

## BIRD–HABITAT RELATIONSHIPS IN INTERIOR COLUMBIA BASIN SHRUBSTEPPE

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**Abstract.** Vegetation structure is important in structuring avian communities. In the sagebrush biome, where continued habitat loss is thought to threaten shrubsteppe-obligate birds, both remotely sensed and field-acquired measures of big sagebrush (*Artemisia tridentata*) cover have proven valuable in understanding avian abundance. Differences in structure between the exotic annual cheatgrass (*Bromus tectorum*) and native bunchgrasses are also expected to be important. We used abundance from 318 point-count locations, coupled with field vegetation measurements and a detailed vegetation map, to model abundance of four shrub- and four grassland-associated avian species in southeastern Washington. Specifically, we ask whether species' abundances in bunchgrass and cheatgrass differ and whether mapped categories of cover adequately explain species' abundances or whether fine-grained, field-measured differences in vegetation are also important in explaining abundance. We found that the abundance of shrub associates did not differ in sagebrush with a cheatgrass vs. bunchgrass understory, but grassland associates tended to use bunchgrass more than cheatgrass grasslands (Horned Lark, *Eremophila alpestris*; Grasshopper Sparrow, *Ammodramus savannarum*), or, in one case, cheatgrass more than bunchgrass (Long-billed Curlew, *Numenius americanus*). In the comparison of map- and field-based models, mapped cover types alone were sufficient for predicting abundance of five species studied, but models containing field-measured sagebrush cover outperformed models based on maps only for three species, the Sage Sparrow (*Amphispiza belli*) (+), Horned Lark (–), and Grasshopper Sparrow (–). We conclude that cover-type maps that consider understory composition and sagebrush density can predict avian distribution and abundance in the sagebrush biome efficiently.

**Key words:** *Artemisia*, bird–habitat relationships, cheatgrass, sagebrush, shrubsteppe.

### Relaciones entre Ave y Ambiente en la Estepa Arbustiva al Interior de la Cuenca de Columbia

**Resumen.** La estructura de la vegetación es importante para estructurar las comunidades de aves. En el bioma de monte de *Artemisia*, donde se piensa que la pérdida continua de hábitat amenaza a las aves obligadas de la estepa arbustiva, las medidas obtenidas con sensores remotos y trabajo de campo de la cobertura de *Artemisia tridentata* han resultado ser valiosas para entender la abundancia de las aves. También se piensa que son importantes las diferencias en estructura entre la especie exótica anual *Bromus tectorum* y las especies nativas. Empleamos la abundancia obtenida a partir de 318 puntos de conteo, en combinación con medidas de campo de la vegetación y con un mapa detallado de vegetación, para modelar la abundancia de cuatro especies de aves asociadas a los arbustales y cuatro a los pastizales en el sudeste de Washington. Específicamente, preguntamos si la abundancia de las especies varió entre los pastizales nativos y exóticos y si las categorías mapeadas de cobertura explican adecuadamente las abundancias de las especies o si las diferencias de la vegetación medidas en el campo a escala detallada son también importantes para explicar la abundancia. Encontramos que la abundancia de las especies asociadas a los arbustos no varían en los montes de *Artemisia* con un sotobosque de *B. tectorum* vs. uno con especies nativas, pero las aves asociadas a los pastizales tendieron a usar más los pastizales nativos que los de *B. tectorum* (*Eremophila alpestris*, *Ammodramus savannarum*), o, en un caso, los de *B. tectorum* más que los pastos nativos (*Numenius americanus*). En la comparación de los modelos basados en los mapas y en los estudios de campo, los tipos de cobertura mapeados fueron por sí solos suficientes para predecir la abundancia de cinco especies estudiadas, pero los modelos que contenían la cobertura medida en el campo de *Artemisia* presentaron un mejor desempeño que los modelos basados en los mapas sólo para tres especies, *Amphispiza belli* (+), *E. alpestris* (–) y *A. savannarum* (–). Concluimos que los mapas de tipo de cobertura que consideraron la composición del sotobosque y la densidad de *Artemisia* pueden predecir eficientemente la distribución y abundancia de las aves en el bioma de *Artemisia*.

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## INTRODUCTION

Vegetation structure, both vertical structure and horizontal patchiness, is considered a key habitat feature influencing avian communities (MacArthur 1964, Willson 1974, Rotenberry and Wiens 1980). In particular, measures of big sagebrush (*Artemisia tridentata*) cover at both the local and landscape scales have proven valuable in understanding shrubsteppe birds' abundance (Rotenberry 1985, Wiens et al. 1987, Knick and Rotenberry 1995, 2002, Rotenberry and Knick 1999, Vander Haegen et al. 2000, Hanser and Knick 2011). In addition to varying in sagebrush cover, shrubsteppe habitats differ in whether the exotic annual cheatgrass (*Bromus tectorum*) or native bunchgrasses constitute the dominant herbaceous vegetation. Differences in structure between cheatgrass, which grows more densely and evenly, and bunchgrasses, which grow in clumps interspersed with bare ground or cryptobiotic soil crust, are expected to influence avian abundance. Here we ask whether shrub- or grassland-associated bird species are distinguishing between bunchgrass- and cheatgrass-dominated cover either as understory in sagebrush shrublands or in grasslands.

Although many studies have examined the importance of multiple spatial scales in models of shrubsteppe birds' habitat (e.g., Knick and Rotenberry 1995, Rotenberry and Knick 1999, Vander Haegen et al. 2000), the effect of resolution is typically ignored. Remotely sensed measurements of vegetation structure are available at relatively low cost and over large geographic extents, while field measurements, although more expensive, are at a finer resolution that is sometimes more appropriate for describing bird-habitat relationships. Indeed, most studies directly comparing avian habitat models based on remotely sensed and field-collected data, including those in woodlands of Great Britain (Mack et al. 1997), forests of eastern (DeGraaf et al. 1998, Betts et al. 2006) and western (Cushman et al. 2008) North America, and montane meadows of the western U.S (Saveraid et al. 2001), have concluded that field-measured data provide important explanatory power beyond those obtained from remote sensing. Here we evaluate parameters at two resolutions in the shrubsteppe biome—mapped, categorical cover types and field measurements. The cover-type map we used was based on remotely sensed data combined with field information, so it can be viewed as intermediate between traditional remotely sensed and field-collected data. Specifically, we ask whether shrubsteppe birds respond to fine-scale differences in sagebrush and grass cover (as would be documented with field measurements) or whether mapped, categorical cover types adequately explain species' distribution and abundance.

Fires in degraded big sagebrush communities can convert native shrubsteppe to cheatgrass grasslands (West and Young 2000, Chambers et al. 2007), and the relatively dense-growing and early senescing cheatgrass, either in pure stands or as understory in sagebrush communities, also shifts fire regimes toward more frequent, severe, and large fires (Young and Evans

1973, Whisenant 1990, Baker 2011). Conversion of a sagebrush or bunchgrass community to annual grassland represents the crossing of an ecological threshold into a new steady state (Westoby et al. 1989, Bestelmeyer et al. 2003, Briske et al. 2006, Holmes and Miller 2010) from which it is difficult, if not impossible, to return to the previous state of native shrubsteppe. A substantial portion of the Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*) in the Columbia Plateau and Great Basin has been converted to annual grasslands dominated by cheatgrass or is at risk of such conversion, having an understory of exotic annual grass (Mac et al. 1998, Knick et al. 2003, Chambers et al. 2007). Suring et al. (2005) estimated that 58% of the remaining sagebrush in the western U.S. is at moderate to high risk of infestation by cheatgrass. In the interior Columbia Plateau of Washington, over 65% of the sagebrush has been lost, primarily as a result of conversion to farmland. Much of the remaining Wyoming big sagebrush has been negatively affected by agriculture, livestock grazing, and fire (McDonald and Reese 1998, Vander Haegen et al. 2000, Chambers et al. 2007). The loss of remaining sagebrush communities is considered a serious threat to shrubsteppe-obligate bird species in the Columbia Plateau and throughout the western United States (Knick and Rotenberry 1997, Knick 1999, Knick et al. 2005). In light of the continued loss of sagebrush communities, identifying habitat features that influence avian abundance and distribution, and developing cost-effective and accurate measurements of those features, is of particular conservation interest.

