

Avian Community Structure Along a Mountain Big Sagebrush Successional Gradient

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ABSTRACT We compared vegetative structure and bird communities among 4 successional states in central Oregon representing a continuum from 1) postburn grassland, 2) mountain big sagebrush–Idaho fescue (*Artemisia tridentata*–*Festuca idahoensis*) shrub–steppe, 3) sagebrush–steppe–juniper (*Juniperus occidentalis*), to 4) old-growth western juniper. Species richness, evenness, and diversity of bird communities were highest in old-growth and mid-successional juniper (22.9 species/tract and 23.6 species/tract, respectively) but lowest in the grasslands (17.6 species/tract). Bird species diversity was positively correlated with physiognomic cover diversity ($r = 0.74$, $P = 0.001$). Density of breeding birds was greatest in old-growth juniper (6.6 birds/ha) and lowest in postburn grasslands (3.6 birds/ha) but similar in shrub–steppe and sagebrush–steppe–juniper (6.0 birds/ha and 5.5 birds/ha, respectively). Old-growth juniper had the highest total densities of both tree and cavity nesters. Mountain chickadees (*Parus gambeli*), Cassin’s finches (*Carpodacus cassinii*), chipping sparrows (*Spizella passerina*), brown-headed cowbirds (*Molothrus ater*), mountain bluebirds (*Sialia currucoides*), dark-eyed juncos (*Junco hyemalis*), Empidonax flycatchers, ash-throated flycatchers (*Myiarchus cinerascens*), and northern flickers (*Colaptes auratus*) were more abundant in cover types dominated by junipers. Vesper sparrows (*Poocetes gramineus*), western meadowlarks (*Sturnella neglecta*), green-tailed towhees (*Pipilo chlorurus*), and horned larks (*Eremophila alpestris*) were associated with grassland communities. Brewer’s sparrows (*Spizella breweri*), sage sparrows (*Amphispiza belli*), sage thrashers (*Oreoscoptes montanus*), and horned larks (*Eremophila alpestris*) were most abundant in sagebrush cover types. Management strategies should restore or maintain the desired proportions of the different successional states to maintain populations of grassland and sagebrush birds while providing habitat for tree and cavity nesting species. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1057–1066; 2007)

DOI: 10.2193/2005-702

KEY WORDS abundance, avian communities, diversity, fire effects, juniper encroachment, richness, shrub–steppe communities.

Avian communities in the semiarid portion of western North America have been subjected to constant temporal and spatial change in plant community distribution, composition, and structure (Miller and Wigand 1994). In the mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana*) alliance, changes in plant composition and structure are dynamic in time and space. The physiognomy of the predominant successional states typically follows a gradient from grassland to shrub–steppe to juniper (*Juniperus* spp.) woodland (Miller and Tausch 2001). Within this alliance, fire is one of the primary disturbance factors that influence plant succession and community structure (Miller and Tausch 2001). In addition, the number of years between fire events (i.e., fire return interval) is a key factor that determines the proportion of these successional states, which persist over time and space (Miller and Tausch 2001, Johnson and Miller 2006). Since the time of Eurasian settlement in the late 1800s, the interval between fires has increased in the mountain big sagebrush alliance (Miller and Rose 1999, Miller and Tausch 2001). This decrease in fire frequency across this alliance has resulted in a decline in the proportion of grassland-dominated communities and an encroachment of piñon (*Pinus* spp.) and juniper into shrub–steppe communities (Miller and Tausch 2001). Since the late 1800s, piñon and juniper woodlands are estimated to have increased 10-fold throughout much of the Intermoun-

tain West north of the Colorado Plateau (Burkhardt and Tisdale 1976; Miller and Rose 1995, 1999). In response, land managers are using fire in attempt to restore vegetative composition and structure at landscape scales, which has increased concern over the response of wildlife species, especially sagebrush obligates.

Shifts in the proportion of early and late-seral shrub–steppe communities and encroachment of juniper woodlands have likely resulted in significant changes in species composition, diversity, and abundance of breeding birds (Rosenstock and van Riper 2001). Most bird communities are influenced by changes in vegetative structure, and bird species diversity is often associated with increased structural complexity of plant communities (McArthur and McArthur 1961, Roth 1976, Cody 1981). However, limited information is available to determine how the different successional states in shrub–steppe systems influence avian communities. The purpose of our study was to describe the vegetative associations of breeding birds along a successional continuum from postburn grasslands to shrub–steppe vegetation to old-growth juniper communities. We predicted that there would be considerable differences in breeding bird communities among the 4 successional states and diversity of bird communities would be related to structural complexity of the vegetation.

STUDY AREA

Study sites were located in the Mazama and High Desert Ecological Provinces (Anderson et al. 1998) in Deschutes

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and Lake Counties in central Oregon, USA. All sites were located on lands managed by the Lakeview and Prineville Districts, Bureau of Land Management (BLM). Elevations of sites ranged from 1,110 m to 1,530 m. Soils were of Aeolian origin and made up largely of fine pumice and lakebed sands. Climate across the study area is characteristic of the northern Great Basin. Mean annual precipitation varied from 25 cm to 38 cm, falling predominantly as winter and spring snow or rain (Taylor 1993). The 30-year average of monthly temperature in spring (Apr–Jun) was 8.8° C (Taylor 1993). Climate in 1998 was relatively cool and one of the wettest years on record, with average spring monthly temperature of 7.6° C and precipitation totaling 150% of average. In 1999, spring conditions were slightly warmer and drier than average. A large portion of the upland vegetation was characterized by mountain big sagebrush steppe and old-growth western juniper woodland. Grasslands occupied portions of the region where fire had occurred within the past 0–20 years, and portions of the shrub–steppe were in different stages of encroachment by western junipers.

