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COMPARATIVE HABITAT USE IN A JUNIPER WOODLAND BIRD COMMUNITY

David C. Pavlacky, Jr.,^{1,2} and Stanley H. Anderson^{1,3}

ABSTRACT.—We compared vegetation structure used by 14 bird species during the 1998 and 1999 breeding seasons to determine what habitat features best accounted for habitat division and community organization in Utah juniper (*Juniperus osteosperma*) woodlands of southwestern Wyoming. Habitat use was quantified by measuring 24 habitat variables in 461 bird-centered quadrats, each 0.04 ha in size. Using discriminant function analysis, we differentiated between habitat used by 14 bird species along 3 habitat dimensions: (1) variation in shrub cover, overstory juniper cover, mature tree density, understory height, and decadent tree density; (2) a gradient composed of elevation and forb cover; and (3) variation in grass cover, tree height, seedling/sapling cover, and bare ground/rock cover. Of 14 species considered, 9 exhibited substantial habitat partitioning: Mourning Dove (*Zenaida macroura*), Bewick's Wren (*Thryomanes bewickii*), Blue-gray Gnatcatcher (*Poliophtila caerulea*), Mountain Bluebird (*Sialia currucoides*), Plumbeous Vireo (*Vireo plumbeus*), Green-tailed Towhee (*Pipilo chlorurus*), Brewer's Sparrow (*Spizella breweri*), Dark-eyed Junco (*Junco hyemalis*), and Cassin's Finch (*Carpodacus cassinii*). Our results indicate juniper bird communities of southwestern Wyoming are organized along a 3-dimensional habitat gradient composed of woodland maturity, elevation, and juniper recruitment. Because juniper birds partition habitat along successional and altitudinal gradients, indiscriminate woodland clearing as well as continued fire suppression will alter species composition. Restoration efforts should ensure that all successional stages of juniper woodland are present on the landscape.

Key words: habitat use, birds, Utah juniper woodland, community organization, succession, vegetation structure.

Juniper woodland is an extensive plant community in the Southwest and Intermountain U.S. In prehistoric times juniper woodland experienced dramatic range fluctuations, and successional trajectories have changed markedly in the last 150 years (Miller and Wigand 1994). Recent changes to juniper plant communities include greater tree density in existing stands, increased recruitment in open areas, and downslope movement into grassland and shrubland (Chambers et al. 1999). Possible explanations for juniper range expansion are fire suppression, livestock grazing, and recent climatic changes (Miller and Wigand 1994, Chambers et al. 1999). If juniper expansion is largely due to human land use, grassland restoration and control of juniper woodland may be necessary. However, changes in bird community organization can be expected from management practices that alter woodland succession (Sedgwick 1987).

Pinyon-juniper bird communities are among the least studied avifauna in the U.S. (Balda and Masters 1980). Little is known about bird

community organization in pure juniper woodlands (Fitton and Scott 1984). Pinyon-juniper bird communities are composed of a few dominant, several common, and many rare species (Balda and Masters 1980). Few avian species demonstrate narrow niche breadth and are considered specialists within the pinyon-juniper plant community (Balda and Masters 1980). Here we investigate differences in habitat used by 14 common species in a juniper woodland bird community (Table 1).

Studies of habitat partitioning are concerned with how coexisting species divide environmental heterogeneity (Wisheu 1998). Patterns of resource segregation in animals often reveal specific habitat features that influence community organization (Schoener 1986). Understanding avian habitat partitioning and community organization may help land managers anticipate the effects of human and/or climatic alteration of successional trajectories in juniper woodlands.

Our objectives were to (1) identify features accounting for habitat division among 14

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TABLE 1. Bird species, alpha codes, and sample sizes used in discriminant function analysis, and percent correct classification, Sweetwater County, Wyoming, 1998–1999.