Hanford Reach National Monument contains some of the largest contiguous stands of shrubsteppe remaining in the central Columbia Basin, is representative of other relatively undisturbed shrubsteppe in the area, and supports regionally significant populations of shrubsteppe birds (TNC 1999). Our study area, the portion of the monument north of the Columbia River, is a matrix of sagebrush with native bunchgrass understory, sagebrush with cheatgrass understory, bunchgrass grasslands, and cheatgrass grasslands. This matrix and a detailed cover-type map recently produced for the monument (Easterly and Salstrom 2004) provide a unique opportunity for investigation of the relationships between avian abundance, mapped cover types, and field measurements of cover by sagebrush, bunchgrasses, and cheatgrass.

We used avian abundance data from 318 point-count locations, coupled with field vegetation measurements and a detailed vegetation map of the monument, to model abundance for eight species. We address the following questions: (1) Which vegetation measurements best explain the abundance of shrub- and grassland-associated shrubsteppe birds? (2) In sagebrush-dominated cover types and within grasslands, does shrubsteppe birds' abundance differ by whether the understory consists of cheatgrass and bunchgrass? (3) Is shrubsteppe birds' abundance best predicted by mapped, categorical cover types or do shrubsteppe species also respond to fine-scale differences in vegetation cover?

## METHODS

### STUDY AREA

Hanford Reach National Monument lies near the confluence of the Columbia and Yakima rivers on the central Columbia Plateau of southeastern Washington. Our study area includes most of the monument north of the Columbia River, including the 130-km<sup>2</sup> Saddle Mountain National Wildlife Refuge Unit and most of the 225-km<sup>2</sup> Wahluke Unit (previously the Wahluke State Wildlife Area). The Saddle Mountain Unit has been closed to the public and livestock grazing since 1943; on the Wahluke Unit, most grazing and farming ceased in 1943, but grazing continued in the north third of the unit until 1998 (TNC 1999). In the northern and eastern parts of the study area, in the 1970s and mid-1990s, respectively, wildfire created large expanses with sparse or no sagebrush. Active management within the sampled study area, other than fire suppression, was minimal in the decades prior to this study and consisted primarily of seeding small areas with native plants (total 1.87 km<sup>2</sup> from 2001 to 2004) or crested wheatgrass (7.5 km<sup>2</sup> in the late 1970s). The monument lies within the hottest and driest part of the Columbia Basin Ecoregion. Average precipitation is 16 cm at low elevations, falling primarily during the winter, and the average high temperature is in July at 24.6 °C.

The study area varies in elevation from 150 to 600 m and encompasses portions of the Wahluke Slope, White Bluffs, and slopes of the Saddle Mountains. The following description is based on a detailed, digitized cover-type map (Easterly and Salstrom 2004). Sagebrush shrublands with varying amounts of shrub cover constitute about half (52%) of the study area, and about 24% of the area remains in community phases dominated by native understory vegetation. Wyoming big sagebrush overstory with bunchgrass understory—primarily Sandberg's bluegrass (*Poa secunda*) and needle-and-thread grass (*Hesperostipa comata*)—constitutes 7%, antelope bitterbrush (*Purshia tridentata*) with Indian ricegrass (*Achnatherum hymenoides*) or needle-and-thread grass understory constitutes 4%, gray rabbitbrush (*Ericameria nauseosa*) or green rabbitbrush (*Chrysothamnus viscidiflorus*) with bunchgrass understory constitutes 5%, and bunchgrass grasslands (primarily needle-and-thread grass) constitute 9%. However, the most common cover types are Wyoming big sagebrush with cheatgrass understory (45%), cheatgrass grasslands (23%), and rabbitbrush or spiny hopsage (*Grayia spinosa*) with cheatgrass understory (6%).

### SAMPLING PLAN

We excluded higher elevations (>600 m) of the Saddle Mountain slope at the extreme northern edge of the study area and nontarget cover types such as riparian areas along the Columbia River, wetlands, gravel pits, and unvegetated dunes (total 40 km<sup>2</sup>). We also excluded areas within 100 m of a road to

avoid potential roadside bias (e.g., Ingelfinger and Anderson 2004, but see Rotenberry and Knick 1995).

We systematically placed potential sampling points 0.7 km apart throughout the study area such that no 100-m-radius buffer extended outside the study area or into excluded cover types. Of the 438 potential points, we randomly chose 318 (73%) to be surveyed. Within each cover type, we randomly assigned subsets of the points to be sampled in each of the three years. We sampled 106 points in 2004, 105 in 2005, and 107 in 2006. Each point was surveyed once during each of three time blocks between 12 April and 4 June, with at least 14 days between surveys. Points surveyed by observer 1 in the first and third time blocks were surveyed by observer 2 in the second time block and vice versa. On the basis of the walking distance between points, we assigned five to six points to a group that could be surveyed by one person of the two-person field crew within 150 min. The order in which points within a group were surveyed (i.e., beginning or ending with the point nearest a road) was chosen at random for the first time block and alternated thereafter.

### POINT COUNTS

We limit our analysis to eight native species that breed on the study area and are associated with shrubsteppe habitat: the Western Meadowlark (*Sturnella neglecta*), Sage Sparrow (*Amphispiza belli*), Lark Sparrow (*Chondestes grammacus*), Horned Lark (*Eremophila alpestris*), Grasshopper Sparrow (*Ammodramus savannarum*), Savannah Sparrow (*Passerculus sandwichensis*), Loggerhead Shrike (*Lanius ludovicianus*), and Long-billed Curlew (*Numenius americanus*). These species were chosen because they were the most abundant shrubsteppe associates recorded, and each was abundant enough to provide reasonable statistical power for habitat models. Observers recorded all birds seen or heard in a 400-m radius of the point during a 5-min period and recorded the distance to birds with a digital rangefinder. In preliminary analyses, we used the program Distance (Buckland et al. 2001) with the hazard-rate detection function to determine a radius within which the probability of detection was high for the eight focal species. Within a 100-m radius, estimated probability of detection was 1.0 for four of the eight species, also very high for the Grasshopper Sparrow ( $0.92 \pm 0.07$ ), moderate for the Sage Sparrow ( $0.65 \pm 0.15$ ) and Savannah Sparrow ( $0.46 \pm 0.05$ ), but insufficient for the Long-billed Curlew. Thus, in the bird-habitat analysis presented here, we use only observations within a 100-m fixed radius of the point, which also ensured that the area of vegetation sampling coincided with avian observations. The study design ensured that cover types were equally distributed across observers, dates, and times of day, reducing potential biases in comparisons by habitat, which are the focus of this study. Surveys were conducted between 0.25 and 2.5 hr after local sunrise and were not conducted during rain or winds >20 km hr<sup>-1</sup>.

#### VEGETATION SAMPLING

We sampled vegetation at each point during the same breeding season in which it was surveyed for birds, along three 50-m transects (for a total of 150 m at each point). Each transect originated 25 m from the point and was oriented north, southeast, or southwest ( $120^\circ$  between transects). We estimated percent shrub cover by line-intercept sampling (Canfield 1941) along the full length of each transect. Shrubs were recorded by species then pooled into two categories: (1) Wyoming big sagebrush, or (2) all other shrubs (i.e., gray and green rabbitbrush, spiny hopsage, and antelope bitterbrush).

We estimated percent ground cover visually to 1% by using a  $20 \times 50$ -cm sampling frame (Daubenmire 1959) that was subdivided into  $10 \times 10$ -cm grid cells. The frame was placed every 5 m along each line intercept transect, and the estimates from the 30 sampling frames at each point-count location were averaged to produce one estimate per point. Grasses and forbs were identified to species and then pooled as annual exotic grasses (i.e., cheatgrass), perennial bunchgrasses (primarily Sandberg's bluegrass, needle-and-thread grass, and squirreltail [*Elymus elymoides*]), annual forbs, and perennial forbs. For the purpose of this study, we pooled crested wheatgrass (*Agropyron cristatum*), even though it is not native, with other perennial bunchgrasses because it has a similar growth form and structure.

