observer error. Even though we were mainly interested in presence or absence of sage-grouse pellets, we recorded the number of single pellets, roost piles, and number of pellets per roost pile for other research objectives. We also surveyed a subset of plots within 1–2 days of initial survey for a simple mark-resight study to estimate naïve pellet detectability and ensure we were detecting most of the pellets within a plot (Pollock et al. 2002).

To estimate songbird abundance, we conducted standard point count surveys at the center of each pellet count plot following distance sampling protocol (Buckland et al. 2001). The protocol included focusing on detections at and surrounding the point, measuring radial distance with rangefinders to the bird or object near the bird to estimate the distance, and recording distance to where we first detected a bird (Buckland et al. 2001). We identified birds aurally and visually within a 6-minute interval at each point and attempted to record individuals only once. We conducted surveys during the breeding season from sunrise to approximately 4 hours after sunrise depending on weather. We did not conduct surveys during inclement weather, such as rain or windy conditions when activity or detectability of the birds was hindered. We also conducted surveys beginning at lower elevation sites earlier in the breeding season and moving up in elevation as the season progressed to capture the phenology of the birds' breeding activity (Hanni et al. 2013). We conducted surveys 1 time a field season at each pellet and songbird plot with the exception of the subset of plots surveyed twice to estimate pellet detectability. Most of the plots (236 out of 300) were only surveyed in 1 year; however, to determine if songbird data could be pooled across years, we surveyed a subset of plots in consecutive seasons to compare songbird densities (eq. 3.102 in Buckland et al. 2001).

Songbird Detection Probabilities

To estimate songbird abundance, we used Program Distance (Distance 6.0, http://www.ruwpa.st-and.ac.uk/distance/, accessed 15 Jul 2014) and examined several detection model forms (e.g., half-normal). We excluded outlier detections based on visual inspection of detection histograms and binned distances accordingly (Buckland et al. 2001). We compared models with detectability variables using the Multiple Covariate Distance Sampling engine. Variables included survey start time, ordinal date of survey, observer, how the bird was detected (i.e., calling, singing, and visual), temperature, cloud cover (i.e., 0 = 0–15% cloud cover, 1 = 16–50% cloud cover, 2 = 51–75% cloud cover, and 3 = 76–100% cloud cover), and wind speed (0 = <0 km/hr, 1 = 1.6–4.8 km/hr, 2 = 6.4–11.3 km/hr, 3 = 12.9–19.3 km/hr, and 4 = 20.9–29.0 km/hr; Hanni et al. 2013). We evaluated models for variables affecting detection probability in 3 model sets: the weather set included the 3 weather variables, the time set included start time and ordinal date, and the observer set included observer and how the bird was detected. We compared univariable models and models with all combinations of variables for each model set (including a null model with no covariates) and retained the best model from each set based on the lowest Akaike's Information Criterion (AIC) score (Burnham and Anderson 1998). We then predicted density estimates for each plot using the best detection model for each species. We used the best detection model for each species to calculate an offset term based on the mean density and survey effort at each point count plot, and included the offset term in subsequent count-based regression models to adjust counts for heterogeneity in detection (Buckland et al. 2009).

Predictor Selection

Given limited information on how sagebrush avifauna scale their environment in northwest Colorado and the importance of a multi-scaled approach to understand habitat relationships (Johnson 1980), we followed a similar hierarchical exploratory approach as outlined in Leu et al. (2011). We first summarized land-cover predictors in ArcMap 10.0 (Environmental Systems Research Institute, Redlands, CA, USA) within 3 moving window scales: 0.56 km, 1 km, and 5 km of each survey point. We chose scales based on previous studies of sage-grouse and sagebrush songbird habitat selection. Previous modeling efforts reported that the amount of sagebrush within 1 km of a used site best explained sage-grouse site selection (Carpenter et al. 2010, Hanser et al. 2011), and sagebrush cover within 5 km of a lek was positively correlated with lek trends across the greater sage-grouse range (Johnson et al. 2011). In the Wyoming Basin region, the top models explaining Brewer's sparrow, green-tailed towhee, sagebrush sparrow, and sage thrasher abundance included variables at multiple scales (e.g., all big sagebrush cover within a 1-km extent and mountain big sagebrush [*A. t. vaseyana*] cover within a 5-km extent; Aldridge et al. 2011). To incorporate a finer scale of habitat selection, we also included the pixel value for land-cover variables at each plot (i.e., 30 m × 30 m; Homer et al. 2012).

To summarize multi-scaled land-cover predictors, we used a remotely sensed layer developed for sagebrush rangelands across Montana, Wyoming, and northern Colorado (Homer et al. 2012). The biotic predictors included percent cover of all sagebrush (all *Artemisia* spp.), big sagebrush, tall sagebrush (i.e., sagebrush > 29 cm), total shrubs, litter, herbaceous understory, and bare ground, shrub height, and sagebrush height (Homer et al. 2012). We did not explore

relationships with anthropogenic features, such as oil or gas wells, because few features occurred throughout the study area.

Model Development and Assessment

We evaluated count-based regression models for songbird counts and logistic regression models for sage-grouse occurrence using the multi-scaled predictors. For songbird models, we excluded songbird counts beyond the truncation distance (as determined by detection histograms) and included an offset term to scale counts for detection heterogeneity across plots (Buckland et al. 2009). If a plot had zero counts, we used the average offset value from plots with a count for each species (Aldridge et al. 2011). For sage-grouse models, we assigned a 1 to plots where we found sage-grouse pellets or roost piles and a 0 to plots where we did not detect any sage-grouse pellets.

For songbirds, we first identified the appropriate data distribution (i.e., Poisson or negative binomial) for each species' count data using an intercept-only model and comparing AIC values for the 2 models. We also used Vuong's test to confirm the appropriate data distribution (Hilbe 2011). We chose not to explore zero-inflated models for 2 reasons. First, a higher frequency of zero counts can be represented with a negative binomial distribution with a low mean and this distribution also accounts for overdispersed data, so the more complicated model structure is unnecessary (Warton 2005, Hilbe 2011). Second, zero-inflated models assume that excessive zeros are partly due to organisms not occurring in the area of interest (Warton 2005), which was not valid for our focal species.