Species	Code	<i>n</i>	Classification
Mourning Dove (<i>Zenaidura macroura</i>)	MODO	25	52
Northern Flicker (<i>Colaptes auratus</i>)	NOFL	25	44
Gray Flycatcher (<i>Empidonax wrightii</i>) ^{ab}	GRFL	45	40
Juniper Titmouse (<i>Baeolophus griseus</i>) ^{ab}	JUTI	45	42
Bewick's Wren (<i>Thryomanes bewickii</i>) ^a	BEWR	45	58
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>) ^a	BGGN	46	50
Mountain Bluebird (<i>Sialia currucoides</i>)	MOBL	26	65
Plumbeous Vireo (<i>Vireo plumbeus</i>) ^b	PLVI	25	60
Black-throated Gray Warbler (<i>Dendroica nigrescens</i>) ^a	BTYW	45	40
Green-tailed Towhee (<i>Pipilo chlorurus</i>)	GTTO	26	81
Chipping Sparrow (<i>Spizella passerina</i>)	CHSP	30	33
Brewer's Sparrow (<i>Spizella breweri</i>)	BRSP	27	100
Dark-eyed Junco (<i>Junco hyemalis</i>)	DEJU	25	88
Cassin's Finch (<i>Carpodacus cassinii</i>)	CAFI	26	62

^aPinyon-juniper specialists (Balda and Masters 1980, Fitton and Scott 1984)

^bEndemic to the Great Basin

breeding bird species and (2) compare differences in avian habitat use along habitat gradients. Because pinyon-juniper specialists in southwestern Wyoming select habitat according to elevation and vegetation structure typical of mature juniper woodland (Pavlacky and Anderson 2001), we predicted that these factors would influence the habitat distribution of breeding birds.

METHODS

Study Site

We studied habitat used by 14 members of a breeding bird community in the Green River basin, southwestern Sweetwater County, Wyoming. Our study area encompasses 345 km² of Utah juniper (*Juniperus osteosperma*) woodland east of Flaming Gorge Reservoir, south of Rock Springs, Wyoming (41°00'–41°30'N, 109°00'–110°30'W). The climate is semiarid with mean annual temperatures ranging from 1.2°C to 14.8°C, and mean annual precipitation of 24 cm. Topography of the region consists of moderately steep rocky ridges and rolling hills dissected by alluvial flats and ephemeral drainages. Mesic northeastern aspects exhibit high-density woodlands with relatively high canopy cover, and xeric, southwestern-facing slopes support open, low-growing woodland. Low elevations are dominated by big sagebrush (*Artemisia tridentata*) and elevations between 1950 m and 3000 m support monotypic stands of Utah juniper. Pinyon pine (*Pinus edulis*) is present in the understory in the southern por-

tion of the study area. Common understory shrubs include big sagebrush, mountain mahogany (*Cercocarpus montanus*), rabbitbrush (*Chrysothamnus* spp.), and bitterbrush (*Purshia tridentata*).

Most woodlands in the study site are located within Bureau of Land Management (BLM) boundaries. Land use includes livestock grazing and oil and natural gas development. Several BLM habitat management projects are aimed at improving forage for livestock and ungulate game species. An extensive unimproved road network supports activities such as hunting and recreation associated with Flaming Gorge Reservoir. Some woodlands show signs of thinning due to firewood and/or fencepost cutting. All woodland patches were subject to livestock grazing and unimproved roads.

Data Collection

We selected 14 of the most frequently encountered bird species for study, representing the core avian community in Utah juniper woodlands of southwestern Wyoming (Table 1; American Ornithologists' Union 1998). We investigated habitat used by breeding birds along 25 transects in 22 woodland patches from 15 May to 8 July 1998, and from 11 May to 3 July 1999. The patches were defined as discrete stands of juniper woodland bounded by sagebrush vegetation. Woodland patches with adequate road access were identified by inspection of 1:24,000 aerial photographs and 7.5-minute topographic maps. We selected woodland patches in a uniform distribution within

the study area using a Geographic Information System (ArcView, version 3.1), representing the range of patch sizes (0.1–22.3 km²) present in the study area (Pavlacky 2000). Of 22 sampled patches, 4 showed signs of woodland thinning, 3 contained edge affiliated with primary road development, 1 had edge associated with pipeline construction, and 1 contained edge created by prescribed fire. We positioned line transects (\bar{x} length = 1.5 km, range = 0.8–2.4 km) from woodland edge toward the interior of each patch using aerial photographs and topographic maps. Starting points and transect bearings were predetermined to maximize transect length. Each transect was navigated using compass orienteering techniques from 0.5 hour after sunrise until 4 hours after sunrise. In both years we visited the transects once early in the breeding season (11 May–11 June) and again during the later part of the season (12 June–8 July).