The grassland sites that we studied had burned within the previous 5 years, each by a different fire. Mean cover of current vegetation was 26.5% herbaceous cover and <5% shrub cover, which was mostly resprouting green rabbitbrush (*Chrysothamnus viscidiflorus*; Reinkensmeyer 2000). Among the shrub–steppe sites, mean vegetation cover was 18.0% herbaceous, 18.6% shrub, and little-to-no western juniper. The lack of charred wood found in a reconnaissance of all 4 shrub–steppe sites and a measured subsample of age (basal stem growth ring counts) in dominant overstory shrubs suggested these sites had not burned for >40 years. We selected the shrub–steppe–juniper sites based on the juniper woodland development model described by Miller et al. (2005). This successional state was a transitional phase between shrub–steppe and juniper woodland. In these stands, grasses, shrubs, and trees were codominant with 13.5% total herbaceous cover, 12.6% shrub cover, and 6.1% tree cover. All trees were postsettlement (<140 yr old) based on morphological characteristics defined by Miller et al. (2005). Old-growth juniper communities were dominated by trees >300 years old, contained relatively abundant cavities and lichens in the tree canopies and had an average of 10 standing dead snags/ha (Waichler et al. 2001). Mean cover was 8.5% herbaceous, 5.4% shrubs, and 23% tree canopy. A map of the entire study area with locations of the study sites can be found in Reinkensmeyer (2000).

METHODS

Stand Selection and Study Design

During 1998 and 1999, we conducted breeding bird surveys on 4 replicates of 4 different successional states (16 total study sites). The 4 successional states included 1) grassland (time since fire <5 yr), 2) shrub–steppe, 3) shrub–steppe–juniper, and 4) old-growth juniper. We used field reconnaissance, aerial photos, and BLM vegetation and soils maps to locate potential study sites within the

mountain big sagebrush–Idaho fescue (*Festuca idahoensis*) plant association. Idaho fescue was the dominant herbaceous species across all 4 successional states, and mountain big sagebrush was the potential dominant shrub. Western juniper was the only tree species present among the successional states. Each study site was spatially separate because no 2 replicates were within the same contiguous block of vegetation. Study sites were >250 ha, and we selected them to be as homogenous as possible based on vegetative structure and topography. We selected sites that were dominated by native shrubs, forbs, and grasses and those where exotic plant species accounted for <1% of the ground cover. Reinkensmeyer (2000) and Waichler et al. (2001) provide complete descriptions of vegetation composition and structure of all 16 study sites.

Bird Community Sampling

We established a 1.6-km transect on each study site, which consisted of 8 permanently marked sample points spaced at 200-m intervals. A sample point was a single station at which we conducted bird surveys and vegetative sampling. We randomly located the starting point for each transect near the northern edge of each successional state, and we placed sampling points systematically along each transect. We oriented transects to maintain the maximum distance from the edge or to exclude inclusions of different successional states. Sample points were always located >100 m from a different successional state.

We surveyed birds during the breeding season from 11 May to 26 June 1998 and from 13 May to 28 June 1999. We visited each transect 6 times/year for a total of 12 visits/transect. At each sampling point, we used the variable circular plot (VCP; Reynolds et al. 1980) or point count method (Buckland et al. 1993) to estimate abundance of birds. A single observer stood at a VCP station for 8 minutes, after a 1-minute waiting period, and all birds detected visually and aurally were recorded. Bird surveys began 10–20 minutes after sunrise and were concluded within 4 hours. We conducted surveys on mornings with wind <15 km/hour and no precipitation. We visually estimated the radial distance from each sample point to individual birds with the aid of rangefinders.

We grouped common species (observed on ≥ 6 visits on ≥ 2 transects; modified from Hagar et al. 1996) into nesting assemblages. We assigned birds to nesting assemblages based on the most common substrate used for nesting as indicated in the literature (DeGraaf and Rappole 1995): ground nesters, shrub nesters, tree-foliage nesters, cavity nesters, variable substrate nesters, and brood parasites. *Empidonax* flycatchers that we observed in this study commonly nested in both trees and shrubs; therefore, we assigned half of their density values to both the shrub and foliage nesting guilds.

Bird Associations with Vegetation Attributes

We evaluated the association between bird species and vegetation attributes at the macrohabitat and microhabitat scales. At the macroscale, the objective was to compare bird

associations among the 4 successional states; therefore, we considered each study site the sampling unit. At the microscale, the objective was to relate bird species abundance to vegetative attributes surrounding each sample point; therefore, we treated sample points as the sampling unit. Because we placed transects and sample points within successional states characterized by distinct vegetation structure, we assumed vegetation around each sample point to be representative of a larger area (Wiens and Rotenberry 1981). We conducted vegetation sampling from 6 July to 20 August 1998.

At the macrohabitat scale, we measured species composition, cover, tree density, and cover of bare ground for all 16 study sites (Reinkensmeyer 2000, Waichler et al. 2001). We sampled microscale characteristics at each of the 128 survey points on the 16 sites. We sampled vegetation along 4 20-m lines, each radiating from the sample point. We placed the lines 90° apart, with the first direction selected at random. We estimated percentage of ground cover in 0.4-m² plots placed at 3-m intervals along each of the 4 20-m lines (20 frames/plot). We estimated ground cover for perennial grasses, annual grasses, perennial forbs, annual forbs, bare ground and rock, litter, and cryptogammic crust. We used the line-intercept method (Canfield 1941) to estimate shrub cover along each 20-m line. We recorded live and dead shrub intercept measurements separately for each species of shrub encountered. We measured maximum shrub height for each individual shrub encountered. We placed a thin rod (5-mm diam) vertically at 3-m increments along each 20-m line and obtained indices of the vertical density of vegetation by counting the number of vegetation contacts with the rod within 10-cm segments (Cody 1968).