For sage-grouse and songbirds, we examined scatterplots of every variable with raw counts at each scale and histograms of counts or occurrence to check for nonlinear relationships, outliers, and variables with limited variation across the study area. If plots showed evidence of nonlinearity, we evaluated a linear and a quadratic model to assess fit of the functional form of the covariate using AIC to determine which model structure to retain (i.e., retained the model form with the lowest AIC score). We then determined the best spatial extent for each variable in the sage-grouse and songbird analyses by evaluating univariable regression models and retaining the scale of each variable with the greatest explanatory power (i.e., lowest AIC score; Leu et al. 2011). We first used Pearson's correlation coefficient as a preliminary screening for correlation among variables (i.e., $r \geq |0.7|$; Zar 2010) and excluded correlated variables from the same model. To ultimately assess multicollinearity, we examined variance inflation factors (VIF) for each species' top model(s) if they contained multiple variables (Menard 1995), excluding models if mean model scores were >2 (Chatterjee et al. 2000). We performed all analyses in R (R Development Core Team 2015).

We developed candidate models from combinations of the top predictor variables (excluding overly correlated variables) and ranked the models according to AIC to determine the best model(s) explaining sage-grouse occurrence and songbird abundance. We determined competitive models as a model with $\Delta AIC \leq 2$ (Burnham and Anderson 1998). To avoid over-fitting models, we did not include >1 variable per 10% of plots with ≥1 songbird or pellet detection in any model (Hosmer and Lemeshow 2000). We also excluded models when coefficients for any variable were unstable and switched direction of influence across models (Arnold 2010).

To assess the fit of models over an intercept-only (null) model, we calculated a McFadden's pseudo-R^2 value for all models, which differs from traditional R^2 values in that it is an estimate of the total variation explained by a model rather than the proportion; a pseudo-R^2 value tends to produce lower values than the traditional R^2 statistic (McFadden 1977). We also used a χ^2 likelihood ratio test with the lrtest function in package lmtest to determine goodness of fit for the top model over an intercept-only model. Because we did not have independent datasets to evaluate the predictive capability of our top models, we evaluated predictive success using 5-fold cross validation (Hastie et al. 2009) with the cvFit function in package cvTools (Alfons 2015). We also evaluated the area under the curve for a receiver operating characteristic (ROC) to determine the predictive performance of our sage-grouse occurrence models (Hosmer and Lemeshow 2000).

Umbrella Concept

To determine the effectiveness of sage-grouse as an umbrella for songbirds in our study area, we used 2 approaches. We first examined the Pearson's correlation coefficient between model-predicted songbird densities and probability of sage-grouse pellet occurrence. We hypothesized that sage-grouse should be an effective umbrella if $r > 0.5$, with greater correlation indicating increasing overlap between species. We then mapped model-predicted songbird densities within the East and West Moffat study sites. In East Moffat, we predicted models to all area within participating landowner property boundaries. This approach was reasonable because our target ecological sites comprised the majority of the study site (USDA NRCS 2013) and we sampled across a range of sagebrush cover (0–26%) from disturbed areas (burned and mechanically treated) to undisturbed areas. We did not sample on dryland agricultural fields, however, and even though sage-grouse use these fields (B. L. Walker, CPW, personal communication), they comprise a small proportion of the study site. In West Moffat, we restricted model predictions to areas similar to our sampling locations because we did not sample across the range of vegetation types and topography in this area. Our sampling locations occurred mainly on ridgetops with sagebrush and salt shrub communities because the valleys contained little sagebrush and access was more difficult. However, we sampled across a gradient of sagebrush cover (0–16%) on the ridgetops.

We model averaged predictions for songbird densities and probabilities of sage-grouse pellet occurrence if there were multiple competitive models (i.e., $\Delta AIC \leq 2$; Burnham and Anderson 1998, Cade 2015). For mapping purposes, we classified the predicted probability of sage-grouse pellet

occurrence as low or high based on the sensitivity-specificity equality threshold (Liu et al. 2005). We used the OptimalCutpoints package in R (R Development Core Team 2015) to determine the optimal threshold, which minimized the absolute value of the difference between sensitivity and specificity (Lòpez-Ratòn et al. 2014). We highlighted areas where sage-grouse were predicted to occur with greater probability to determine if songbird densities were greatest in these areas. We then estimated average songbird densities in areas where sage-grouse were more and less likely to occur for comparison.

We also calculated a richness index for the songbird species following Aldridge et al. (2011). We classified the predicted densities as a 1 using the minimum density to support a songbird territory or 1 breeding pair. We based the largest territory size on what was reported for each species in the Birds of North America species' accounts (Rodewald 2015) or CPW species' accounts (Boyle and Reeder 2005). For green-tailed towhee, we could not find a reliable source for largest territory size reported, so we used the minimum density reported for Bureau of Land Management lands in Colorado from 2011 to 2017 (Bird Conservancy of the Rockies 2017). Finally, we estimated songbird richness in areas where sage-grouse were more likely to occur and also where sage-grouse were less likely to occur for comparison.

RESULTS

We surveyed 300 plots for sage-grouse pellets and songbirds: 198 plots in East Moffat and 102 plots in West Moffat. We detected 854 Brewer's sparrows (on 233 plots), 158 green-tailed towhees (on 76 plots), 216 sagebrush sparrows (on 77 plots), 263 sage thrashers (on 133 plots), and single pellets or roost piles on 151 plots ($\bar{x} = 15$ pellets and 2 piles per plot). Of the 151 plots on which we detected sage-grouse pellets or roost piles, we detected Brewer's sparrows on 132 plots, green-tailed towhees on 53 plots, sage thrashers on 84 plots, and sagebrush sparrows on 31 plots. We detected few sagebrush sparrows in the East Moffat site (8 birds on 6 plots), so we included only count data from West Moffat for subsequent sagebrush sparrow models and predicted only the best model(s) to West Moffat.