We determined habitat use by centering 0.04-ha circular vegetation quadrats on positions where individual birds were sighted (James 1971, Larson and Bock 1986). To ensure independent observations, we used the 1st bird-centered location for each observed individual. Bird-centered locations along identical transects between years were treated as independent samples. We chose bird-centered vegetation sampling because it represents an improvement over correlation techniques in its ability to identify a greater number of specific habitat features used by individuals within the bird community (Larson and Bock 1986). This method is similar to that used by Sedgwick (1987) except that we marked locations of all adult birds encountered rather than only singing males, thus avoiding bias in vegetation height associated with singing perches (Larson and Bock 1986). Birds encountered along line transects were engaged in a variety of behaviors including vocalizing, perching, nesting, and foraging. Because breeding bird territories must contain vegetation structure suitable for each of these behavioral activities (Balda 1975, Anderson 1980), we pooled all observations to assess habitat used by each species. This spatial scale of investigation is designed to identify the use of habitat features within bird territories (Johnson 1980) for local populations of several species (Wiens et al. 1986).

Habitat use was quantified by measuring 24 habitat variables in each 0.04-ha bird-cen-

TABLE 2. Habitat variables measured within 0.04-ha vegetation quadrats, Sweetwater County, Wyoming, 1998–1999.

Description
Elevation (m)
Slope (%)
Seedling and sapling (main stem < 10 cm dbh) density (stems · ha ⁻¹)
Mature tree (main stem 10–35 cm dbh and < 5 m height) density (stems · ha ⁻¹)
Dominant tree (main stem > 35 cm dbh and > 5 m height) density (stems · ha ⁻¹)
Total mature tree (main stem > 10 cm) density (stems · ha ⁻¹) ^a
Sapling and seedling (main stem < 10 cm dbh) canopy cover (%)
Mature tree (main stem 10–35 cm dbh and < 5 m height) canopy cover (%) ^a
Dominant tree (main stem > 35 cm dbh and > 5 m height) canopy cover (%) ^a
Overstory tree (main stem > 10 cm) canopy cover (%)
Canopy height (m)
Effective understory foliage height (cm)
Asteraceae shrub density (mean distance from center point)
Rosaceae shrub density (mean distance from center point)
Total shrub density (mean distance from center point)
Grass cover (%)
Shrub cover (%)
Forb cover (%)
Litter and stick (< 7 cm diameter) cover (%)
Down log and stump (> 7 cm diameter) cover (%)
Bare ground and rock cover (%)
Snag (> 20 cm dbh and 2 m height) density (stems · ha ⁻¹)
Dead limb (> 20 cm dbh and 2 m height) density (stems · ha ⁻¹)
Decadent tree (> 25% dead limbs) density (stems · ha ⁻¹)

^aHighly correlated habitat variables removed from analysis

tered quadrat (Table 2). We selected the habitat variables best able to distinguish between vegetation structure (Anderson 1980) of juniper woodland successional stages (Blackburn and Tueller 1970, Barney and Frischknecht 1974, Koniak 1985). Habitat features were measured using the modified techniques of James and Shugart (1970) and Noon (1981). Elevation (m) above sea level was derived from 7.5-minute topographic maps. Using a Biltmore reach stick, we determined the size class of trees by measuring the diameter-at-breast-height (dbh) of the main tree stem. Juniper trees were classified as seedling/sapling (main stem < 10 cm dbh), mature trees (main stem 10–35 cm dbh, < 5 m height), and dominant trees (main stem > 35 cm dbh, > 5 m height). We determined density (stems · ha⁻¹) by counting the number

of stems in each tree class per vegetation quadrat. For each tree class, canopy cover (%) was measured as the proportion of hits to misses while sighting upward along a meter stick at 40 standard locations along 2 transects intersecting the bird location. Overstory juniper cover (%) was considered canopy cover for mature trees (main stem > 10 cm). We estimated tree height (m) as the mean height of canopy within the vegetation quadrat. Understory foliage height (cm) was defined as the mean height of vegetation not greater than breast height along the 4 segments of the intersecting transects. Using an ocular tube with cross hairs, we measured ground cover (%) by sighting vertically at 40 standard locations along 2 intersecting transects. Decadent trees were those visually estimated to have >25% dead limbs (Sedgwick 1987).