We counted all individual juniper trees, snags, and downed logs within a 20-m radius of each sample point to estimate juniper density. We measured basal diameter, height, maximum canopy width, and foliage width at 3-m height increments (3 m, 6 m, 9 m, and 12 m) for each tree. We computed canopy cover estimates by multiplying the square of half the canopy diameter by π . We obtained an index of canopy volume for each tree by summing the 3-m increment canopy-cover measurements. We counted the total number of cavities in each plot. We defined tree cavities as naturally occurring or excavated holes or cracks with openings >3 cm in diameter and >10 cm deep occurring in the trunks or large branches of trees. We measured or computed 32 vegetative characteristics at each sample point during the summer of 1999. The variables and their acronyms include percentage of cover by perennial grasses (PGRS%), annual grasses (AGRS%), bare ground (BGND%), ground litter (LITR%), microbotics (MICR%), perennial forbs (PFORB%), annual forbs (AFORB%), rocks (RCK%), sagebrush (ARTR%), dead shrubs (DEAD%), green rabbit brush (CHVI%), other shrubs (OTHSHRB%), and all shrubs (ALLSHRUB%); average shrub height (AVGSHBHT); maximum shrub height (MAXSHBHT); density of juvenile (<4 m tall) junipers (DENS1&2), young (>4 m tall) junipers

(DENS3), mature junipers (DENS4), senescent junipers (DENS5&6), juniper snags (DENS7), and all junipers (TOTDENS); vertical density index (ALLHITS); vertical density index for shrubs 0–30 cm (SHBHIT1), shrubs 30–60 cm (SHBHIT2), shrubs >60 cm (SHBHIT3), herbaceous vegetation <10 cm (HCHITS<10), herbaceous vegetation >10 cm (HCHITS>10); percent slope (SLOPE); average height of juniper trees (AVGTRHT); sum of juniper canopy cover (CANCVM); index of juniper canopy volume (CANVOL); and number of tree cavities (CAVS).

Data Analysis

Macrohabitat vegetative data.—We computed means and standard errors for each vegetative variable and each transect and analyzed the data with 1-way analysis of variance (ANOVA) using General Linear Models in SAS (SAS Institute 1988). When response variables were not normally distributed or lacked unequal variances, we converted them by \log_e ; $\log_e(Y + 1)$, for variables with zero values; or square-root transformations to meet ANOVA assumptions. We used Tukey's Studentized Range test as the multiple comparison procedure to test all pairwise comparisons among successional states, and we set the overall familywise confidence level at 95% (Ramsey and Schafer 1997).

We used physiognomic cover diversity (PCD, Wiens and Rotenberry 1981) as an index of vegetative complexity. We categorized vegetative cover into 3 physiognomic or structural groups for this analysis. These groups included all herbaceous plants, all shrubs, and juniper (>1 m); they collectively include the total coverage of live vegetation. We calculated PCD through the substitution of percentage of cover values for each major physiognomic vegetative group into the Shannon–Wiener index (Shannon and Weaver 1963): $H' = -\sum p_i(\log_e p_i)$, where p_i is the proportional coverage of the i th physiognomic group.

Bird associations.—We used bird abundance, species richness, diversity, and evenness to evaluate changes in bird associations among successional states. We calculated relative abundance of each species for each transect as the average of the total number of individuals detected on all sample points during 6 visits for each year. We used all bird species observed in each replicate of each successional state in the calculations of bird species richness, diversity, and evenness. We calculated bird species richness as the sum of the number of individual species observed on each site during 6 visits for each year. We used the Shannon–Wiener index to calculate bird species diversity (H'). We divided H' by \log_e of species richness to estimate bird species evenness (J'). We averaged species richness and diversity between years for each treatment because there were no significant ($F < 1.00$, $P > 0.05$) year-by-treatment interactions. We used simple linear regression (SAS Institute 1988) to evaluate the relation between bird species diversity and habitat complexity (PCD).

Estimation of avian density.—We found it difficult to distinguish between dusky flycatchers (*Empidonax oberhol-*

Table 1. Bird community measures for all detections among 4 successional states in central Oregon, USA, 1998 and 1999.

Community measure	Postburn grassland		Shrub-steppe		Mid-successional juniper		Old-growth juniper	
	\bar{x}^a	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Species richness (species/transect)	17.6A ^b	1.3	11.5B	2.2	23.6C	1.4	22.9C	1.5
Species diversity (H')	1.82A	0.08	1.64A	0.06	2.41B	0.10	2.49B	0.05
Species evenness (J')	1.47A	0.05	1.65B	0.06	1.76B	0.05	1.85B	0.03

^a \bar{x} is based on 6 visits/transect/2 yr; 4 transects/cover type.

^b Tukey's mean separation test used to determine differences among means; means with different letters within rows represent significant differences at $\alpha = 0.05$ or $P < 0.05$.

seri) and gray flycatchers (*Empidonax wrightii*) during surveys; therefore, we combined the 2 species for analysis and refer to them collectively as *Empidonax* flycatchers. We selected only those species observed on >6 visits on >2 transects for density estimation. We estimated density (birds/ha) for these common species on each study site using distance sampling (Buckland et al. 1993) and the program DISTANCE version 3.5 (Thomas et al. 1998). We pooled all detections of each bird species for both years and each successional state to develop a single detection function for each species in each successional state. Examination of histograms of the distance data revealed an abundance of observations at certain distances for nearly all species and, in some instances, evidence of minor movement in response to the observer. We ameliorated these problems by grouping the distance data into appropriate, but different, intervals for each species before selection of the final detection function. We truncated approximately 10% of the outermost distance data to eliminate outliers and facilitate model fitting (Buckland et al. 1993). We selected the final models based on Akaike's Information Criterion and chi-square goodness-of-fit statistics (Buckland et al. 1993). We computed total density of birds for each successional state as the sum of densities of individual species. We also compared total density of birds in each nesting guild among successional states.

Comparison of bird associations among successional states.—We compared density, diversity, evenness, and species richness among successional states and years with a repeated measures, 2-way ANOVA using General Linear Models in SAS. We used successional states as treatments and year in the treatment-by-year interaction. When response variables were not normally distributed or lacked equal variances, we used the square root, \log_e , or $\log_e(Y + 0.01)$ transformations to meet ANOVA assumptions. We used Tukey's Studentized Range test as the multiple comparison procedure to test all pairwise comparisons among succession states. We set the familywise confidence level at 95% (Ramsey and Schafer 1997).