Detection Probabilities

We did not find a difference in songbird density estimates from 64 plots surveyed in consecutive years; therefore, we combined detections across the 3 field seasons. For Brewer's sparrows, we truncated distances >200 m and binned the data into 7 bins *post hoc* to improve density estimates (Buckland et al. 2001). The best detection model was the hazard rate function with simple polynomial adjustments and no detection variables. Average Brewer's sparrow density was 1.92 birds/ha. For green-tailed towhees, sagebrush sparrows, and sage thrashers, we truncated distances >220–250 m and binned the data into 6 or 7 bins. The best detection model for green-tailed towhees was a half-normal function with how the bird was detected, observer, temperature, and cloud cover. Average green-tailed towhee density was 0.16 birds/ha. The best detection model for sagebrush sparrows was the half-normal function with how the bird was detected and start time. Average sagebrush sparrow density was 0.25 birds/ha. The best detection model for sage thrashers was a half-normal function with no adjustments and how the bird was detected and cloud cover. Average sage thrasher density was 0.15 birds/ha. From the mark-resight study, we estimated high sage-grouse pellet detectability (i.e., >0.8), so we did not considered it an issue in subsequent modeling efforts.

Model Development

Both Vuong's test and AIC suggested the negative binomial distribution was the best model structure for Brewer's sparrows, green-tailed towhees, and sage thrashers. For sagebrush sparrows, Vuong's test indicated a negative binomial model was best, though the strength of that selection was weak ($P = 0.10$) and the data were not overdispersed ($\bar{x} = 2.01$, variance = 2.58). Including a shrub or sagebrush cover variable resulted in a lower AIC value for the Poisson model and a lack of convergence in the negative binomial model, so we used a Poisson distribution for subsequent sagebrush sparrow models.

Big sagebrush cover, all sagebrush cover, tall sagebrush cover, and total shrub cover were highly correlated at all scales, so we retained only the best shrub structure variable for each species (Table 1). Further, we could not include tall sagebrush cover in sagebrush sparrow models because of a limited occurrence of this predictor in the West Moffat site. For the top sage-grouse models, the model including tall sagebrush cover within 1 km and herbaceous cover within 5 km was competitive (Table 2). However, herbaceous cover was highly correlated with litter in the second-best model ($r \geq |0.7|$) and was thus, excluded as redundant. All supported models of songbird abundance and pellet occurrence included a quadratic relationship for the sagebrush cover variables and with the exception of sage thrashers, supported models also included a relationship with herbaceous cover or litter (Table 3; Fig. 2). Although we did not use confidence limits to exclude uninformative parameters, we present 85% confidence limits because AIC includes parameters at a 0.157 α level (Arnold 2010), and we wanted to show biological relevance rather than statistical relevance at the standard 0.05 α level.

Umbrella Concept

For the model-predicted songbird densities and probability of sage-grouse pellet occurrence, the correlation was positive with Brewer's sparrows ($r = 0.72$), green-tailed towhees ($r = 0.72$), and sage thrashers ($r = 0.68$) but negative with sagebrush sparrows ($r = -0.79$ for West Moffat only). All correlations between probability of pellet occurrence and predicted songbird densities were significant ($P < 0.001$).

We estimated greater densities for Brewer's sparrows and green-tailed towhees in areas with a high probability of sage-grouse occurrence, whereas sagebrush sparrow predicted densities were lower in areas more likely to contain

Table 1. Best scale (30 m, 564 m, 1 km, 5 km) and form (L = linear and Q = quadratic) for predictors used in logistic and count-based regression models for greater sage-grouse and sagebrush-associated songbirds in northwest Colorado, USA, 2013–2015. Best base refers to the best sagebrush predictor from total shrub cover (shrub), all sagebrush cover (all sage), big sagebrush cover (big sage), and tall sagebrush cover (tall sage). We retained only 1 sagebrush predictor for each species because of high correlation among the sagebrush predictors. We also present the best scale and form for shrub height, sagebrush shrub height (sage height), and percent cover of bare ground (bare), herbaceous understory (herb), and litter (litter).

Predictor	Brewer's sparrow	Green-tailed towhee	Sagebrush sparrow	Sage thrasher	Sage-grouse pellets
Shrub 30 m	Q, best	Q	L	L	Q
Shrub 564 m	L	Q, best	Q	L	Q
Shrub 1 km	L	Q	Q, best	L, best	Q, best
Shrub 5 km	L	Q	Q	L	Q
All sage 30 m	L, best	Q	L	L, best	Q, best
All sage 564 m	L	Q, best	Q	L	Q
All sage 1 km	L	Q	Q, best base	L	Q
All sage 5 km	L	L	Q	L	Q
Big sage 30 m	Q, best	Q	L	L, best	Q
Big sage 564 m	L	Q, best	Q	L	Q
Big sage 1 km	L	Q	Q	L	Q, best
Big sage 5 km	L	Q	Q, best	L	Q
Tall sage 30 m	L	L	NA[a]	L	L
Tall sage 564 m	Q	Q	NA	Q, best base	Q
Tall sage 1 km	Q, best base	Q, best base	NA	Q	Q, best base
Tall sage 5 km	Q	Q	NA	Q	Q
Shrub height 30 m	L, best	Q	L	L, best	Q, best
Shrub height 564 m	L	Q	L	L	Q
Shrub height 1 km	L	Q	L, best	L	Q
Shrub height 5 km	L	Q	L	L	Q
Sage height 30 m	L, best	Q	L	L, best	Q
Sage height 564 m	L	Q	L	L	Q, best
Sage height 1 km	L	Q	L	L	Q
Sage height 5 km	L	Q	L, best	L	Q
Bare 30 m	L, best	L, best	Q	L, best	L, best
Bare 564 m	L	L	Q	L	L
Bare 1 km	L	L	Q, best	L	L
Bare 5 km	L	L	Q	L	L
Herb 30 m	L	L	Q	L	Q
Herb 564 m	L	L	Q	L	Q
Herb 1 km	L	L	Q	L	Q
Herb 5 km	L, best	L, best	Q, best	L, best	L, best
Litter 30 m	L	L, best	L	L	L, best
Litter 564 m	L, best	L	Q	L, best	L
Litter 1 km	L	L	Q, best	L	L
Litter 5 km	L	L	Q	L	L

[a] Tall sagebrush cover not included in sagebrush sparrow models because of a limited occurrence of this predictor in the West Moffat site.

sage-grouse (Table 4; Fig. 3). Sage thrasher densities were slightly higher in areas with a high probability of sage-grouse occurrence. Species richness of 1 (20%) or 2 (69%) species was more common than species richness of 3 (11%) or 4 (0%) species in areas with a low probability of sage-grouse occurrence. Richness of 3 species was most common (80%) in areas with a greater probability of sage-grouse occurrence (1 species = 8%, 2 species = 12%, 4 species = 0%; Fig. 4).