Statistical Analyses

We used discriminant function analysis (DFA; SPSS, version 8.0) to compare habitat use of 14 bird species with ≥ 25 observations (Table 1; $n = 461$). Discriminant function analysis produces 1 or more independent, linear combinations of habitat variables that maximize Mahalanobis distance between group (bird) centroids (Klecka 1980, Williams 1983). The discriminant functions that emerge are composed of habitat variables that best differentiate between habitat used by members of the avian community (Sedgwick 1987). We used the discrimination procedure to identify variables accounting for differences in habitat use, and classification analysis to assess the fit and predictive ability of the discriminant functions (Klecka 1980, Williams 1983). Pearson product moment correlation was used to avoid problems attributed to multicollinearity (Minitab, version 12.21). When 2 highly correlated habitat variables were encountered ($r > 0.70$, $P < 0.05$), we retained the most biologically explainable variable in the analysis (Anderson and Shugart 1974). A final set of 21 habitat variables was used to perform all DFA (Table 2). We interpreted each statistically significant discriminant function ($\alpha = 0.05$) according to habitat variables exhibiting the highest structure coefficients (Klecka 1980, Williams 1983). Ordination of bird species in 3-dimensional habitat space was achieved by plotting group (bird) centroids in relation to the habitat gradients. We generated classification statistics using

quadratic DFA, which relaxes the assumption of homogeneity within the variance-covariance matrix (Klecka 1980). Prior probabilities of group membership were adjusted to reflect the sample size of bird species included in the analysis (Table 1). We considered classification rates of $\geq 50\%$ as evidence of habitat partitioning (Sedgwick 1987).

RESULTS

We differentiated between habitat used by 14 bird species along 3 significant ($P < 0.05$) discriminant functions (Table 3). Discriminant function 1 (DF1), defined by a gradation of shrub cover, overstory canopy cover, mature tree density, and decadent tree density, accounted for the greatest differences in habitat use within the breeding bird community (Wilk's $\lambda = 0.319$, $df = 273$, $P < 0.001$, canonical $R^2 = 0.33$). Discriminant function 2 (DF2) explained changes in habitat use along a gradient of elevation and forb cover (Wilk's $\lambda = 0.476$, $df = 240$, $P < 0.001$, canonical $R^2 = 0.17$). Discriminant function 3 (DF3) described a habitat gradient composed of grass cover, tree height, seedling/sapling cover, and bare ground/rock cover (Wilk's $\lambda = 0.573$, $df = 209$, $P = 0.038$, canonical $R^2 = 0.13$).

The DFA correctly classified 56% of the 461 bird observations into habitat space used by 14 bird species. The fit of the habitat model is 48% better than chance, considering classification of 7% would be expected from a random distribution. Of the 14 species considered, 9 exhibited $\geq 50\%$ correct classification (Table 1). Bird-centered locations for each species were primarily perching sites (34%), followed by singing stations (31%) for territorial defense. The Mountain Bluebird (*Sialia currucoides*) was the only species represented by a large percentage of known nest sites (31%).

Ordination of 14 species suggests 3 general subgroups: 10 species associated with closed canopy, 3 with open canopy, and 1 with young woodland (DF1; Fig. 1). The 10 species in the closed canopy group used woodlands with greater overstory juniper cover and density of mature and decadent trees, and lower shrub cover and understory height than other species. The Northern Flicker (*Colaptes auratus*), Green-tailed Towhee (*Pipilo chlorurus*), and Chipping Sparrow (*Spizella passerina*) used increasingly

TABLE 3. Discriminant functions, habitat variables, and range of habitat conditions accounting for differences in habitat used by 14 bird species, Sweetwater County, Wyoming, 1998–1999.

Discriminant functions (DF) Habitat variables	Range		Structure coefficients	P
	Min	Max		
DF1: Woodland maturity				< 0.001
Shrub cover (%)	0.0	57.5	-0.71	
Overstory juniper cover (%)	0.0	77.5	0.52	
Mature tree density (stems · ha ⁻¹)	0.0	500.0	0.48	
Understory height (cm)	23.0	148.0	-0.43	
Decadent tree density (stems · ha ⁻¹)	0.0	325.0	0.38	
DF2: Elevation				< 0.001
Elevation (m)	1927.3	2242.4	-0.69	
Forb cover (%)	0.0	50.0	-0.49	
DF3: Juniper recruitment				0.038
Grass cover (%)	0.0	60.0	-0.66	
Tree height (m)	1.5	6.5	-0.53	
Seedling/sapling cover (%)	0.0	30.0	0.47	
Bare ground/rock cover (%)	0.0	67.5	0.39	