Multivariate analysis.—We compiled 32 habitat attributes, which were either measured or derived from the microhabitat data, into a separate matrix. The habitat matrix consisted of 32 habitat attributes by 128 sample points. We divided individual habitat attributes (columns) within the habitat matrix by column maximum values to standardize habitat attributes measured on different scales. We compiled

density estimates of selected species at each VCP point into a matrix of species by sample units. We retained species that occurred within 5% of sample units for analysis. The final species matrix consisted of 22 species by 128 sample points. We used the multiresponse permutation procedure (Mielke 1984) in program PC-ORD (McCune and Mefford 1997) to test whether bird communities differed when grouped by successional state. We conducted ordination of the habitat attribute matrix using nondimensional multiple scaling (Kruskal 1964, Mather 1976) to describe the dominant vegetative gradients at each bird survey point. We performed overlays of bird species onto the habitat gradients to explore the strongest associations between bird species densities and vegetative structure. For more detail on these analyses, see Reinkensmeyer (2000).

RESULTS

Relative Abundance, Richness, Diversity, and Evenness

We recorded 14,633 detections of 62 species on the study sites during 1998 and 1999. There were no significant year-by-treatment interactions for all tests ($F = 1.04$, $P > 0.39$). Bird species richness, diversity (H'), and evenness (J') were significantly higher in the shrub-steppe-juniper, and old-growth juniper (Table 1) compared with the other 2 successional states ($F > 310.1$, $P < 0.001$). The presence of juniper cover in the shrub-steppe-juniper and old-growth juniper successional states resulted in significantly higher PCD values than those in the grassland and shrub-steppe successional states (Fig. 1). Greater equitability of cover among the physiognomic categories resulted in PCD being slightly higher in shrub-steppe-juniper than in old-growth juniper. Bird species diversity was positively correlated with PCD ($r = 0.735$, $P = 0.001$; Fig. 2), indicating an increase in bird species diversity with increases in structural complexity of vegetation along the successional gradient.

Bird Densities

Total density (no./ha) was significantly greater in 1999 than in 1998 ($F = 7.18$, $P = 0.013$) and varied among successional states ($F = 312.6$, $P < 0.001$; Table 2). Total density was significantly higher in old-growth juniper (6.6 birds/ha) and lowest in grasslands (3.6 birds/ha; Table 2). Species composition also varied as 16 bird species had significantly different densities ($F > 4.00$, $P \leq 0.05$) among the 4 successional states (Table 2). There were no significant year or year-by-treatment interactions ($F < 1.0$, $P > 0.05$) on density estimates for any species. We detected *Empidonax*

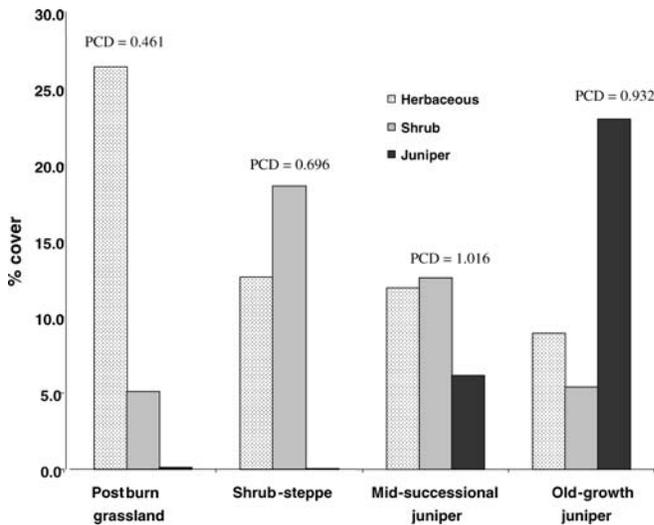


Figure 1. Vegetative cover and physiognomic cover diversity (PCD) among 4 successional states in central Oregon, USA, 1999.

flycatchers, brown-headed cowbirds (*Molothrus ater*), and northern flickers (*Colaptes auratus*) in all 4 successional states, but most species were more abundant in 1 or 2 successional states. The only obligate brood parasite encountered was the brown-headed cowbird, whose density was highest in old-growth juniper.

We estimated densities of 15 species in the grassland successional state (Table 2). Vesper sparrows (*Poocetes gramineus*), western meadowlarks (*Sturnella neglecta*), and green-tailed towhees had significantly higher densities in grasslands compared with the other successional states ($F > 6.50$, $P < 0.003$), but densities of the latter 2 species were low. The combined densities of vesper sparrows, horned larks, and Brewer's sparrows (*Spizella breweri*) comprised approximately 82% of total bird density in grasslands.

We estimated densities of 10 species in the shrub-steppe successional state (Table 2). Sage sparrows (*Amphispiza belli*), Brewer's sparrows, and sage thrashers (*Oreoscoptes montanus*) had significantly higher densities in the shrub-steppe versus the other successional states ($F > 48.0$, $P < 0.001$). The combined densities of sage sparrows, Brewer's sparrows, and horned larks comprised approximately 91% of total bird density in shrub-steppe.

We estimated densities of 18 species in the shrub-steppe-juniper successional state (Table 2). No species had a higher density in shrub-steppe-juniper ($P > 0.05$). Species consistently detected in shrub-steppe-juniper included chipping sparrows (*Spizella passerina*), mountain chickadees (*Parus gambeli*), Cassin's finches (*Carpodacus cassinii*), ash-throated flycatchers (*Myiarchus cinerascens*), and dark-eyed juncos (*Junco hyemalis*). The combined density of *Empidonax* flycatchers, Brewer's and sage sparrows, brown-headed cowbirds, chipping sparrows, and mountain bluebirds comprised approximately 80% of total species density in shrub-steppe-juniper. We found no species exclusively in shrub-steppe or shrub-steppe-juniper states.