DISCUSSION

When evaluating model-predicted songbird densities across the study area, our first prediction was met for Brewer's sparrow, green-tailed towhee, and sage thrasher. Densities were higher in areas with a higher probability of sage-grouse occurrence, although only slightly higher for sage thrashers (Fig. 3). These results suggest sage-grouse could be an effective umbrella for these 3 species and they align with several previous studies. Brewer's sparrows, green-tailed towhees, and sage thrashers have greater overlap with sage-grouse along a multi-scaled environmental gradient across the Intermountain West region, although the strength and direction of association between sage-grouse and songbirds varies across scales (Hanser and Knick 2011). Brewer's sparrow and sage thrasher abundance throughout the western United States is greater for landscapes containing active sage-grouse leks, which is attributed to greater sagebrush cover surrounding leks (Donnelly et al. 2016). Finally, Brewer's sparrow and green-tailed towhee abundance has been reported to increase for 3 years following juniper (*Juniperus* spp.) removal to restore sage-grouse habitat (Holmes et al. 2017).

In our study, there was greater correlation between sage-grouse and Brewer's sparrows, green-tailed towhees, and sage thrashers because they all selected for similar features, often at similar scales (Table 2). All 4 species were associated with moderate tall sagebrush cover at intermediate scales (564 m or 1 km). Brewer's sparrow density peaked at approximately 17% sagebrush cover, green-tailed towhee density peaked at 13% sagebrush cover, sage thrasher density peaked at 9% sagebrush cover, and sage-grouse occurrence was greatest at 10% sagebrush cover (Fig. 2). These results are not surprising

Table 2. Logistic and count-based regression models for greater sage-grouse use and sagebrush-associated songbird density in northwest Colorado, USA, 2013–2015. For each model, we report log-likelihood (LL), number of parameters (*K*), Akaike's Information Criterion (AIC), difference in AIC compared to lowest AIC of the model set (ΔAIC), AIC weight (*w*), pseudo-R^2 value, root mean squared prediction error from 5-fold cross validation for count-based models (songbirds) or receiver operating characteristic score (ROC) for logistic models (sage-grouse), and *P* value from likelihood ratio test.

	Model[a]	LL	*K*	AIC	ΔAIC	*w*	R^2	Error or ROC	*P*
Brewer's sparrow	Tall sage 1 km + (tall sage 1 km)^2	618.53	4	1245.1	0.00	0.48	0.04	3.07	<0.001
	Tall sage 1 km + (tall sage 1 km)^2 + herb 5 km	617.84	5	1245.7	0.61	0.35	0.04	3.08	<0.001
	Sage height 30 m + herb 5 km	619.76	4	1247.5	2.44	0.14	0.03	3.07	<0.001
	Shrub height 30 m + herb 5 km	622.29	4	1252.6	7.51	0.01	0.03	3.08	<0.001
	Sage height 30 m	623.76	3	1253.5	8.46	0.01	0.03	3.08	<0.001
	Sage height 30 m + litter 564 m	623.75	4	1255.5	10.43	0.00	0.03	3.08	<0.001
	Herb 5 km	625.39	3	1256.8	11.72	0.00	0.03	3.08	<0.001
	Shrub height 30 m	628.20	3	1262.4	17.34	0.00	0.02	3.09	<0.001
	Shrub height 30 m + litter 564 m	627.87	4	1263.7	18.67	0.00	0.02	3.09	<0.001
	Bare 30 m	629.68	3	1265.4	20.29	0.00	0.02	3.09	<0.001
	Litter 564 m	633.71	3	1273.4	28.35	0.00	0.01	3.10	<0.001
Green-tailed towhee	Tall sage 1 km + (tall sage 1 km)^2 + herb 5 km	232.51	5	475.0	0.00	0.99	0.20	2.78	<0.001
	Tall sage 1 km + (tall sage 1 km)^2	238.42	4	485.2	10.18	0.01	0.18	2.50	<0.001
	Sage height 564 m + (sage height 564 m)^2	246.07	4	500.1	25.11	0.00	0.15	2.60	<0.001
	Bare 30 m	248.53	3	503.1	28.02	0.00	0.14	2.54	<0.001
	Herb 5 km	248.63	3	503.3	28.24	0.00	0.14	2.49	<0.001
	Tall sage 1 km + (tall sage 1 km)^2 + litter 30 m	237.61	5	503.7	28.70	0.00	0.18	3.31	<0.001
	Shrub height 564 m + (shrub height 564 m)^2	257.11	4	522.2	47.19	0.00	0.11	2.29	<0.001
	Litter 30 m	259.53	3	525.1	50.03	0.00	0.10	2.58	<0.001
Sagebrush sparrow	All sage 1 km + (all sage 1 km)^2 + herb 5 km + (herb 5 km)^2	155.29	6	320.6	0.00	0.91	0.19	3.21	<0.001
	All sage 1 km + (all sage 1 km)^2	160.21	4	326.4	5.86	0.05	0.16	2.91	<0.001
	Shrub height 1 km + herb 5 km + (herb 5 km)^2	160.38	5	328.8	8.20	0.02	0.16	2.89	<0.001
	Bare 1 km + (bare 1 km)^2	161.52	4	329.1	8.48	0.01	0.16	2.42	<0.001
	Litter 1 km + (litter 1 km)^2	162.85	4	331.7	11.12	0.00	0.15	2.62	<0.001
	Shrub height 1 km	164.01	3	332.0	11.46	0.00	0.14	2.06	<0.001
	Sage height 5 km	164.24	3	332.5	11.90	0.00	0.14	2.06	<0.001
	Herb 5 km + (herb 5 km)^2	175.30	4	356.6	36.03	0.00	0.09	2.06	<0.001
Sage thrasher	Tall sage 564 m + (tall sage 564 m)^2	354.19	4	716.4	0.00	0.63	0.01	1.55	0.016
	Sage height 30 m	357.31	3	720.6	4.25	0.07	0.00	1.53	0.155
	Null	358.32	1	720.7	4.27	0.07	0.00	1.52	1.0
	Herb 5 km	357.50	3	721.0	4.62	0.06	0.00	1.52	0.20
	Shrub height 30 m	357.81	4	721.6	5.25	0.05	0.00	1.53	0.344
	Bare 30 m	358.11	3	722.2	5.84	0.03	0.00	1.52	0.513
	Sage height 30 m + herb 5 km	357.20	4	722.4	6.02	0.03	0.00	1.54	0.326
	Litter 564 m	358.23	3	722.5	6.08	0.03	0.00	1.53	0.664
	Shrub height 30 m + herb 5 km	357.47	4	722.9	6.56	0.02	0.00	1.52	0.426
Sage-grouse	Tall sage 1 km + (tall sage 1 km)^2	185.24	3	376.5	0.00	0.54	0.11	0.71	<0.001
	Tall sage 1 km + (tall sage 1 km)^2 + litter 30 m	184.98	4	378.0	1.49	0.26	0.11	0.72	<0.001
	Tall sage 1 km + (tall sage 1 km)^2 + herb 5 km	185.21	4	378.4	1.95	0.20	0.11	0.71	<0.001
	Shrub height 30 m + (shrub height 30 m)^2 + herb 5 km	194.06	4	396.1	19.65	0.00	0.07	0.67	<0.001
	Shrub height 30 m + (shrub height 30 m)^2	195.16	3	396.3	19.86	0.00	0.06	0.66	<0.001
	Litter 30 m	196.32	2	396.6	20.17	0.00	0.06	0.65	<0.001
	Sage height 564 m + (sage height 564 m)^2	195.63	3	397.3	20.78	0.00	0.06	0.69	<0.001
	Bare 30 m	196.79	2	397.6	21.10	0.00	0.05	0.65	<0.001
	Herb 5 km	197.48	2	399.0	22.49	0.00	0.05	0.63	<0.001