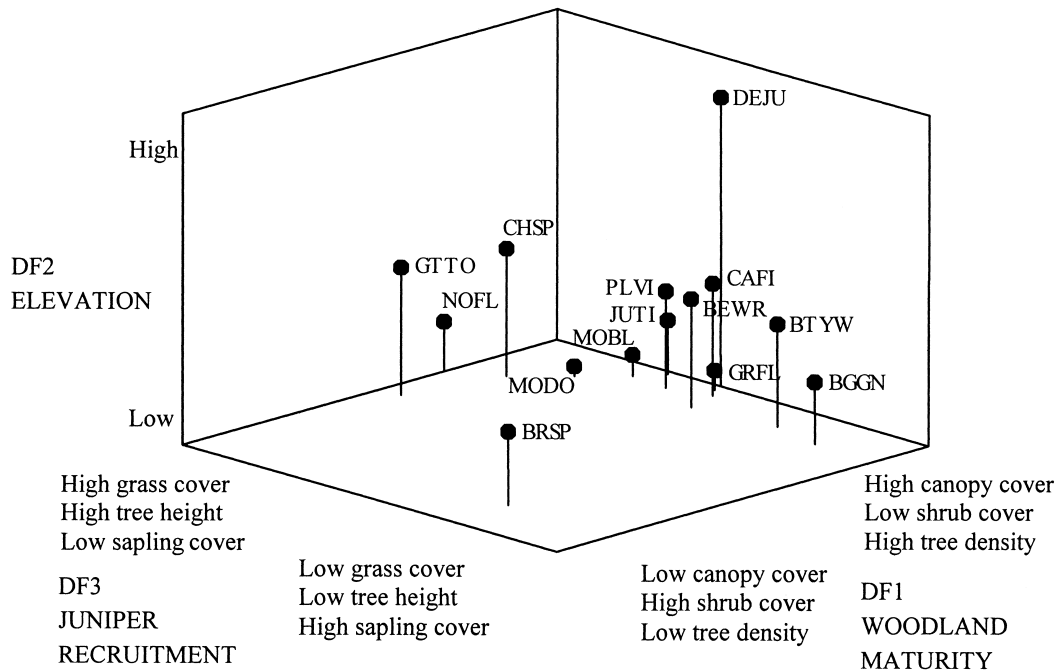


Fig. 1. Ordination of 14 bird species along 3 discriminant axes defined by woodland maturity, elevation, and juniper recruitment, Sweetwater County, Wyoming, 1998–1999. Species codes are given in Table 1.

open woodland with taller trees, moderately shrubby understory, higher grass cover, and lower seedling/sapling cover than did other members of the avifauna. Brewer’s Sparrows (*Spizella breweri*) used woodlands with lower

overstory juniper cover, density of mature and decadent trees, tree height, and grass cover; and greater shrub cover, seedling/sapling cover, and understory height than other species in the community.

Habitat utilized by most species was concentrated in woodlands at intermediate elevations with moderate herbaceous cover (DF2; Fig. 1). Dark-eyed Juncos (*Junco hyemalis*) used woodlands at higher elevations with greater forb cover, while Mourning Doves (*Zenaidura macroura*), Gray Flycatchers (*Empidonax wrightii*), and Mountain Bluebirds used woodlands at lower elevations with less herbaceous ground cover.

Along habitat gradient DF3, Blue-gray Gnatcatchers (*Poliophtila caerulea*) and Black-throated Gray Warblers (*Dendroica nigrescens*) used woodlands with lower grass cover and tree height, and greater seedling/sapling and bare ground/rock cover than other species (Fig. 1). Gray Flycatcher, Bewick's Wren (*Thryomanes bewickii*), Dark-eyed Junco, and Cassin's Finch (*Carpodacus cassinii*) habitat was intermediate with respect to grass cover, tree height, seedling/sapling, and bare ground/rock cover. The Mourning Dove, Juniper Titmouse (*Baeolophus griseus*), Mountain Bluebird, and Plumbeous Vireo (*Vireo plumbeus*) used woodlands with greater grass cover and tree height and lower seedling/sapling and bare ground/rock cover than other members of the bird community.