#### MAPPED COVER TYPES

We used a cover-type map of existing vegetation based on 1996 aerial photos and extensive field work during 2003 and 2004 (Easterly and Salstrom 2004). Easterly and Salstrom drew polygon boundaries to reflect changes in the cover of high- and medium-priority plant species (i.e., big sagebrush, antelope bitterbrush, spiny hopsage, needle-and-thread grass, and Indian ricegrass), with lower-priority species also mentioned in the names of mapped units (gray and green rabbitbrush, Sandberg's bluegrass, cheatgrass). For the purpose of this study, we pooled the mapped cover types into five categories: (1) sagebrush–bunchgrasses ( $19.7 \text{ km}^2$ ), (2) bunchgrass grasslands ( $23.3 \text{ km}^2$ ), (3) sagebrush–cheatgrass ( $120.7 \text{ km}^2$ ), (4) cheatgrass grasslands ( $62.2 \text{ km}^2$ ), and (5) areas dominated by other shrubs (i.e., rabbitbrush,  $28.7 \text{ km}^2$ , and bitterbrush,  $12.8 \text{ km}^2$ ).

#### CATEGORICAL COMPARISON OF CHEATGRASS VS. BUNCHGRASS AND SAGEBRUSH–CHEATGRASS VS. SAGEBRUSH–BUNCHGRASS COVER TYPES

To compare avian abundance by cover type, we first assigned each point to one of the five cover types described above according to the majority mapped cover type in its 100-m-radius circle. For this analysis, we were interested in a direct comparison of sagebrush vs. grassland and cheatgrass vs. native; we excluded points with other shrub as the majority cover type because the overstory was neither sagebrush nor grassland and the understory was a mix of cheatgrass and bunchgrass. For each point, we used the total number of individuals of each species

observed during the three surveys. We used one-way ANOVA to test for familywise significance, followed by Fisher's protected least-significant difference tests for pairwise comparisons if the ANOVA was statistically significant.

#### HABITAT MODELS

To identify vegetation parameters that best explain avian abundance and to evaluate whether mapped cover types are sufficient to predict abundance or whether field measurements of more fine-scale differences in vegetation are also needed, we constructed models by using parameters derived from the cover-type map (map resolution), field measurements (field resolution), and a combination of map and field measurements (combined resolution). Candidate models, parameters, and model selection are described below. For most species, we modeled bird–habitat relationships by using general linear models with a negative binomial (Western Meadowlark, Horned Lark) or zero-inflated Poisson (Grasshopper Sparrows, Savannah Sparrows, Sage Sparrows) distribution. The response variable for each point-count location was the total number of individuals observed across the three surveys; counts rather than averages are needed for negative binomial and Poisson regression (SAS Institute 2004). Because our data contained a large percentage of zeros, we began with zero-inflated negative binomial distribution, but, for a given species, we reverted to negative binomial if the full model at each resolution using negative binomial was  $>2$  Akaike's information criterion (AIC) units lower than that using zero-inflated negative binomial (Burnham and Anderson 2002), or we reverted to zero-inflated Poisson distribution if the overdispersion factor was not significant or too small to be estimated in the full models at each resolution (Proc CountReg, SAS Institute 2004). We used logistic regression for three species (Loggerhead Shrike, Long-billed Curlew, and Lark Sparrow) for which the response variable was almost always 0 or 1 (i.e.,  $>92\%$  of points had 0 or 1 individual per point).

We used an information-theoretic approach to choose the best subset of models for each species at each resolution (Burnham and Anderson 2002). We considered the model with the lowest AIC score the most parsimonious model and included models within 4 AIC units of it in the subset of best models. Following Arnold (2010), we do not include models  $<2$  AIC from the most parsimonious model that differed from it by only one parameter (or  $<4$  AIC if differing by two parameters); such models are not considered truly competitive, and the additional parameter does not explain any important additional variance (Burnham and Anderson 2002:170, Arnold 2010). We then used model averaging across the best subset of models at each resolution to calculate the model-averaged regression coefficient ( $\pm$  SE) for each parameter at each resolution (Burnham and Anderson 2002), and we interpret only statistically significant model-averaged coefficients.

Map parameters used in univariate models were percent cover types of sagebrush–bunchgrass, sagebrush–cheatgrass,

other shrubs, cheatgrass, and bunchgrass within the 100-m radius. In addition, we included two derived map variables as univariate predictors; “sage” cover, defined as sagebrush–bunchgrass plus sagebrush–cheatgrass cover, and “grass” cover, defined as bunchgrass plus cheatgrass cover. We excluded sage, grass, and sagebrush–cheatgrass from multivariate map models because they were highly negatively correlated with other cover types: otherwise, we used all possible combinations of map parameters, for a total of 20 map models (7 univariate and 13 multivariate).

Field parameters used in univariate models were percent cover of sagebrush, perennial bunchgrasses, cheatgrass, and other shrubs. We excluded annual forb cover, litter, and cheatgrass from multivariate models because they were highly correlated with other parameters measured in the field (annual forb with sagebrush, litter with bunchgrass, and cheatgrass negatively with bunchgrass); otherwise, we used all combinations of field parameters. We also included cover of perennial forbs and bare ground for the Lark Sparrow and bare ground for the Horned Lark because the literature suggested their importance as predictors of those species’ abundance (e.g., Bock and Webb 1984, Bock and Bock 1992). If we found them to be significant univariate predictors, we added these parameters to the best model to create an additional candidate model. Thus for most species we considered nine field models (four univariate, four multivariate, and the null), with an additional one or two univariate and multivariate models considered for the Lark Sparrow and Horned Lark.

We considered field-resolution models better than map models if they were >2 AIC units lower. To determine whether combined models, i.e., those with both map and field parameters, could improve upon the best single-resolution model, we started with either the best map or best field model (whichever had the lowest AIC) and added parameters from the best model at the other resolution in single and multiple combinations. This created one to six combined models for each species. We also tested for interactions between parameters in the best field and map models and added significant interaction terms to the best combined model to create one additional candidate model for two species and three for one species. We considered combined-resolution models better than map models if they were >2 AIC units lower and that field parameters improved on map-resolution models if they had significant model-averaged coefficients in combined-resolution models.

## RESULTS

We recorded 45 species at the 318 points. The eight species investigated here, in order of decreasing abundance, were the Horned Lark ( $\bar{x}$  = 1.27 individuals per station-visit), Western Meadowlark (1.23), Sage Sparrow (0.71), Savannah Sparrow (0.48), Grasshopper Sparrow (0.44), Lark Sparrow (0.30), Loggerhead Shrike (0.10), and Long-billed Curlew (0.05).

### DOES SHRUBSTEPPE BIRD ABUNDANCE IN SAGEBRUSH-DOMINATED COVER TYPES OR WITHIN GRASSLANDS DIFFER BY WHETHER THE UNDERSTORY IS CHEATGRASS OR NATIVE GRASS?

Species typically considered shrub associates were more common at sagebrush-dominated points, and grassland associates were more common at grassland-dominated points (Fig. 1). None of the four shrub associates differed in abundance according to whether the understory was cheatgrass or bunchgrass. However, three of the four grassland associates differed in abundance in cheatgrass and bunchgrass grasslands—the Horned Lark and Grasshopper Sparrow were more common in bunchgrass grasslands than in any other cover type, and the Long-billed Curlew was found almost exclusively in cheatgrass grasslands. Also, both the Horned Lark and Grasshopper Sparrow were more common in the sagebrush–bunchgrass than in the sagebrush–cheatgrass cover type, and the Savannah Sparrow exhibited the same tendency although the difference was not significant. This apparent avoidance of sagebrush–cheatgrass by grassland associates is consistent with field measurements of greater sagebrush cover ( $15.1\% \pm 0.8$  vs.  $10.0\% \pm 2.6$ , respectively,  $t = 1.88$ ,  $P = 0.08$ ), and lower bunchgrass cover ( $0.42\% \pm 0.14$  vs.  $3.0\% \pm 1.0$ , respectively,  $t = 2.55$ ,  $P = 0.01$ ) for the sagebrush–cheatgrass relative to sagebrush–native grass cover type (Table 1).