[a] Predictors include percent cover of tall sagebrush (tall sage), all sagebrush (all sage), herbaceous understory (herb), litter (litter), and bare ground (bare), sagebrush shrub height (sage height) and shrub height. Scales included 30-m, 564-m, 1-km, and 5-km moving windows.

given the positive relationship between Brewer's sparrows, green-tailed towhees, sage thrashers, and sage-grouse with sagebrush cover (Braun et al. 1976).

Brewer's sparrow and green-tailed towhee densities and sage-grouse occurrence were also positively associated with greater ground cover: herbaceous cover at the largest scale (5 km) for the songbirds and litter at the smallest scale (30 m) for sage-grouse. Optimal sage-grouse breeding habitat (i.e., lekking, nesting, and brood-rearing) should contain ≥15% herbaceous cover (Connelly et al. 2000), and in our study, herbaceous cover and litter were highly correlated. In addition, litter could provide more insects for foraging sage-grouse or nest concealment from predators (Kirol et al. 2012). Green-tailed towhees typically feed on the ground and below shrub cover, so greater herbaceous cover would provide foraging opportunities for seeds and insects (Dobbs et al. 2012). Brewer's sparrows exhibited a weaker relationship with herbaceous

Table 3. Beta coefficient estimates (β), standard errors (SE), and 85% confidence intervals for predictors in the top (i.e., ΔAIC < 2) logistic and count-based regression models for greater sage-grouse occurrence and sagebrush-associated songbird density in northwest Colorado, USA, 2013–2015.

	Coefficients[a]	β	SE	85% Lower	85% Upper
Brewer's sparrow					
Model 1	Intercept	0.29	0.09	0.16	0.42
	Tall sage 1 km	0.12	0.03	0.08	0.16
	(Tall sage 1 km)^2	−0.004	0.001	−0.006	−0.001
Model 2	Intercept	0.14	0.15	−0.08	0.36
	Tall sage 1 km	0.09	0.03	0.04	0.14
	(Tall sage 1 km)^2	−0.002	0.002	−0.005	<0.001
	Herb 5 km	0.010	0.008	−0.002	0.022
Green-tailed towhee					
Model 1	Intercept	−6.24	0.67	−7.28	−5.32
	Tall sage 1 km	0.47	0.09	0.34	0.60
	(Tall sage 1 km)^2	−0.019	0.004	−0.025	−0.013
	Herb 5 km	0.09	0.02	0.05	0.13
Sagebrush sparrow					
Model 1	Intercept	−12.00	3.75	−17.46	−6.66
	All sage 1 km	0.81	0.24	0.48	1.18
	(All sage 1 km)^2	−0.14	0.04	−0.20	−0.09
	Herb 5 km	1.92	0.63	1.02	2.83
	(Herb 5 km)^2	−0.08	0.03	−0.12	−0.04
Sage thrasher					
Model 1	Intercept	−1.84	0.15	−2.06	−1.62
	Tall sage 564 m	0.14	0.05	0.07	0.20
	(Tall sage 564 m)^2	−0.007	0.003	−0.011	−0.003
Sage-grouse					
Model 1	Intercept	−1.03	0.21	−1.34	−0.73
	Tall sage 1 km	0.44	0.07	0.34	0.56
	(Tall sage 1 km)^2	−0.02	0.01	−0.03	−0.02
Model 2	Intercept	−1.21	0.32	−1.68	−0.75
	Tall sage 1 km	0.40	0.09	0.27	0.54
	(Tall sage 1 km)^2	−0.02	0.01	−0.03	−0.01
	Litter 30 m	0.01	0.02	−0.01	0.04

[a] Predictors included percent cover of tall sagebrush (tall sage), all sagebrush (all sage), herbaceous understory (herb), and litter (litter). Scales included 30-m, 564-m, 1-km, and 5-km moving windows.

cover (Table 3), but they will also feed on seeds and insects on the ground (Rotenberry et al. 1999).