DISCUSSION

Our interpretation of the discriminant functions suggests the core bird community in southwestern Wyoming is organized along a 3-dimensional habitat gradient composed of woodland maturity, elevation, and juniper recruitment (Fig. 1). The structure coefficients for DF1 (woodland maturity) correspond to a successional series proceeding from immature to mature woodland (Table 3). Increased overstory juniper cover, mature tree density, and decadent tree density along with the corresponding decrease in shrub cover are expected as succession advances toward mature woodlands (Koniak 1985). The density and canopy cover of mature trees increase substantially in stands 100–150 years of age (Barney and Frischknecht 1974). Utah junipers past 137 years of age begin to senesce, becoming decadent after 241 years (Blackburn and Tueller 1970).

Discriminant function 2 (elevation) and associated structure coefficients parallel a habitat gradient of elevation and forb cover (Table 3). Elevation is a complex variable, and relationships can be expected to arise from several

interrelated factors. We accounted for autocorrelation between habitat variables along the elevation by removing highly correlated habitat variables from consideration prior to the analysis. In pinyon pine and Utah juniper woodlands of northwestern Colorado, mean annual temperature decreases by 1% for every 100 m increase in elevation (Weldon et al. 1990). High elevations receive more October–June precipitation and exhibit greater herbaceous productivity than low elevations (Tausch and Tueller 1990, Vaitkus and Eddleman 1991).

We interpreted the structure coefficients for DF3 (juniper recruitment) as a successional gradient proceeding from low to high juniper recruitment (Table 3). As succession advances from early to mid-successional stages, seedling/sapling and bare ground/rock cover increase while grass cover decreases (Koniak 1985). However, grass production is positively correlated with increasing tree height due to ecological release from competing shrubs (Vaitkus and Eddleman 1991). Saplings <3 m tall provide most of the canopy cover in woodlands 22–46 years of age (Barney and Frischknecht 1974). In general, early successional woodlands are characterized by maximum age classes of <100 years (Vaitkus and Eddleman 1991).

Another interpretation of DF3 describes a grazing-induced successional pathway in Utah juniper woodlands (Baker and Kennedy 1985). According to Baker and Kennedy (1985), livestock grazing can influence woodland succession by decreasing native grass species and increasing shrubs, forbs, and exotic grasses. High grazing pressure by domestic livestock can result in the ecological release of less palatable juniper seedlings (Miller and Wigand 1994). However, other ecological processes, such as reduced fire frequency and climate change, can result in decreased grass cover and increased juniper recruitment in pinyon-juniper woodlands (Miller and Wigand 1994, Chambers et al. 1999).

Habitat used by 10 of 14 bird community members was concentrated toward the end of the woodland maturity gradient (Fig. 1). Bird species richness is positively associated with successional age of pinyon-juniper woodlands (Rosenstock and van Riper 2001) due to increased vegetation complexity of later successional stages (Germano and Lawhead 1986). The habitat used by 10 species associated with mature woodland is subdivided along DF3

according to juniper recruitment in the mid-level canopy (Fig. 1). Our results are similar to those of Willson (1974), where the addition of a mid-canopy tree layer increases vegetation structure and promotes differential habitat utilization. Late-successional juniper woodlands are often composed of multiple age classes ranging from seedlings and saplings to trees several hundred years old, with most trees in an intermediate age class (Burkhardt and Tisdale 1969).

Although habitat use was largely concentrated at intermediate elevations, a few species occupied the elevation gradient extremes (Fig. 1). Stevens (1992) suggests bird distribution along elevation gradients is a function of species ability to tolerate a range of microclimates. Several pinyon-juniper specialists show selection for aspect and elevation in southwestern Wyoming (Pavlacky and Anderson 2001). However, bird communities may segregate habitat according to variation in vegetation structure along elevational gradients (Finch 1989). As mentioned previously, relationships along elevation gradients may arise from several inter-related variables. For instance, nest sites used by Dark-eyed Juncos are associated with forb cover (Dumas 1950), which often increases with elevation (Tausch and Tueller 1990).

