

## REGIONAL CORRESPONDENCE AMONG SHRUBSTEPPE BIRD HABITATS<sup>1</sup>

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**Abstract.** Habitats of Brewer's Sparrows (*Spizella breweri*) and Green-tailed Towhees (*Pipilo chlorurus*) were compared (as biological replicates) in Colorado, Nevada, and Utah to identify regional commonalities in vegetation species, structure, and vigor among habitats of shrubsteppe passerines. Sparrow habitats were in landscapes dominated by sagebrush (*Artemisia* spp.) whereas towhee habitats were better described as ecotones between sagebrush and other shrub species. Individuals of both species selected bushes of comparable vegetative vigor across the three states even though species populations were allopatric in two of the states. For each species, measures of vegetation structure and vigor were compared between breeding habitats in Colorado and Nevada (near the longitudinal extremes of the continental distribution of each species at 42°N latitude) in 1983. Sparrow habitats in the two states were similar in four measures of vigor but differed in all structural variables measured. Towhee habitats were similar between Colorado and Nevada for three measures of vigor and three measures of structure. Independent tests of the Colorado/Nevada conclusions were conducted near the center of the species' ranges (Utah) in the subsequent breeding season (1984). Those tests confirmed the validity of all measures of vegetation vigor as descriptors of sparrow habitat and one measure of vigor plus two of vegetation structure as descriptors of towhee habitat. Thus, sparrow habitats were best characterized regionally by measures of sagebrush vigor, whereas towhee habitats were characterized by shrub vigor and structure. Our tests and conclusions generally support recent, correlational studies that identify vegetative physiognomy as the primary descriptor of passerine habitats at a regional scale and floristic composition as the primary descriptor at a local scale. We add that individuals of these two species selected habitats from a mosaic of patches of varying vegetation vigor (supplemented by structural information for towhees) within a locale. Measures of vegetation vigor are rarely used to describe passerine habitats, although vigor surely correlates better with food abundance and cover for nests than vegetation structure. These observations suggest an hierarchical approach for viewing habitat selection by shrubsteppe birds.

**Key words:** *Brewer's Sparrow*; *Spizella breweri*; *Green-tailed Towhee*; *Pipilo chlorurus*; *Colorado*; *Nevada*; *Utah*; *shrubsteppe*; *habitat*; *habitat selection*; *Artemisia*; *Cercocarpus*.

### INTRODUCTION

The process of habitat selection by birds has historically been of major interest to ornithologists (Hildën 1965, Cody 1985). Current understanding of the relation between habitat structure and use of a site by birds has been based upon correlative studies performed in different habitats, multivariate ordinations at single study areas,

and natural and manipulative experiments (Morse 1985).

Manipulative experiments of habitat selection are difficult to design for field studies (Wiens et al. 1986). Correlative and ordination approaches have predominantly addressed habitat selection within localized populations and conclusions are almost never tested with independent data for a population of the species from a distant location. Where tested, vegetation variables strongly associated with a species' habitat locally are rarely supported as predictors of species' presence or population density at regional or continental scales of investigation (Wiens 1985a).

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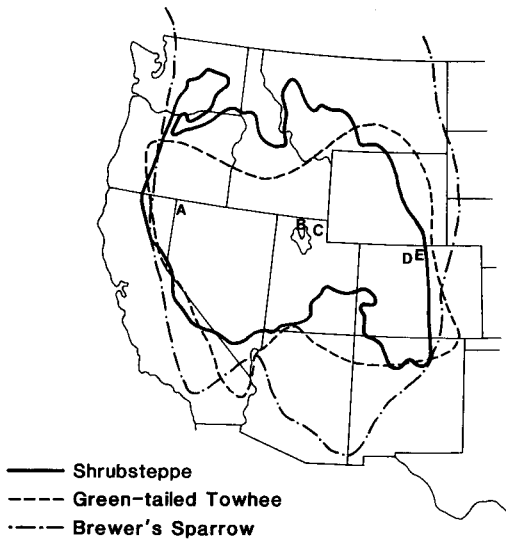


FIGURE 1. Distribution of shrubsteppe communities (developed from Bailey and Cushwa 1981) and breeding populations of Brewer's Sparrows and Green-tailed Towhees in the western United States. Study areas for Brewer's Sparrows and Green-tailed Towhees included an area of sympatric populations in Humboldt County, Nevada (A), and areas of allopatric species populations in Box Elder (B) and Cache (C) counties, Utah, and Jackson (D) and Larimer (E) counties, Colorado.

Regionwide similarities in the structural characteristics of habitats have been identified in correlative studies of passerine birds of deciduous forests (Cody 1978, Noon et al. 1980, James et al. 1984). However, studies of single species in forests (Collins 1983) and avian assemblages in western shrubsteppe communities (Wiens and Rotenberry 1981) reported very dissimilar structuring of species' habitats regionally, the latter study implicating floristic composition as a better predictor of species' habitats. The importance of floristics also is supported by a regional analysis by Rotenberry (1985) and local studies in forest communities (Franzreb 1978, Holmes and Robinson 1981, Rice et al. 1984, Robinson and Holmes 1984).

This study was designed as an independent test of the relevance of using vegetation measurements to define passerine habitats at multiple scales (continental/regional/local) of investigation. We chose sagebrush-dominated landscapes (generally referred to as the North American shrubsteppe) of the western United States for

these tests due to their extensive distribution yet simple physiognomy, floristic composition, and structure.