### WHICH VEGETATION MEASUREMENTS BEST EXPLAIN ABUNDANCE OF SHRUBSTEPPE BIRDS?

In species-specific habitat-association models at the map resolution, sagebrush cover types were significant predictors for five species and grassland cover types were significant for five species (Tables 2 and 3). At the field resolution, field-measured sagebrush cover was a significant predictor for all eight species (Fig. 2); cover by other shrubs and bunchgrass cover were each significant for two species.

Among shrub associates, for the Sage Sparrow and Western Meadowlark, the mapped sagebrush cover type (sage–cheat and sage–native combined) remained a significant positive predictor of abundance at the combined resolution (Tables 2 and 3). For the Sage Sparrow, field-measured sagebrush cover also remained significant in combined-resolution models, but the positive effect of field-measured sagebrush cover tended to be less pronounced when percent cover by the mapped sagebrush cover-type was high, as indicated by the significant interaction term (Table 3, Fig. 3). For the other two shrub associates, the Loggerhead Shrike and Lark Sparrow, the mapped grassland and cheatgrass grassland cover types, respectively, were significant negative predictors of presence (Table 2 and 3). Although field-measured sagebrush cover was a significant positive predictor in field-resolution models for all four shrubland associates (Fig. 2, Tables 2 and 3), it remained significant in combined models only for the Sage Sparrow.

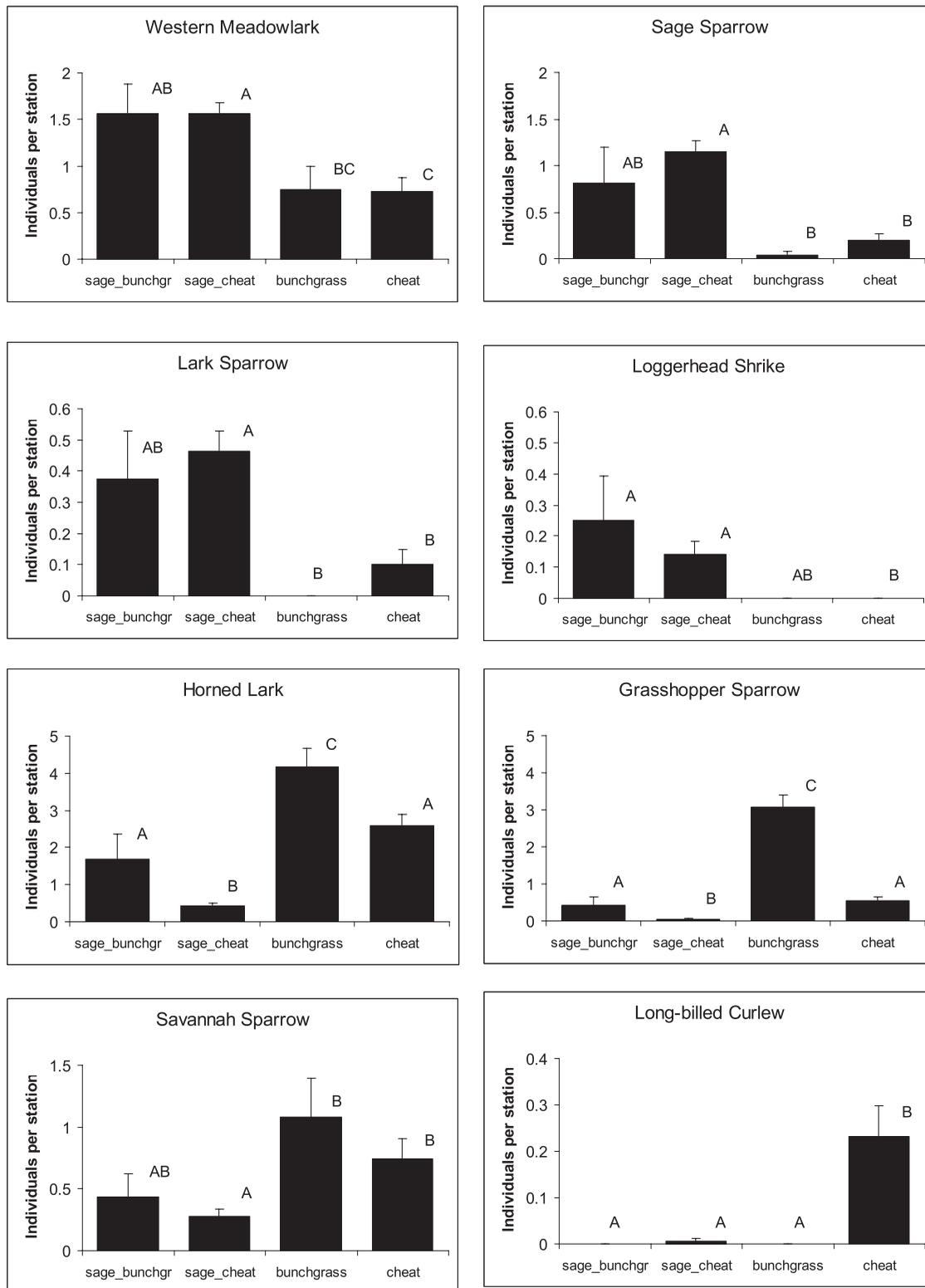


FIGURE 1. Mean relative abundance ( $\pm$ SE) of shrubsteppe and grassland species at 100-m fixed-radius point counts in four cover types. Points were classified by the cover type most common within a 100-m radius; points at which the shrub overstory consisted primarily of rabbitbrush and bitterbrush are not considered in this descriptive analysis. Statistical tests from one-way ANOVA followed by Fisher's LSD for post-hoc tests. Cover types sharing a letter do not differ significantly in relative abundance. Number of points dominated by sagebrush–bunchgrass cover type was 16, sagebrush–cheatgrass 168, bunchgrass grassland 24, and cheatgrass grassland 69.

TABLE 1. Percent field-measured vegetative cover at point-count locations categorized into five mapped cover types based on the majority cover type within a 100-m radius of the point.

Mapped cover type	Percent cover of field-measured parameters ( $\pm$ SE)				
	Sagebrush	Bunchgrass	Cheatgrass	Forbs	Bare ground
Sage–cheatgrass ( <i>n</i> = 168)	15.08 (0.79)	5.55 (0.33)	19.35 (0.98)	4.00 (0.45)	24.60 (1.10)
Sage–bunchgrass ( <i>n</i> = 16)	9.96 (2.60)	9.26 (2.00)	14.73 (2.49)	6.84 (2.74)	25.13 (3.62)
Cheatgrass ( <i>n</i> = 69)	1.12 (0.36)	5.86 (0.62)	29.60 (1.88)	4.45 (0.50)	13.69 (1.92)
Bunchgrass ( <i>n</i> = 24)	0.17 (0.10)	16.71 (1.36)	6.97 (1.89)	4.80 (0.82)	27.82 (3.85)
Other shrub ( <i>n</i> = 41)	3.50 (0.84)	6.21 (1.06)	15.57 (2.10)	5.13 (0.74)	32.41 (2.95)

TABLE 2. Significant model-averaged predictors at the map and field resolutions indicated by the sign (+ or –) of the coefficient. Significant model-averaged coefficients in the best combined model (i.e., models both with field and map parameters) are enclosed in boxes. For zero-inflated models, the sign is of the non-zero-inflated coefficient and indicates that both the zero-inflated and non-zero-inflated coefficients were significant unless noted otherwise. Based on counts at 318 points.