Of 14 species considered, Northern Flickers, Green-tailed Towhees, and Chipping Sparrows used woodlands with greater tree height and grass cover, moderate overstory and shrub cover, and lower seedling/sapling cover than other members of the community, indicating an association with open seral woodland (Fig. 1). Contrary to our results, Sedgwick (1987) found Green-tailed Towhees and Chipping Sparrows negatively associated with crown height in pinyon-juniper woodlands of northwestern Colorado. We suggest this discrepancy is due to different study objectives. While Sedgwick (1987) sampled chained and unchained woodland, we investigated a range of variation in a naturally patchy woodland. Paleobotanical evidence indicates juniper woodland once existed in an open, savanna-like condition over much of the Intermountain region (Miller and Wigand 1994). Although Chipping Sparrows and Green-tailed Towhees use woodland openings created by chaining (Sedgwick 1987), it is likely that these species have a historical association with open savanna-woodland interspersed with large

trees created by natural disturbance. In addition, the presence of open woodland may benefit secondary cavity-nesting species by providing habitat for the primary cavity-nesting Northern Flicker.

The Brewer's Sparrow was the only species associated with immature woodland characterized by low canopy cover and density of mature trees, and high shrub and seedling/sapling cover (Fig. 1). Often considered a sagebrush specialist, the Brewer's Sparrow is common in early successional juniper woodland (Wauer 1964) as well as large sagebrush openings within pinyon-juniper vegetation (Sedgwick 1987).

Habitat partitioning along environmental gradients results from natural selection, where habitat overlap imposes fitness costs among coexisting species (Martin 1996). Although competition is commonly invoked as a causal factor (Schoener 1986), different processes can produce identical patterns of habitat segregation (Wisheu 1998). Habitat division may arise from a combination of abiotic and biotic factors (Martin 2001), as well as the physiological, morphological, and behavioral attributes of the constituent species (Wisheu 1998). While the underlying causal processes are unknown, succession appears to strongly influence avian community organization in juniper woodlands (Rosenstock and van Riper 2001).

We recognize 3 limitations to results of our study. First, because we considered habitat use relative to other species in the community, our results may not reflect the habitat preferences of individual species. For example, Bewick's Wrens, Blue-gray Gnatcatchers, and Black-throated Gray Warblers select breeding territories with greater shrub cover than is available in the environment (Pavlacky and Anderson 2001). Results presented here show that these species use woodlands with lower shrub cover than several other members of the bird community. Second, because DFA determines habitat features best able to differentiate among members of the bird community, habitat associations shared by species cannot be ascertained. Finally, although sample effort for each species was equal along the transects, the range of conditions sampled may not reflect the actual proportion of habitat features in the study area. For instance, mature woodland may have been overrepresented along the habitat gradient.

CONCLUSIONS

Ranchers and land managers are concerned with increasing land cover of juniper and declining forage production for livestock and ungulate game species (Burkhardt and Tisdale 1969, Terrel and Spillet 1975). In addition, encroachment of juniper woodland into grasslands will change species composition and abundance within grassland bird communities (Rosenstock and van Riper 2001). Woodland clearing may benefit certain wildlife species, but certain woodland-dwelling birds may decline in response to habitat loss (Terrel and Spillet 1975, Sedgwick 1987). However, if juniper expansion is largely due to human land use, grassland restoration and woodland control may be necessary.

Restoration efforts must consider recent changes to juniper plant communities (Chambers et al. 1999), as well as the possibility of climate-induced range expansion (Miller and Wigand 1994). As succession proceeds from grasslands to tree-dominated woodlands, bird species enter and leave the community in predictable sequences, according to specific habitat requirements (Rosenstock and van Riper 2001). Because juniper birds appear to partition habitat along successional and altitudinal gradients, both indiscriminate woodland clearing and fire suppression may alter species composition, resulting in the elimination of certain avian species. Mature woodlands are often targeted for woodland clearing due to low forage productivity of late successional stages (Vaitkus and Eddleman 1991, Chambers et al. 1999). Yet, 6 of 10 species using mature Utah juniper in the present study are considered pinyon-juniper specialists in the Intermountain region (Balda and Masters 1980).

Burkhardt and Tisdale (1969) and Rosenstock and van Riper (2001) conclude that juniper control would be more beneficial on recently invaded alluvial sites than mature upland woodlands. While we agree, fire must also be returned to woodlands because certain species have historical associations with open mid-seral woodlands. Some woodland-dwelling species may benefit from increased juniper recruitment and stand density, but juniper expansion may negatively affect other species using grass understories and open woodlands (Fig. 1). The integrity of juniper woodland bird communities will be enhanced by ensur-

ing that all successional stages are present on the landscape (Anderson 1980).

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