For sagebrush sparrows, the opposite pattern occurred. Correlation between probability of pellet occurrence and sagebrush sparrow density was negative; thus, lower sparrow densities were within areas with a higher probability of sage-grouse occurrence (Fig. 3). Similarly, in central Wyoming, the relationship between sagebrush sparrow abundance and sage-grouse pellet counts at a fine scale is negative (Carlisle 2017). In our study, sagebrush sparrows were associated with less sagebrush and herbaceous cover (Fig. 2) compared to sage-grouse. Sagebrush sparrows were prevalent in only the more arid portion of our study area (West Moffat), which had less shrub and ground cover compared to East Moffat. Sagebrush sparrows do not appear to occur throughout all sagebrush rangelands in Colorado but are restricted to a few sub-regions where shrub and ground cover are less (Boyle and Reeder 2005, Bird Conservancy of the Rockies 2017). In a nearby study site in northwest Colorado, sagebrush sparrows were associated with the ecological site containing larger gaps between shrubs and a greater density of shorter shrubs compared to other ecological sites (Williams et al. 2011). Sagebrush sparrow abundance in the Wyoming Basin was similarly greater for sagebrush landscapes containing lower sagebrush cover (Aldridge et al. 2011). These birds appear to prefer more open areas with less shrub and herbaceous cover, possibly because they walk to and from nests and forage on the ground (Martin and Carlson 1998).

In contrast with sagebrush sparrow density, sage-grouse population density is higher in the East Moffat region based on annual lek counts (CPW 2008). Indeed, our models predicted a higher probability of sage-grouse pellet occurrence across the East Moffat study site compared to West Moffat (Fig. 3). If we had examined overlap between sagebrush sparrow densities and sage-grouse probability of occurrence across a larger extent, such as a multi-state region, we may have found a positive relationship as previous studies have found (Hanser and Knick 2011, Donnelly et al. 2016). At larger distributional scales, landscape requirements may be similar, whereas local vegetation conditions within sagebrush rangelands (e.g., ground cover) appear to be different.

Given the negative correlation between sage-grouse and sagebrush sparrows in our study, our second hypothesis predicting high species richness in areas with a high probability of sage-grouse occurrence was only partially met. Species richness was higher in areas more likely to be used by sage-grouse. However, all 4 sagebrush-associated songbirds occurred in <1% of both study areas, regardless of sage-grouse probability of occurrence (Fig. 4). To date greater sage-grouse have not been evaluated as an umbrella in northwest Colorado and it would be easy to assume that managing for sage-grouse habitat would benefit

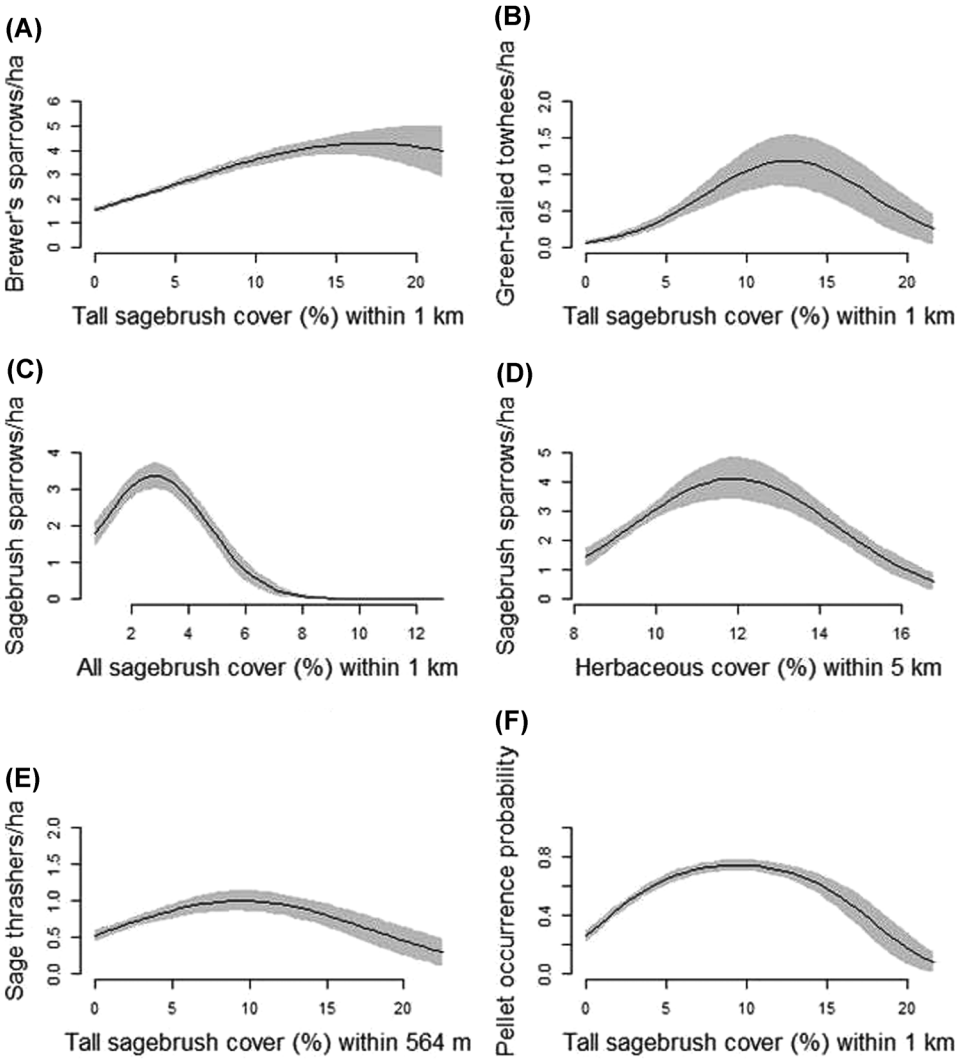

Figure 2. Predicted variable relationships and 95% confidence intervals for the top A) negative binomial model of Brewer's sparrows and tall sagebrush cover within 1 km, B) negative binomial model of green-tailed towhees and tall sagebrush cover within 1 km, Poisson models of sagebrush sparrows and C) all sagebrush cover within 1 km and D) herbaceous cover within 5 km, E) negative binomial model of sage thrashers and tall sagebrush cover within 564 m, and F) negative binomial model of greater sage-grouse pellets and tall sagebrush cover within 1 km in northwest Colorado, USA, 2013–2015.

Table 4. Comparison of sagebrush-associated songbird average density in areas with a high probability of greater sage-grouse pellet occurrence (probability >0.50) versus areas with a low probability of pellet occurrence in northwest Colorado, USA, 2013–2015.