Resolution and parameter <sup>a</sup>	Shrub associates <sup>b</sup>				Grassland associates <sup>b</sup>			
	WEME	SAGS	LOSH	LASP	HOLA	SAVS	GRSP	LBCU
<b>Map</b>								
msage	+	+ <sup>c</sup>						
msage_cheat						– <sup>d,e</sup>		
msage_bunchgr					+		+ <sup>d</sup>	
mothshrub				– <sup>f</sup>				
mgrass			–					
mcheat				– <sup>f</sup>	+		+ <sup>d</sup>	+
mbunchgr					+		+ <sup>c</sup>	
<b>Field</b>								
fsage	+	+ <sup>g</sup>	+	+	–	– <sup>d</sup>	– <sup>g</sup>	–
fothshrub					–		– <sup>g</sup>	
fbunchgr							+	
<b>Map × field interaction</b>								
msage_bunchgr × fsage					+			
msage × fsage		– <sup>g</sup>						
mcheat × fbunchgr				+ <sup>f</sup>				

<sup>a</sup>Parameters (percent of each cover type within 100 m of point) based on maps named with “m” as first letter; those based on field measurements named with “f” as first letter.

<sup>b</sup>WEME = Western Meadowlark, SAGS = Sage Sparrow, LOSH = Loggerhead Shrike, LASP = Lark Sparrow, HOLA = Horned Lark, SAVS = Savannah Sparrow, GRSP = Grasshopper Sparrow, LBCU = Long-billed Curlew.

<sup>c</sup>In the combined-resolution model, only the non-zero-inflated coefficient is significant. Both zero- and non-zero-inflated coefficients are significant in single-resolution models.

<sup>d</sup>Only the zero-inflated coefficient is significant.

<sup>e</sup>For the Savannah Sparrow at the map resolution, model averaging is not used because the two parameters in question, msage and msage\_cheat, are interpreted as nearly equivalent. Msage\_cheat constitutes 91% of msage (msage = msage\_cheat + msage\_native). For other species, the subset of best models did not include models with both msage and msage\_cheat.

<sup>f</sup>For the Lark Sparrow, model-averaged coefficients for mcheat and mothshrub were marginally or not significant at the map resolution ( $P = 0.054$  and  $0.12$ , respectively) but significant at the combined resolution ( $P < 0.0001$  and  $0.02$ , respectively); mcheat × fbunchgr was marginally significant at the combined resolution ( $P = 0.07$ ).

<sup>g</sup>In the combined-resolution model, only the zero-inflated coefficient is significant. Both zero- and non-zero-inflated coefficients are significant in single-resolution models.

TABLE 3. Model-averaged regression coefficients ( $\pm$ SE) at the map, field, and combined resolutions. For species in which zero-inflated models were used (Sage Sparrow, Savannah Sparrow, Grasshopper Sparrow), zero-inflated coefficients left of slash predict the species' absence, and coefficients to right of slash predict the species' abundance given that it is present. Statistically significant coefficients in bold. Levels of significance: (\*)  $P < 0.10$ , \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Based on counts at 318 points.

Shrubland associates				
Parameter <sup>a</sup>	Sage Sparrow	Western Meadowlark	Lark Sparrow	Loggerhead Shrike
Map				
msage	<b>-0.02 (0.005)***/0.01 (0.004)**</b>	<b>0.008 (0.003)**</b>	0.004 (0.007)	
mothshrub		-0.001 (0.002)	-0.01 (0.009)	
mgrass				<b>-0.043 (0.019)*</b>
mcheat		-0.002 (0.003)	<b>-0.02 (0.009)(*)</b>	
mbunchgr		-0.001 (0.002)	-0.16 (0.18)	
Field				
fsage	<b>-0.12 (0.02)***/0.03 (0.008)***</b>	<b>0.03 (0.006)***</b>	<b>0.06 (0.01)***</b>	<b>0.05 (0.02)**</b>
fbunchgr			-0.13 (0.11)	
Combined				
msage	-0.01 (0.009)/ <b>0.01 (0.007)*</b>	<b>0.008 (0.002)***</b>		
mothshrub			<b>-0.01 (0.007)*</b>	
mgrass				<b>-0.04 (0.02)*</b>
mcheat			<b>-0.03 (0.006)***</b>	
mbunchgr			-0.19 (0.19)	
fsage	<b>-0.35 (0.14)*</b> /0.07 (0.04)	0.01 (0.008)		0.02 (0.02)
fbunchgr			-0.17 (0.12)	
msage $\times$ fsage	<b>0.003 (0.001)*</b> /-0.0005 (0.0004)			
mcheat $\times$ fbunchgr			<b>0.01 (0.006) (*)</b>	
Grassland associates				
	Savannah Sparrow	Grasshopper Sparrow	Horned Lark	Long-billed Curlew
Map				
msage	<b>0.017 (0.004)***</b> /-0.001 (0.003) <sup>b</sup>			
msage_cheat	<b>0.018 (0.004)***</b> /0 (0.003) <sup>b</sup>			
msage_bunchgr		<b>-0.03 (0.01)**</b> /0 (0.006)	<b>0.02 (0.004)***</b>	
mcheat		<b>-0.03 (0.007)***</b> /0 (0.005)	<b>0.02 (0.002)***</b>	<b>0.04 (0.01)***</b>
mbunchgr		<b>-0.08 (0.02)***</b> /0.01 (0.004)**	<b>0.03 (0.003)***</b>	
Field				
fsage	<b>0.06 (0.02)**</b> /-0.02 (0.02)	<b>0.23 (0.10)*</b> /-0.06 (0.03)*	<b>-0.11 (0.01)***</b>	<b>-0.35 (0.16)*</b>
fothshrub		<b>1.18 (0.50)*</b> /-0.15 (0.06)*	<b>-0.15 (0.03)***</b>	
fbunchgr		<b>-3.08 (1.26)*</b> /0.07 (0.01)***	<b>0.04 (0.02)*</b>	-0.28 (0.24)
Combined				
msage_cheat	<b>0.015 (0.005)**</b> /0.003 (0.004)			
msage_bunchgr			0.005 (0.005)	
mcheat			<b>0.009 (0.002)***</b>	<b>0.04 (0.01)***</b>
mbunchgr		0.04 (0.05)/ <b>0.01 (0.003)***</b>	<b>0.01 (0.003)***</b>	
fsage	0.015 (0.03)/-0.03 (0.02)	<b>0.32 (0.14)*</b> /-0.02 (0.03)	<b>-0.11 (0.02)***</b>	-0.11 (0.14)
fothshrub		<b>1.53 (0.64)*</b> /-0.08 (0.06)	<b>-0.10 (0.03)***</b>	
fbunchgr		<b>-3.93 (1.62)*</b> /0.04 (0.02)*	0.02 (0.02)	
msage_bunchgr $\times$ fsage			<b>0.001 (0.0003) **</b>	

<sup>a</sup>Parameters (percent of each cover type within 100 m of point) based on maps named with "m" as first letter; those based on field measurements named with "f" as first letter.

<sup>b</sup>For the Savannah Sparrow at the map resolution, model averaging is not used because the two parameters in question, msage and msage\_cheat, should be interpreted as nearly equivalent. Msage\_cheat constitutes 91% of msage (msage = msage\_cheat + msage\_native). For other species, the subset of best models did not include models with both msage and msage\_cheat.