We estimated densities of 17 species in old-growth juniper

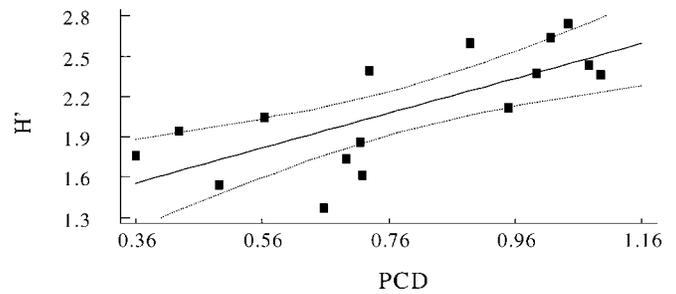


Figure 2. Relationship between bird species diversity (H') and physiognomic cover diversity (PCD) at 16 sites in central Oregon, USA, in 1998 and 1999. Solid line represents predicted values, and dotted lines represent 95% confidence limits.

(Table 2). Thirteen species had significantly higher densities in old-growth juniper, including *Empidonax* spp. flycatchers, brown-headed cowbirds, chipping sparrows, mountain bluebirds (*Sialia currucoides*), mountain chickadees, Cassin's finches, northern flickers, dark-eyed juncos, pinyon jays (*Gymnorhinus cyanocephalus*), mourning doves (*Zenaida macroura*; $F > 4.03$, $P < 0.03$). We found house finches (*Carpodacus mexicanus*), red-breasted nuthatches (*Sitta canadensis*), and American kestrels (*Falco sparverius*) exclusively in old-growth juniper. The combined densities of flycatchers, brown-headed cowbirds, chipping sparrows, mountain chickadees, and mountain bluebirds comprised approximately 82% of total species density in old-growth juniper.

Comparisons Among Nesting Assemblages

Total density of ground nesting birds was greatest in grasslands, where they accounted for nearly 75% of the total bird density and over 30% of the species composition (Table 3). Variable substrate nesters had the highest densities in grasslands; however, only 6% of the total bird density and 13% of the species composition were composed of this nesting assemblage. Total density of shrub nesting species was highest in the shrub-steppe state, and shrub nesters accounted for 73% of the total bird density and 45% of the species composition within shrub-steppe. Shrub-steppe-juniper supported nesting assemblages that were important in both shrub-steppe and old-growth juniper, although to lesser amounts. Shrub, tree, and cavity nesters comprised 87% of the total density of breeding birds in shrub-steppe-juniper. Ground-nesting birds, however, substantially declined in shrub-steppe-juniper, decreasing to 4.5% and 7.6% of grassland and shrub-steppe densities, respectively. Old-growth juniper had the highest total densities of both tree and cavity nesters, which accounted for 67% of the total bird density and 66% of the species composition in old-growth juniper.

Vegetation Attributes Among Successional States

We selected a 2-dimensional solution (cumulative $r^2 = 91.6\%$) from a direct ordination to describe bird species associations with vegetative attributes. The first dimension (axis 1) explained 37.8% of the variation in the original matrix of vegetative characteristics. The second and

Table 2. Mean densities (birds/ha/yr) of bird species that we detected on ≥ 6 visits and on ≥ 2 bird-survey transects and total bird density among 4 successional states in central Oregon, USA, in 1998 and 1999.

Species	Postburn grassland		Shrub-steppe		Mid-successional juniper		Old-growth juniper	
	\bar{x}^a	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Sage sparrow	0.09A	0.07	2.60B	0.25	0.75C	0.12	+ ^b	
Brewer's sparrow	0.41A	0.08	1.64B	0.09	1.29C	0.10	+	
<i>Empidonax</i> spp. flycatcher	0.03A	0.01	0.01B	0.01	1.34C	0.19	1.41C	0.15
Vesper sparrow	1.80A	0.16	0.38B	0.16	0.04B	0.01	+	
Horned lark	0.71A	0.27	1.17A	0.27	+		0 ^b	
Brown-headed cowbird	0.01A	0.01	0.01A	0.01	0.48B	0.12	1.08B	0.23
Chipping sparrow	+		+		0.49A	0.12	1.07B	0.04
Mountain bluebird	0.02A	0.00	+		0.45B	0.06	0.89B	0.28
Mountain chickadee	+		0		0.10A	0.03	0.90B	0.09
Cassin's finch	0		+		0.15A	0.04	0.42B	0.12
American robin	0.20A	0.05	+		0.12A	0.02	0.13A	0.04
Northern flicker	0.02A	0.01	0.01A	0.01	0.11B	0.01	0.14B	0.02
Ash-throated flycatcher	+		+		0.13A	0.06	0.11A	0.03
Western meadowlark	0.13A	0.02	0.04B	0.02	0.04B	0.01	+	
Dark-eyed junco	0		0		0.02A	0.01	0.15B	0.03
Green-tailed towhee	0.11A	0.03	0.01B	0.01	+		+	
Sage thrasher	0.01A	0.01	0.09B	0.01	0.01A	0.01	0	
Pinyon jay	0.01A	0.01	+		0.01A	0.01	0.08B	0.04
Rock wren	0.01A	0.01	+		0.02A	0.01	0.02A	0.01
Mourning dove	0.01A	0.01	+		0.01A	0.01	0.05B	0.01
House finch	0		+		0		0.05	0.03
Red-breasted nuthatch	0		0		+		0.05	0.03
American kestrel	+		+		+		0.01	0.01
Total density	3.57A	0.33	5.97B	0.25	5.54B	0.31	6.55B	0.57

^a Mean density (individuals/ha) of birds detected during 6 visits/transect/2 yr; 4 transects/cover type; means with different letters within rows represent significant differences ($P < 0.05$) in pairwise comparison.

^b 0 = species absent from cover type, + = species present within cover type but observed infrequently (<6 visits) or on only one transect.

dominant dimension (axis 2) explained 53.7% of the variation in the vegetative characteristics. Axis 1 of nonmetric multidimensional scaling described a gradient ranging from a mixture of juniper and shrub vegetation on the lower end of the gradient to the prevalence of herbaceous vegetation on the upper end of the gradient (Fig. 3). Specific vegetative attributes with the largest negative correlations with axis 1 included average tree height (AVGTRHT, $r = -0.639$), litter cover (LITR%, $r = -0.622$), juniper canopy cover (CANCVM, $r = -0.550$),

microbiotic crust cover (MICRO%, $r = -0.519$), and total tree density (TOTDENS, $r = -0.515$; Table 4). Specific habitat attributes with the highest positive correlations with axis 1 included vertical density of herbaceous vegetation both below 10 cm and above 10 cm (HCHIT<10, $r = 0.841$ and HCHIT>10, $r = 0.776$, respectively), total vertical density of all understory vegetative functional groups (ALLHITS, $r = 0.789$), and perennial grass cover (PGRAS%, $r = 0.748$).