	Songbird density (birds/ha) in areas of low probability of pellet occurrence		Songbird density (birds/ha) in areas of high probability of pellet occurrence	
Species	$\bar{x}$	**Range**	$\bar{x}$	**Range**
Brewer's sparrow	1.9	1.7–4.7	3.0	1.7–4.7
Green-tailed towhee	0.1	0.01–1.5	0.7	0.02–3.0
Sagebrush sparrow	1.7	0.0–4.4	<0.01	0.0–0.75
Sage thrasher	0.5	0.2–0.8	0.8	0.4–1.0

sagebrush-associated songbirds. Although greater sage-grouse did not receive federal protection in 2015 (USFWS 2015), populations continue to decline throughout their range (Garton et al. 2011), and local and large-scale efforts promoting sage-grouse habitat continue. Therefore, biologists could benefit from a better understanding of how efforts to promote sage-grouse habitat could affect songbirds that are also of conservation concern. Knowing where songbird density is greatest within areas that have a high probability of sage-grouse occurrence could guide management or conservation efforts because areas of greater songbird density reflect resources promoting greater fitness (Boyce and McDonald 1999). Understanding environmental features and scales that species select in these areas should further guide efforts to manage for resources to sustain or enhance populations.

Another approach that represents an alternative to umbrella species management is a multi-species strategy whereby a set of focal species dictate management and conservation efforts (Roberge and Angelstam 2004). A multi-species focus is ideal when an ecosystem contains several species of conservation concern because there could be conflicting needs for ≥2 focal

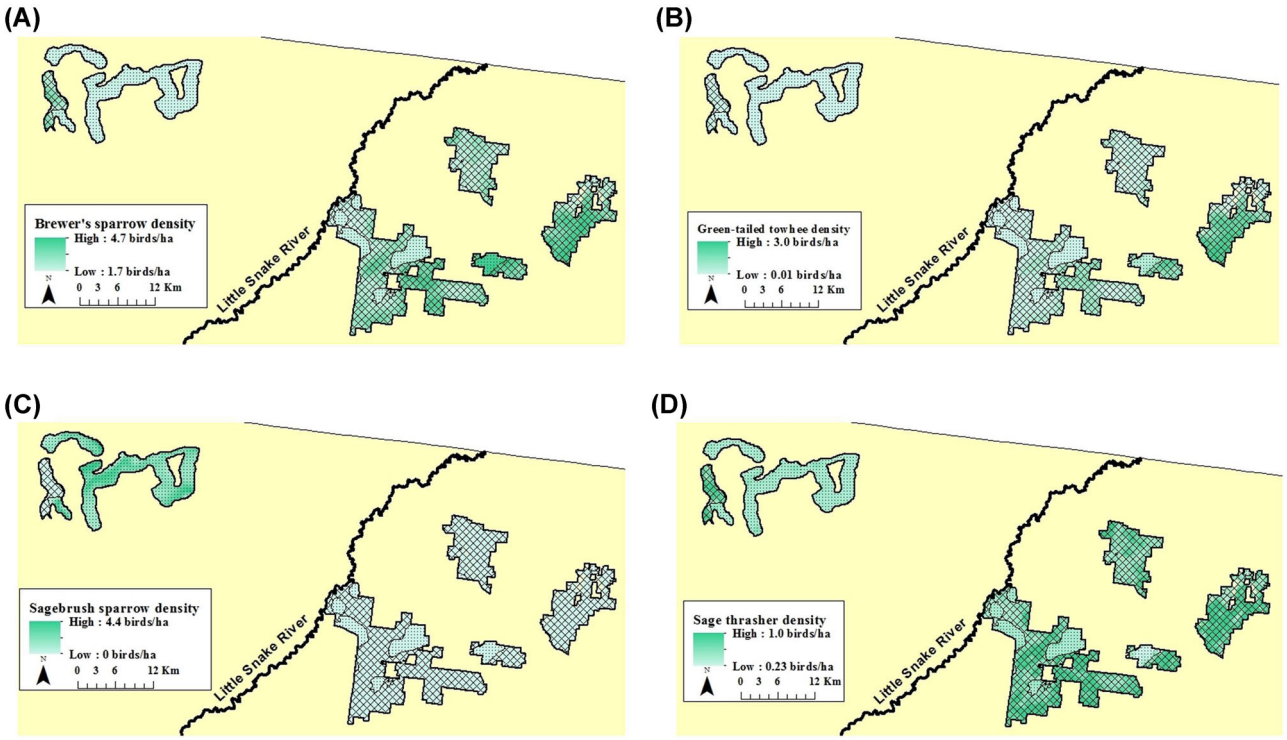

Figure 3. Predicted Brewer's sparrow (A), green-tailed towhee (B), sagebrush sparrow (C), and sage thrasher (D) density within 2 study sites in northwest Colorado, USA (West Moffat study site to the west of Little Snake River and East Moffat study site east of the river). Cross-hatched areas indicate areas of greater occupancy probability for sage-grouse (probability >0.5) and stippled areas indicate lower occurrence probability for sage-grouse.