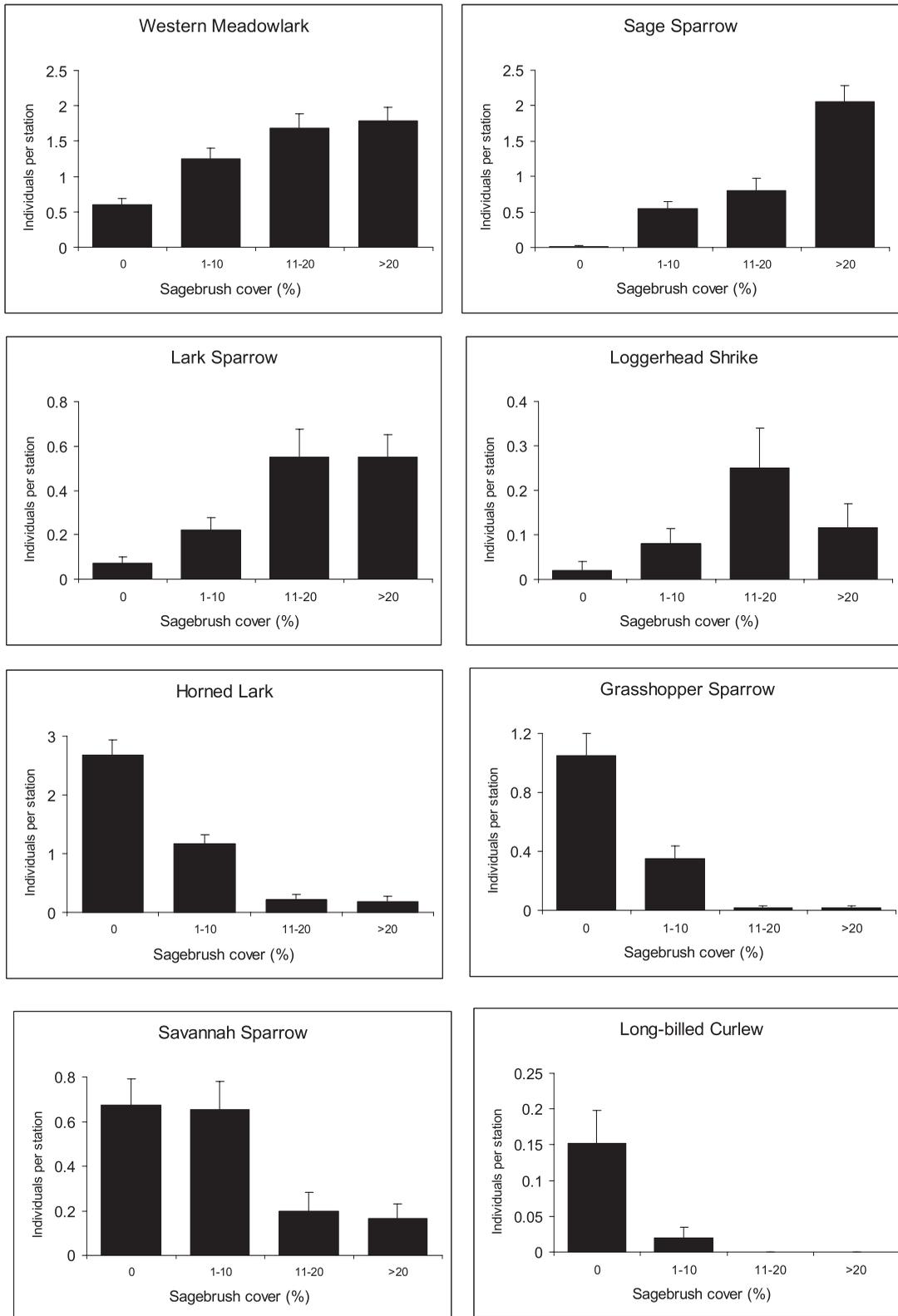


FIGURE 2. Mean relative abundance ( $\pm$ SE) of shrubsteppe species in relation to percent field-measured sagebrush cover in 100-m-radius point counts. Sagebrush cover was a significant predictor in field-resolution models for all species (see Tables 2 and 3). Number of points in the four sagebrush-cover categories reported on the x-axis was 99, 99, 60, and 60, respectively.

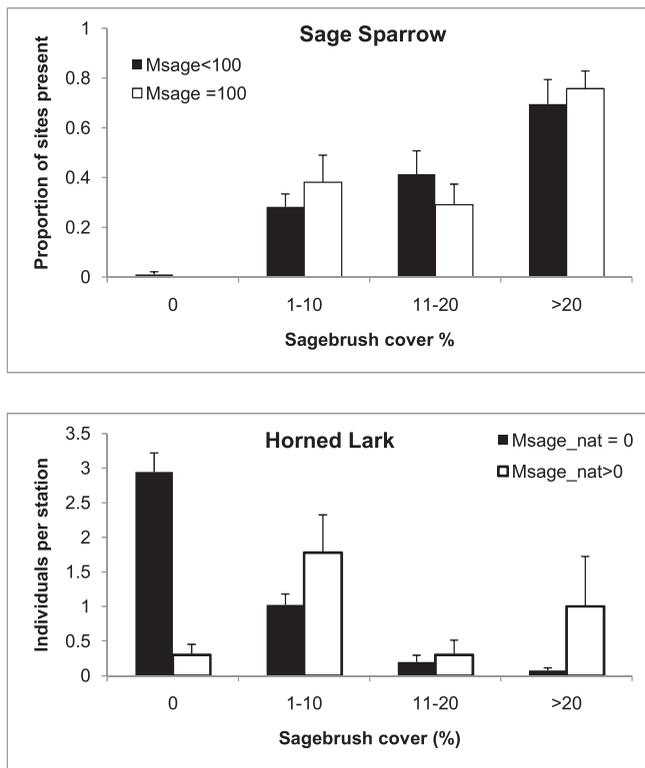


FIGURE 3. Mean relative abundance ( $\pm$ SE) of shrubsteppe species in relation to mapped and field-measured parameters whose interaction terms in combined resolution models were significant. Interactions were among continuous variables; categories are for illustration and were chosen on the basis of sample size. For Sage Sparrow presence, field-measured sagebrush cover had a greater effect when the mapped sagebrush cover type ( $M_{\text{sage}}$ ) covered <100% of the point circle (number of points in each category on the x-axis was 95, 4, 78, 21, 29, 31, 23, and 37, respectively). For Horned Lark abundance, field-measured sagebrush cover had a greater effect when the mapped sagebrush-native cover type ( $M_{\text{sage\_nat}}$ ) was present (number of points in each category on the x-axis was 89, 10, 81, 18, 50, 10, 53, and 7, respectively).

For grassland associates, mapped grassland cover types were significant positive predictors for three species (Tables 2 and 3). Specifically, for the Horned Lark and Grasshopper Sparrow, which were most common in bunchgrass grasslands (Fig. 1), significant predictors were mapped bunchgrass grasslands (+) and field-measured bunchgrass (+), sagebrush (-), and other shrub cover (-) in combined-resolution models. In addition, for the Horned Lark, mapped cheatgrass grassland (+) was also a significant predictor, and the negative effect of sagebrush cover was less pronounced when field-measured bunchgrass was also incorporated in the model, as indicated by the significant interaction term (Table 3, Fig. 3). For the Long-billed Curlew, which occurred almost exclusively in cheatgrass-dominated grasslands, the only significant predictor in combined models was the mapped cheatgrass cover type (+). For the Savannah Sparrow, which

was least common in sagebrush-cheatgrass, the only significant predictor in combined models was mapped sagebrush-cheatgrass (-). Field-measured sagebrush cover was a significant negative predictor for all four grassland associates in field-resolution models (Fig. 2, Tables 2 and 3), but it remained significant in the combined models only for the Horned Lark and Grasshopper Sparrow.

#### IS ABUNDANCE OF SHRUBSTEPPE BIRDS BEST PREDICTED BY MAPPED CATEGORICAL COVER TYPES OR DO SHRUBSTEPPE SPECIES ALSO RESPOND TO FINE-SCALE DIFFERENCES IN VEGETATION DENSITY?

For five of the eight species, models based entirely on mapped, categorical cover types performed as well or better than those based on field measurements (Tables 4 and 5). For the Western Meadowlark, Loggerhead Shrike, Lark Sparrow, Savannah Sparrow, and Long-billed Curlew, models at the map resolution clearly performed as well or better than field-based models—map models were 2.8 to 15.3 AIC units *lower* than those based on field measurements alone. For these species, sagebrush cover was the only significant predictor at the field resolution, and it did not remain significant in models combining map and field resolutions (Tables 3). For these species, combined models did not have more explanatory power than map models ( $\Delta\text{AIC} < 1.8$ , except for the Lark Sparrow, where  $\Delta\text{AIC} = 3.5$ ). For the Lark Sparrow, because the combined and map models differed by <4 AIC and by 2 parameters, the combined model should not be interpreted as explaining more variance (Arnold 2010); furthermore, model-averaged coefficients of the added field parameters were not significant, although one approached significance (i.e., the interaction between mapped cheatgrass and field bunchgrass,  $P = 0.07$ ).