Axis 2 described a gradient ranging from the predom-

Table 3. Characteristics of bird species nesting assemblages among 4 vegetative cover types in central Oregon, USA, 1998 and 1999. Total density values represent sum of mean densities (bird/ha/yr) of species we observed within each cover type and nesting assemblages. Number of species represents count of most common species (bird species detected on ≥ 6 visits and on ≥ 2 transects).

Nesting assemblage ^a	Postburn grassland		Shrub-steppe		Mid-successional juniper		Old-growth juniper	
	Total density ^b	No. species						
Ground	2.663	5	1.590	3	0.121	4	0.172	2
Shrub ^c	0.633	4.5	4.355	4.5	2.722	3.5	0.707	0.5
Tree ^c	0.020	1.5	0.001	0.5	1.317	3.5	2.328	4.5
Cavity	0.036	2	0.009	1	0.775	4	2.084	6
Variable	0.210	2	0.000	0	0.125	2	0.184	2
Brood parasite	0.007	1	0.013	1	0.483	1	1.075	1
Cover type total	3.569	15	5.968	10	5.542	18	6.551	16

^a Nesting assemblages = ground nesters: vesper sparrow, horned lark, western meadowlark, dark-eyed junco, rock wren; shrub nesters: sage sparrow, Brewer's sparrow, sage thrasher, green-tailed towhee, *Empidonax* spp. flycatcher; tree nesters: chipping sparrow, Cassin's finch, pinyon jay, house finch, *Empidonax* spp. flycatcher; cavity nesters: northern flicker, mountain chickadee, mountain bluebird, ash-throated flycatcher, red-breasted nuthatch, American kestrel; variable substrate nesters: American robin, mourning dove; and brood parasite: brown-headed cowbird.

^b \bar{x} density (individuals/ha) of all birds detected during 6 visits/transect/2 yr; 4 transects/cover type.

^c *Empidonax* spp. flycatchers encountered in this study (dusky and gray flycatchers) commonly nest in both trees and shrubs; therefore, we halved their density value and count and assigned them to both the tree- and shrub-nesting assemblages.

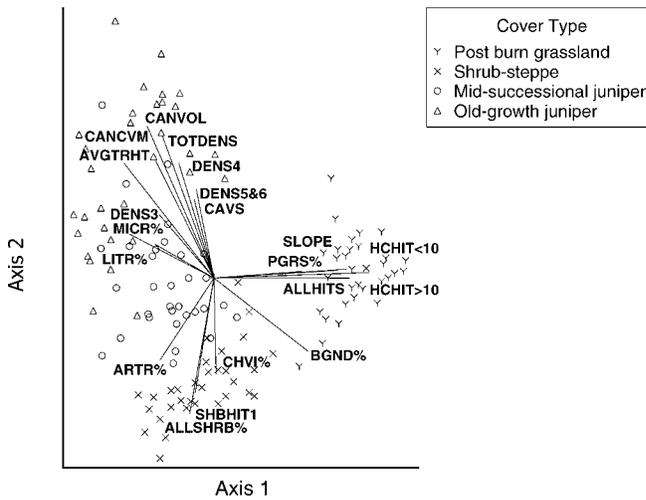


Figure 3. Ordination of sample units (variable circular plot survey points) in habitat attribute space with overlay of habitat attributes. Radiating vectors represent habitat attributes originating from the centroid of the points. Length of vector is proportional to the correlation coefficient of the habitat attribute; the direction of the line corresponds to increasing values on the graph. Acronyms for habitat variables are CANVOL = canopy volume, TOTDENS = total juniper density, DENS4 = density of mature junipers, DENS5&6 = density of senescent junipers, CAVS = number of tree cavities, CANCVM = juniper canopy cover, AVGTRHT = average height of junipers, DENS3 = density of young junipers, MICR% = percent cover of microbotics, LITR% = percent ground litter, SLOPE = percent slope, PGRS% = percent cover of perennial grasses, HCHIT<10 = vertical density of herbaceous vegetation <10 cm, HCHIT>10 = vertical density of herbaceous vegetation >10 cm, ALLHITS = vertical density index, BGND% = percent cover of bare ground, CHVI% = percent cover of rabbit brush, SHBHIT1 = vertical density of shrubs 0–30cm tall, ALLSHRB% = percent cover of all shrubs, ARTR% = percent cover of sagebrush.

inance of juniper vegetation on the lower end of the gradient to the dominance of shrub vegetation on the upper end of the gradient (Fig. 3). Vegetative characteristics with the highest positive correlations with axis 2 included total cover of all shrub species (ALLSHRB%, $r = 0.788$), cover of green rabbitbrush and sagebrush (CHVI%, $r = 0.0664$, and ARTR%, $r = 0.613$, respectively), vertical density of shrubs within 60 cm of the ground (SHRBHIT1, $r = 0.726$), and bare ground (BGRND%, $r = 0.579$; Table 4). Vegetative characteristics with the largest negative correlations with axis 2 included juniper canopy cover (CANCVM, $r = -0.833$), canopy volume (CANVOL, $r = -0.805$), total tree density (TOTDENS, $r = -0.730$), and average tree height (AVGTRHT, $r = -0.726$).