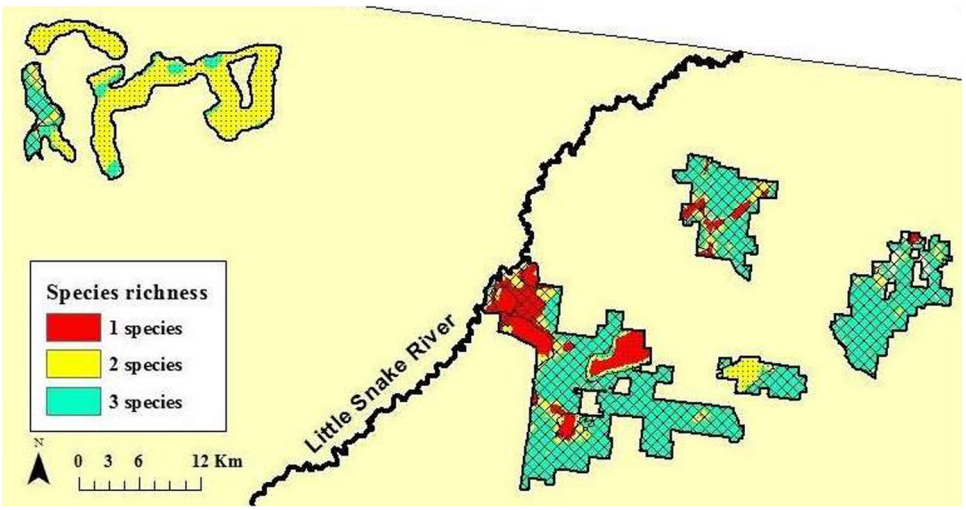

Figure 4. Predicted species richness for Brewer's sparrows, green-tailed towhees, sagebrush sparrows, and sage thrashers within 2 study sites in northwest Colorado, USA (West Moffat study site to the west of Little Snake River and East Moffat study site east of the river). Cross-hatched areas indicate areas of greater occupancy probability for sage-grouse (probability >0.5) and stippled areas indicate lower occurrence probability for sage-grouse. We calculated richness based on a minimum density to support a songbird territory (i.e., 0.42 Brewer's sparrows/ha, 0.11 green-tailed towhees/ha, 0.59 sage thrashers/ha, and 0.14 sagebrush sparrows/ha; Boyle and Reeder 2005, Rodewald 2015, Bird Conservancy of the Rockies 2017).

species that must be balanced within the overall ecosystem (Simberloff 1998). All species included in our analyses have experienced population declines either range-wide or within Colorado and could warrant federal protection in the future (Knick et al. 2003). The selected focal species for an ecosystem should also span spatial scales in terms of resource requirements and response to disturbances (Roberge and Angelstam 2004), such as sage-grouse and songbirds. Sage-grouse and other sagebrush-associated species require sagebrush rangelands year-round or during the breeding season (Braun et al. 1976), but within sagebrush rangelands, species respond to different features at different scales and quantities; thus, sagebrush landscapes should be managed for heterogeneity (Wiens et al. 1987, Connelly et al. 2011, Hanser and Knick 2011). Biologists and managers also need to support multiple species and a diversity of habitat characteristics within an

ecosystem because we lack complete knowledge about requirements for all species at all scales (Roberge and Angelstam 2004, Leu et al. 2011). Relative to our findings, this approach could entail managers and biologists focusing sage-grouse conservation and management efforts in areas with a richness of 3 species (i.e., Brewer's sparrow, green-tailed towhee, and sage thrasher; Fig. 4), and avoiding sage-grouse habitat management in areas where sagebrush sparrow densities are high (Fig. 3). Given the disparate habitat associations for sage-grouse and sagebrush sparrows in our study, a multi-species management approach would ensure that management of sage-grouse habitat was not at the expense of sagebrush sparrows.

Our results should be considered relative to a few caveats. Our Brewer's sparrow and sage thrasher models had reduced explanatory power compared to the other species (Table 2). For Brewer's sparrows, this could be due to their common occurrence throughout the study area, making it more difficult to discriminate local habitat relationships. Our results, however, are still biologically relevant and informative because Brewer's sparrows are often the most common songbird in sagebrush rangelands (Rotenberry et al. 1999), so managing for sage-grouse habitat will likely benefit this species. Further, we detected Brewer's sparrows at a majority of the plots where sage-grouse were detected, which our model-predicted relationships reflect. Our top sage thrasher model also included greater model uncertainty, which could mean we did not include relevant features for sage thrasher habitat in our study area. Amount of landscape fragmentation was an important predictor for sage thrashers in previous studies (Knick and Rotenberry 1995, Vander Haegen 2007), and Aldridge et al. (2011) also reported sage thrashers select environmental features at scales larger than 5-km extents. Our study area, however, had relatively little fragmentation from roads and energy development, and because of the extent of coverage of our remotely sensed products in northwest Colorado, we could not investigate scales >5 km. Our count data for thrashers contained many zeroes with mostly single counts and few plots containing multiple detections. Therefore, we examined logistic regression models *post hoc* for tall sagebrush cover within 564 m and for a null model with no predictors to see if we could better predict sage thrasher occurrence. The logistic regression models had ROC scores of 0.50–0.56, indicating little improvement over current count models (Hilbe 2011). Therefore, sage thrashers in our study area may simply occur across most sagebrush areas, albeit at low densities, limiting our ability to model habitat relationships. We also could have underestimated abundance for these 2 species if we missed initial territorial establishment for males when they are more likely to be singing and detected (Walker 2000), but that was unlikely based on timing of breeding from regional monitoring protocol (Hanni et al. 2013) and local breeding bird survey efforts (Wickersham 2016).

There is also potential bias with sage-grouse pellet surveys. With our sampling methods, we could not discern seasonal habitat preferences for sage-grouse. To do so, we would need to count and remove pellets during each distinct seasonal stage (lekking, nesting, brood-rearing, winter). Therefore, our pellet data likely captured multiple seasons for sage-grouse. On the basis of Dahlgren et al. (2006), the majority of pellets decompose within a 10-month period in a higher elevation, wetter region. Thus, our pellets, which were collected in May–June in a lower elevation and more arid study region, likely reflected breeding (i.e., lekking and nesting) and winter habitat. Further, because of sample sizes, we could not model roost piles and individual pellets separately, which could reflect different fine-scale habitats (e.g., resting vs. foraging habitat; Patterson 1952, Hanser et al. 2011). On the basis of the estimated sage-grouse range in northwest Colorado, both the East and West Moffat sites primarily provide nesting and winter habitat with a small proportion of brood habitat (CPW 2011). For sage-grouse to be an effective umbrella, their various seasonal habitats should encompass habitat for multiple species. If only distinct sage-grouse seasonal habitats matched habitat needs for sagebrush-obligate songbirds, then managing for sage-grouse as an umbrella would not be efficient or effective. We feel our approach is useful and informative because many biologists manage for sage-grouse habitat year-round rather than for distinct seasonal habitats.

MANAGEMENT IMPLICATIONS

Managing for maximum sagebrush-associated species richness is not an effective management strategy in northwest Colorado because although greater sage-grouse appear to be an effective umbrella for Brewer's sparrows, green-tailed towhees, and sage thrashers, sage-grouse habitat does not capture sagebrush sparrow habitat. Any practice to promote greater shrub or ground cover for sage-grouse in this region could be harmful for sagebrush sparrows, so sage-grouse habitat management should be considered in light of sagebrush sparrow habitat relationships. Specifically, sage-grouse management and conservation efforts would be most effective in areas where predicted Brewer's sparrow, green-tailed towhee, and sage thrasher densities are high and predicted sagebrush sparrow densities are low.

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