In contrast, for three species—two grassland associates, the Horned Lark and Grasshopper Sparrow, and one sagebrush associate, the Sage Sparrow—field-resolution models performed substantially better than those based on mapped, categorical parameters (Tables 4 and 5). For the Horned Lark and Grasshopper Sparrow, the field-resolution model, which included sagebrush (-), other shrub (-), and bunchgrass (+) cover as significant predictors, was substantially better than the map-resolution model ( $\Delta\text{AIC} = 25.0$  and 33.5, respectively). For the Sage Sparrow, the field-resolution model, which included sagebrush cover (+) as the only significant predictor, was substantially better than the map model ( $\Delta\text{AIC} = 31.6$ ), which included mapped sagebrush cover (+) as the only significant predictor. For these three species, models containing both mapped and field parameters (i.e., combined-resolution models) were substantially better than either single-resolution model ( $\Delta\text{AIC} > 41.0$ , Tables 4 and 5) and included interaction terms between field- and map-measured sagebrush cover for two species (Horned Lark and Sage Sparrow). The interaction indicates that field-measured sagebrush

TABLE 4. Comparison of models at field, map, and combined resolutions for predicting avian abundance. Combined-resolution models contained both map-based and field-based parameters. Field- or combined-resolution models were considered to improve map models if they decreased AIC by  $>2$ . See Table 5 for  $w_i$  and  $\Delta$ AIC of individual models. Based on counts at 318 points.

Species	Field-based better than map-based?	$\Delta$ AIC field-map	Combined better than map-based?	$\Delta$ AIC combined-map
Shrub associates				
Western Meadowlark	No	10.9	No	-0.3
Lark Sparrow	No	12.6	No <sup>a</sup>	-3.5
Loggerhead Shrike	No	9.6	No	1.4
Sage Sparrow	Yes	-31.6	Yes	-41.2
Grassland associates				
Savannah Sparrow	No	2.8	No	1.8
Long-billed Curlew	No	15.3	No	1.1
Horned Lark	Yes	-25.0	Yes	-56.7
Grasshopper Sparrow	Yes	-33.5	Yes	-42.6

<sup>a</sup>For the Lark Sparrow, because the combined and map models differed by  $<4$  AIC and by 2 parameters, the combined model should not be interpreted as explaining more variance (Arnold 2010); furthermore, the model-averaged coefficient of the field parameter (i.e., the interaction between mapped cheat and field bunchgrass) was only marginally significant ( $P = 0.07$ ).

cover has a greater effect when the mapped sagebrush-native cover type is included in the model (Horned Lark) or when the mapped sagebrush covers  $<100\%$  of the 100-m circle (Sage Sparrow) (Fig. 3).

## DISCUSSION

We found that (1) grassland-associated species, but not shrub-associated species, differed in abundance by habitat with bunchgrass vs. cheatgrass understory and (2) for five of eight species mapped cover types explained the species' presence or abundance as well as or better than field-measured parameters.

Among grassland associates, the Horned Lark and Grasshopper Sparrow were more common in bunchgrass than in cheatgrass grasslands and least common in sagebrush-cheatgrass, the Savannah Sparrow showed the same tendencies but differences were not significant, and the Long-billed Curlew was the only species more common in cheatgrass than in bunchgrass grasslands. Similarly, in habitat models, the Horned Lark and Grasshopper Sparrow were associated with field-measured bunchgrass (+), sagebrush (-), and other shrub (-) cover, the Savannah Sparrow was associated with the mapped sagebrush-cheatgrass cover type (-); and the Long-billed Curlew was associated with the mapped cheatgrass cover type (+). Several studies confirm that grassland species are affected by grassland type and structure. Vander Haegen et al. (2000) found the Horned Lark and Grasshopper Sparrow associated with perennial bunchgrasses rather than with cheatgrass in the shrubsteppe of eastern Washington. Similarly, Holmes and Miller (2010) found that the Grasshopper Sparrow was more common in bunchgrass than in

cheatgrass grasslands and least common in sagebrush without bunchgrass. Other studies confirm an association with sparse vegetation and patchy bare ground, characteristics typical of bunchgrass grasslands (e.g., Table 1), for both the Grasshopper Sparrow (Vickery 1996, Reinking 2005, Powell 2008) and Horned Lark (Bock and Webb 1984, Wiens et al. 1987). The Savannah Sparrow did not strongly prefer bunchgrass over cheatgrass grasslands, but it showed a strong affinity for grasslands here and elsewhere (Wheelwright and Rising 1993). We found the Long-billed Curlew, in contrast to the other grassland associates, almost exclusively in cheatgrass-dominated grasslands, as have others in this region (Allen 1980, Pampush and Anthony 1993). It is possible that the height profile of cheatgrass, lower than that of bunchgrass or shrublands, is attractive to Long-billed Curlews, which breed commonly in short-grass prairies of the Midwest (Pampush and Anthony 1993).

In contrast to grassland associates, in sagebrush cover types, shrub associates did not differ in abundance whether the understory was bunchgrass or cheatgrass, but they were much more common in sagebrush than in grassland cover types (Fig. 1). Similarly, in habitat models, the Western Meadowlark was associated with the mapped sagebrush (+) cover type, the Sage Sparrow was associated with mapped (+) and field-measured (+) sagebrush; Lark Sparrow was associated with mapped bunchgrass (-) and other shrub (-), and the Loggerhead Shrike was associated with the mapped grassland (-) cover type. Several studies confirm the importance of sagebrush cover for the Sage Sparrow (Wiens and Rotenberry 1985, Knick and Rotenberry 1995, 1999, Vander Haegen et al. 2000, McIntyre 2003, Vander Haegen 2007), Western Meadowlark (Wiens and Rotenberry 1981, Knick

TABLE 5. Subset of best models at the map, field, and combined resolutions (i.e., those within 4 AIC of the model with the lowest AIC within each resolution). Best model at each resolution in bold; parameters with nonsignificant coefficients in parentheses;  $\Delta$ AIC and  $w_i$  calculated across all resolutions<sup>a</sup>. Parameters (percent of each cover type within 100 m of point) based on maps named with “m” as first letter; those based on field measurements named with “f” as first letter. Models with interaction terms also contained the respective main effects. Based on counts at 318 points.