Bird Associations and Vegetation Attributes

Bird species with the largest negative correlations with axis 1 included chipping sparrows ($r = -0.660$), flycatchers ($r = -0.652$), mountain chickadees ($r = -0.637$), brown-headed cowbirds ($r = -0.623$), Cassin's finches ($r = -0.580$), ash-throated flycatchers ($r = -0.544$), and northern flickers ($r = -0.526$; Fig. 4). Vesper sparrows ($r = 0.771$), western meadowlarks ($r = 0.638$), green-tailed towhees ($r = 0.537$), and horned larks ($r = 0.381$) had positive correlations with axis 1 (Table 4). Species with the largest negative correlations with axis 2 included mountain chickadees ($r =$

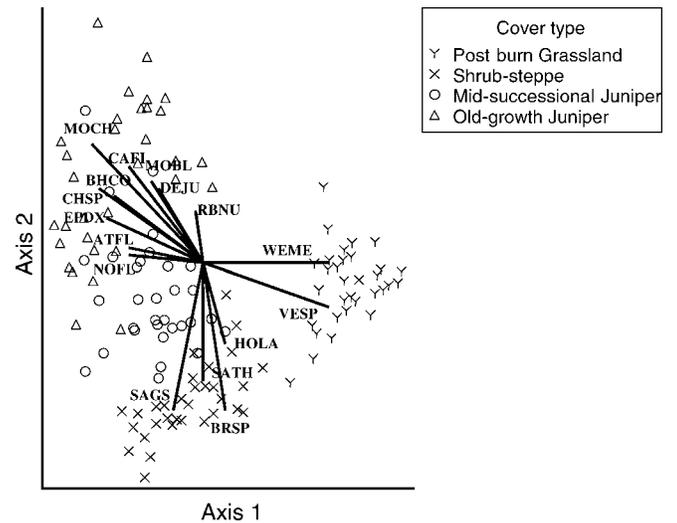


Figure 4. Ordination of sample units (survey points) in habitat attribute space with overlay of bird species. Radiating vectors represent species originating from the centroid points. Length of vector is proportional to the correlation coefficient of the species; the direction of the line corresponds to increasing values of species density on the graph. Acronyms for bird species names are: MOCH = mountain chickadee, CAFE = Cassin's finch, MOBL = mountain bluebird, DEJU = dark-eyed junco, RBNU = red-breasted nuthatch, NOFL = northern flicker, ATFL = American kestrel, EPDX = *Empidonax* flycatchers, CHSP = chipping sparrow, CHCO = brown-headed cowbird, WEME = Western meadowlark, VESP = vesper sparrow, HOLA = horned lark, SATH = sage thrasher, BRSP = Brewer's sparrow, SAGS = sage sparrow.

-0.719), Cassin's finches ($r = -0.711$), chipping sparrows ($r = -0.667$), brown-headed cowbirds ($r = -0.647$), mountain bluebirds ($r = -0.643$), and dark-eyed juncos ($r = -0.606$). Densities of Brewer's sparrows ($r = 0.769$), sage sparrows ($r = 0.735$), sage thrashers ($r = 0.614$), and horned larks ($r = 0.517$) were positively correlated with axis 2 (Table 4).

DISCUSSION

Avian Community Composition

Grassland, sagebrush, and juniper communities are examples of a successional gradient in the mountain big sagebrush alliance resulting from stand-replacing fires. Species composition, diversity, richness, evenness, and densities of breeding birds varied considerably among the 4 successional states, which confirmed our original prediction. In addition, bird species diversity (H') was positively correlated with PCD indicating an increase in avian diversity with an increase in structural complexity of vegetation. Similar to previous studies (Coppedge et al. 2001, Rosenstock and van Riper 2001), the dramatic increase in bird species diversity in shrub-steppe-juniper and old-growth juniper in contrast to the grassland and shrub-steppe states was associated with the additional vegetative layer provided by juniper trees. Maximum densities of 7 tree-nesting species in our study were in old-growth juniper, and 4 of 5 cavity-nesting species had higher densities in old-growth juniper than in shrub-steppe-juniper stands. Clearly, tree decadence and associated cavities were important structural components of old-growth juniper that were not as prevalent in shrub-steppe-juniper and absent from other cover types. The difference

Table 4. Bird species' habitat associations ($r > 0.30$) in 4 plant communities from nonmetric, multidimensional scaling ordination, central Oregon, USA, in 1998 and 1999.

Negative				Positive			
Bird species	r	Habitat variable ^a	r	Bird species	r	Habitat variable	r
Axis 1							
Chipping sparrow	-0.66	AVGTRHT	-0.64	Vesper sparrow	0.77	HCHIT>10	0.84
<i>Empidonax</i> flycatchers	-0.65	LITR%	-0.62	Western meadowlark	0.64	ALLHITS	0.79
Mountain chickadee	-0.64	CANCVM	-0.55	Green-tailed towhee	0.54	HCHIT<10	0.78
Brown-headed cowbird	-0.62	MICR%	-0.52	Horned lark	0.38	PGRS%	0.75
Cassin's finch	-0.58	TOTDENS	-0.52			BGND%	0.65
Ash-throated flycatcher	-0.54	DENS3	-0.50			SLOPE	0.63
Northern flicker	-0.53	ARTR%	-0.50			AFRB%	0.47
Mountain bluebird	-0.47	CANVOL	-0.49			PFRB%	0.40
Dark-eyed junco	-0.43	DEADS%	-0.45			AGRS%	0.35
Pinyon jay	-0.42	DENS1&2	-0.42			DENS7	0.32
House finch	-0.37	DENS4	-0.40				
		ALLSHRB%	-0.33				
		CAVS	-0.30				
Axis 2							
Mountain chickadee	-0.72	CANCVM	-0.83	Brewer's sparrow	0.77	ALLSHRUB%	0.79
Cassin's finch	-0.71	CANVOL	-0.81	Sage sparrow	0.74	SHBHIT1	0.73
Chipping sparrow	-0.67	TOTDENS	-0.73	Sage thrasher	0.61	CHVI%	0.66
Brown-headed cowbird	-0.65	AVGTRHT	-0.73	Horned lark	0.52	ARTR%	0.61
Mountain bluebird	-0.64	DENS4	-0.72			BGND%	0.58
Dark-eyed junco	-0.61	DENS5&6	-0.64			SHBHIT2	0.46
<i>Empidonax</i> flycatchers	-0.59	CAVS	-0.60			DEAD%	0.37
Red-breasted nuthatch	-0.56	RCK%	-0.54				
American robin	-0.52	DENS3	-0.54				
Mourning dove	-0.44	DENS1&2	-0.45				
Ash-throated flycatcher	-0.43	LITR%	-0.45				
Northern flicker	-0.42	MICR%	-0.39				
House finch	-0.42						

^a See Methods section for definition of habitat variables.

between avian communities in shrub-steppe and shrub-steppe-juniper was small, as the common species found within the shrub-steppe communities were also present in shrub-steppe-juniper, but in lower densities. The resulting species composition in shrub-steppe-juniper was a mixture of shrub- and tree-associated species, which resulted in relatively high richness and diversity of breeding birds. Our results indicated that the proportion of these successional states, which persist across landscapes, will significantly influence the abundance and species composition of breeding birds in the Great Basin of western North America.

Breeding Birds and Vegetative Associations

Grasslands.—Total breeding-bird densities (3.6 individuals/ha) were significantly lower in this successional state compared with the other 3 states but comparable to densities reported in other studies for sagebrush steppe (Rotenberry and Wiens 1980, Medin 1992). Vesper sparrows, green-tailed towhees, and western meadowlarks (ground nesters) had highest densities in this state. About 25% of this bird association was comprised of 12 other bird species, which were primarily shrub nesters. In contrast, Sedgwick (1987) and Braun et al. (1976) found green-tailed towhees to be most abundant in sagebrush steppe communities. The near absence of sagebrush (<1% cover) in grasslands resulted in a 30-fold decline in density of sage sparrows and nearly a 7-

fold decline in shrub nesters compared with shrub-steppe (see below).

Shrub-steppe.—Total bird density in the shrub-steppe community in our study (6.0 individuals/ha) was greater than densities reported for other sagebrush communities (Rotenberry and Wiens 1978, Medin 1992). We found sage and Brewer's sparrows, sage thrashers, and horned larks, which accounted for 73% of the breeding bird density, to be the most abundant birds in shrub-steppe. These species were found at lower densities in the grassland and shrub-steppe-juniper, and they avoided old-growth juniper. We found sage sparrows, Brewer's sparrows, and sage thrashers to be highly associated with sagebrush communities and were likely obligates of this successional state. Sage sparrows have been reported to be sensitive to declines in sagebrush cover due to herbicide treatment (Wiens and Rotenberry 1985) or fire (Rotenberry and Wiens 1978).

Shrub-steppe-juniper.—Shrub-steppe-juniper is a transitional state between shrub-steppe and juniper, which often persists for 30–100 years before it becomes a juniper-dominated woodland (Miller et al. 2005, Johnson and Miller 2006). Similar to other studies (Sedgwick 1987, LaRue 1994), we found greater species richness, diversity, and evenness in this successional state compared with the shrub-steppe or grassland states, which was due to greater structural complexity. Although shrub-steppe-juniper was structurally different from either the shrub-steppe or the

old-growth juniper successional states, it supported species common to both. No species preferred this state above the other 3 successional states. Bird species observed in this state that we did not observe in the grassland or shrub-steppe successional state were the chipping sparrow, mountain bluebird, mountain chickadee, Cassin's finch, American robin, ash-throated flycatcher, and dark-eyed junco. Shrub cover was a significant component of the vegetative structure (12% cover) in this successional state, which resulted in continued use by several shrub nesting species; however, sage sparrow densities were 81% lower than in shrub-steppe, indicating a low tolerance to juniper encroachment. Our results were similar to those of Noson et al. (2006) who concluded that vesper sparrows, sage sparrows, and western meadowlarks were absent or scarce in shrub-steppe-juniper.

Old-growth juniper.—There was considerable overlap in tree and cavity nesting species between the shrub-steppe-juniper and old-growth juniper successional states. *Empidonax* flycatchers, mountain bluebirds, and ash-throated flycatchers were common in both these states compared with the grassland and shrub-steppe states. Shrub and ground-nesting species were absent or observed only occasionally in old-growth juniper due to low coverage of herbaceous vegetation. However, the high abundance of cavity-nesting birds in this state resulted in relatively high species richness, diversity, and evenness. Total density of cavity-nesting birds was about 37% higher in old-growth juniper than that in shrub-steppe-juniper. Compared with shrub-steppe-juniper, 4 of 5 cavity nesters were more abundant in old-growth juniper, indicating tree decadence and associated cavities were important structural components. In addition, we detected American kestrels only in old-growth juniper, and red-breasted nuthatches in only 2 of 4 old-growth juniper sites. We found a total bird density of 6.5 individuals/ha in this state, which was higher than the 4.8 individuals/ha in old-growth juniper reported by Gashwiler (1977).

MANAGEMENT IMPLICATIONS

Historically, the proportions of grasslands, sagebrush-steppe, sagebrush-steppe-juniper, and old-growth juniper have changed over time as the result of fire suppression, cattle grazing, and invasion of exotic species. Under historic conditions grasslands, sagebrush-steppe, and old-growth juniper were the predominant vegetation across the sagebrush biome. However, during the past 140 years, large areas of mountain big sagebrush-steppe have been in transition or have been converted to juniper woodlands. Our results suggest this transition has likely resulted in the decline of grassland- and shrub-nesting birds, particularly sagebrush obligates. Long-term management strategies should restore or maintain the desired proportions of grasslands, shrub-steppe, and old-growth juniper to maintain high diversity of avian communities in this biome. The goal of managing young juniper stands should be to replace or maintain the desired proportion of old-growth woodlands to provide habitat for tree- and cavity-nesting birds.

ACKNOWLEDGMENTS

This project was funded by the Eastern Oregon Agricultural Research Center, Oregon Department of Fish and Wildlife, and BLM. S. Knick and D. Robinson provided valuable comments on an earlier draft of the manuscript. The study was conducted under the auspices of the Oregon Cooperative Fish and Wildlife Research Unit with the Wildlife Management Institute, Oregon State University, Oregon Department of Fish and Wildlife, and the United States Geological Survey cooperating.

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Associate Editor: Greenberg.