Species	Resolution	Model	$w_i$	$\Delta$ AIC
Western Meadowlark	<b>Combined</b>	<b>msage (fsage)</b>	<b>0.50</b>	<b>0.0</b>
	<b>Map</b>	<b>msage</b>	<b>0.43</b>	<b>0.3</b>
	Map	mcheat mbunchgr mothshrub	0.07	3.9
	<b>Field</b>	<b>fsage</b>	<0.01	<b>11.2</b>
Sage Sparrow	<b>Combined</b>	<b>msage <math>\times</math> fsage</b>	<b>0.99</b>	<b>0.0</b>
	<b>Field</b>	<b>fsage</b>	<0.01	<b>9.6</b>
	<b>Map</b>	<b>msage</b>	<0.01	<b>41.2</b>
Lark Sparrow	<b>Combined</b>	<b>mcheat <math>\times</math> fbunchgr mothshrub (mbunchgr)</b>	<b>0.74</b>	<b>0.0</b>
	<b>Map</b>	<b>mcheat mothshrub (mbunchgr)</b>	<b>0.13</b>	<b>3.5</b>
	Combo	mcheat mothshrub (mbunchgr) (fbunchgr)	0.10	3.9
	Map	msage	0.03	6.3
	<b>Field</b>	<b>fsage (fbunchgr)</b>	<0.01	<b>16.1</b>
	Field	fsage	<0.01	18.7
Loggerhead Shrike	<b>map</b>	<b>mgrass</b>	<b>0.67</b>	<b>0.0</b>
	<b>combined</b>	<b>mgrass (fsage)</b>	<b>0.33</b>	<b>1.4</b>
	<b>field</b>	<b>fsage</b>	<0.01	<b>9.6</b>
Horned Lark	<b>Combined</b>	<b>msage_bunchgr <math>\times</math> fsage mcheat mbunchgr fothshrub (fbunchgr)</b>	<b>1.0</b>	<b>0.0</b>
	<b>Field</b>	<b>fsage fothshrub fbunchgr</b>	<0.01	<b>31.8</b>
	Field	fsage fothshrub	<0.01	35.3
	<b>Map</b>	<b>mcheat mbunchgr msage_bunchgr</b>	<0.01	<b>56.7</b>
Grasshopper Sparrow	<b>Combined</b>	<b>fsage fbunchgr fothshrub mbunchgr</b>	<b>0.99</b>	<b>0.0</b>
	<b>Field</b>	<b>fsage fbunchgr fothshrub</b>	<b>0.01</b>	<b>9.1</b>
	<b>Map</b>	<b>mcheat mbunchgr msage_bunchgr</b>	<0.01	<b>42.6</b>
Savannah Sparrow	<b>Combined</b>	<b>msage_cheat (fsage)</b>	<b>0.56</b>	<b>0.0</b>
	<b>Map</b>	<b>msage_cheat</b>	<b>0.23</b>	<b>1.8</b>
	Map	msage	0.15	2.7
	<b>Field</b>	<b>fsage</b>	<b>0.06</b>	<b>4.6</b>
Long-billed Curlew	<b>Map</b>	<b>mcheat</b>	<b>0.64</b>	<b>0.0</b>
	<b>Combined</b>	<b>mcheat (fsage)</b>	<b>0.37</b>	<b>1.1</b>
	<b>Field</b>	<b>fsage (fbunchgr)</b>	<0.01	<b>15.3</b>
	Field	fsage	<0.01	18.6

<sup>a</sup>Lowest AIC = 942.6 (Western Meadowlark), 595.4 (Sage Sparrow), 284.9 (Lark Sparrow), 142.9 (Loggerhead Shrike), 793.9 (Horned Lark), 342.2 (Grasshopper Sparrow), 558.0 (Savannah Sparrow), and 82.4 (Long-billed Curlew).

and Rotenberry 1995), and Loggerhead Shrike (Woods and Cade 1996, Humple and Holmes 2006). Only a few studies have investigated the effect of understory structure on shrub associates, and those studies did not directly compare bunchgrass and cheatgrass understories. For example, the Lark Sparrow is thought to be associated with edge habitats such as the sagebrush-grassland ecotone (Martin and Parrish 2000) and with disturbed areas having substantial bare ground and forb cover (Bock and Webb 1984, Bock and Bock 1987, 1992). In our study, both sagebrush-bunchgrass and sagebrush-cheatgrass sites had substantial cover by grasses (24–25%) and bare ground (25%) (Table 1) and may have been similar structurally to the edge and disturbed sites of studies in other regions. The Western Meadowlark tends to be more common in areas with sparse sagebrush cover (Knick and Rotenberry 1995), but otherwise its habitat preferences are broad (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981). In the eastern U.S., the Loggerhead Shrike is often described as using understories with shorter grass and more bare ground rather than habitats with tall, dense grass (Yosef 1996), but in the western U.S. this likely corresponds to sagebrush with an understory of either bunchgrass or cheatgrass (e.g., Cade and Woods 1997).

Our results indicate that maps of cover-type categories explained species' presence or abundance as well or better than field-measured parameters for five of eight species studied in the sagebrush biome. In contrast, in many studies like ours that attempt to compare resolutions at a constant spatial scale, traditional remotely-sensed data perform poorly relative to field-based or combined models in predicting avian abundance in forest (Mack et al. 1997, DeGraaf et al. 1998, Betts et al. 2006, Cushman et al. 2008) and meadow habitats (Saveraid et al. 2001). Many other studies confound resolution and spatial scale; however, it is clear that an important advantage of remote-sensed data is its availability at the landscape scale. The addition of landscape-scale, remotely-sensed parameters often results in better models than those based solely on smaller scale, fine-resolution field parameters (Knick and Rotenberry 1995, Saab 1999, Mitchell et al. 2001, Jeganathan et al. 2004, Betts et al. 2006). Knick and Rotenberry (1995) found that landscape-scale parameters, especially those related to fragmentation, were important predictors of presence for sagebrush-obligates (Sage and Brewer's Sparrow, Sage Thrasher) but not for other shrubsteppe species (Western Meadowlark, Horned Lark). The cover type map used here, which was based on both remotely-sensed and field data, was of higher resolution than data obtained solely by remote sensing and this may explain the success of our map-based models relative to other studies. Recently, LiDAR (Light Detection And Ranging) remote sensing has produced vegetation cover estimates in forested landscapes that are as effective in predicting avian abundance as field-collected data (Muller et al. 2009, 2010), and is an encouraging development

for avian-habitat modeling. In the sagebrush biome, remote-sensing technology continues to improve and large-scale mapping efforts are ongoing (e.g., <http://sagemap.wr.usgs.gov/ShrubMap.aspx>). Our work suggests that remote-sensing techniques that can distinguish among understory structures, e.g., perennial bunchgrasses vs. cheatgrass, and differences in percent sagebrush cover may be particularly valuable in predicting abundance of shrubsteppe birds.

Field models outperformed map models for two grassland associates that showed strong preferences for bunchgrass over cheatgrass, the Horned Lark and Grasshopper Sparrow, and one sagebrush obligate, the Sage Sparrow. Among these species, field-measured bunchgrass (+), sagebrush (–), and the interaction between field-measured and the mapped sagebrush cover type were important predictors. Elsewhere, fine-scaled field measurements of sagebrush cover have proven useful in predicting abundance of the Sage Sparrow and other sagebrush obligates (Wiens and Rotenberry 1985, Knick and Rotenberry 1995, McIntyre 2003, Holmes 2007). These findings are in keeping with predictions that fine-resolution variables may be more important for habitat specialists than for generalists (Betts et al. 2006).

The value of the cover-type map in predicting patterns of distribution within the sagebrush biome is heartening because extensive field measurements of canopy cover in sagebrush and grassland are expensive and time consuming. In fact, in this bird-focused study, we spent nearly three times more person-hours of field work estimating vegetation cover than in estimating bird abundance. Despite the obvious cost savings of using cover-type maps, incorporating field measurements may be advantageous in patchy landscapes, for habitat specialists, and when precise bird-habitat relationships are needed for endangered species or controversial management practices. In addition, avian abundance and the strength of bird-habitat relationships is not always a reliable indicator of habitat quality as measured by avian productivity or survival (Van Horne 1983). The relationship of coarse-scale parameters to habitat quality may be more likely to be indirect than that of fine-scale parameters, and, if so, models based solely on remotely sensed data may be more easily decoupled from avian productivity, and less reliably extrapolated, across spatial and temporal gradients (Jegenathan et al. 2004, Betts et al. 2006). As a result, intensive field-based studies relating habitat features to abundance and productivity will be particularly important for declining or otherwise jeopardized avian species.

Native bunchgrasses, in addition to their direct value as avian habitat as documented here, also play an important role in maintaining the resilience of Wyoming big sagebrush communities. Native bunchgrasses, both as sagebrush understory and as grasslands in a healthy shrubsteppe matrix, increase community resilience by decreasing the risk of large, severe fires and conversion to cheatgrass grasslands. Maintaining

this resilience is critical because restoring Wyoming big sagebrush communities that have transitioned to cheatgrass grasslands is both expensive and problematic (Henstrom et al. 2002, Briske et al. 2006, Chambers et al. 2007, Pyke 2011).

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