## THE APPROACH

Whereas field studies of a species-specific habitat traditionally look for significant local differences between used vs. random (or "unused") sites, we sought to identify those vegetation characteristics that were common to two local, but distant habitats of a species. Our approach described the habitat of a species near the longitudinal extremes (eastern vs. western edges) of its continental distribution, with fieldwork conducted simultaneously at both study areas. Those habitat variables that did *not* differ statistically between the areas were hypothesized to have biological meaning to that species. We subsequently located a population of that bird species at an independent place (in the middle of its continental distribution) and time (during the following breeding season) to test conclusions drawn regarding habitat descriptors.

We chose the Brewer's Sparrow (*Spizella breweri*) for the study because of its strong association with a simple woody community, sagebrush (*Artemisia* spp.) steppe. Because we were interested in evaluating the generality of the approach to habitat studies rather than providing a single-species test, we replicated the test by simultaneously collecting information on Green-tailed Towhees (*Pipilo chlorurus*). The towhee has a similar continental distribution at 42°N latitude, is considered a near-obligate of sagebrush landscapes (Braun et al. 1976), and its habitat was most frequently misclassified as Brewer's Sparrow habitat in a vegetation ordination from northwestern Colorado (Sedgwick 1987).

## STUDY AREAS AND METHODS

### HABITAT SIMILARITIES BETWEEN AREAS

Study areas were located in Colorado and Nevada, near the eastern and western edges of the continental distribution of both species (Fig. 1). In Colorado, Green-tailed Towhee habitats were surveyed on the Colorado Division of Wildlife's Lone Pine Management Unit (1,909 m elevation), 11 km west of Livermore, Larimer County (40°47'N, 105°20'W). Vegetation was a xeric shrub association dominated by true mountain mahogany (*Cercocarpus montanus*), fragrant sumac (*Rhus aromatica*), antelope bitterbrush

(*Purshia tridentata*), gooseberries (*Ribes* spp.), and Rocky Mountain juniper (*Juniperus scopulorum*). Brewer's Sparrow habitats were surveyed on the Arapaho National Wildlife Refuge (2,500 m elevation), 10 km south of Walden, Jackson County (40°38'N, 106°15'W). The topography was gently rolling slopes and woody vegetation was exclusively big sagebrush (*A. tridentata*). In Nevada, habitats of both species were measured at the Sheldon National Wildlife Refuge (2,100 m elevation), Humboldt County, Nevada (41°37'N, 119°18'W). The vegetation also was a xeric association, comprising curlleaf mountain mahogany (*C. ledifolius*), big sagebrush and antelope bitterbrush.

At each study area, we located 50 different individuals of each bird species by slowly walking transects between 06:00 and 10:00 hr between 11 June and 8 July 1983. To assure a robust characterization of habitat for the two species, we recorded the activity and location of the first 50 individuals of each species seen irrespective of behavior (singing, foraging, nest site). The bush in which a bird was sighted was flagged for vegetation measurements later that afternoon. When a bird was first observed foraging on the ground, we waited until it moved to a bush during its foraging activity. Individuals that flushed from the ground to a bush in response to the investigator were not included. When birds flushed from a nest, we recorded information at the nest site rather than at the location to which the bird flew.

The objective of the habitat measurements was to describe species, structure, and vigor of the central bush (where the bird was seen) plus horizontal and vertical patterning and vigor of the shrub patch from the perspective of a bird sitting in that bush. The habitat description methodology was developed in 1980 for studies of riparian birds in willow (*Salix*) shrub communities (Knopf et al. 1988) and is akin to the "organism-centered view" of habitat since advocated by Wiens (1985b). Briefly, we recorded height, maximum diameter, and species of the bird-centered bush. Distance to nearest bush was measured in each of four quadrants delineated by the cardinal compass directions, and measurements taken at the center bush were repeated at the closest bush in each quadrant. Petersen and Best (1985) defined the importance of vigor in identifying bushes used by Brewer's Sparrows; following their methodology, we classified bushes according to

TABLE 1. Vegetation variables measured, or calculated, for locations within Brewer's Sparrow and Green-tailed Towhee habitats in Colorado, Nevada, and Utah.

Variable	Definition
Shrub variables	
HTC	Height of central bush
DIAC	Diameter of the central bush
VIGC	Vigor index for the central bush
DNB	Distance to the nearest bush in any quadrant
Shrub patch variables	
MSEP	Mean distance to nearest bush/quadrant
CVSEP	Coefficient of variation of distance to nearest bush/quadrant
MHT	Mean height of nearest bush/quadrant
CVHT	Coefficient of variation of height of nearest bush/quadrant
MDIA	Mean diameter of nearest bush/quadrant
CVDIA	Coefficient of variation of diameter of nearest bush/quadrant
MVIG	Mean vigor index for nearest bush/quadrant
CVVIG	Coefficient of variation of vigor of nearest bush/quadrant
MHB	Mean index for herbaceous biomass/quadrant
CVHB	Coefficient of variation of herbaceous biomass/quadrant

percentage of live branches (<25%, 25–49%, 50–74%, or 75–100%). Standing herbaceous biomass was indexed midway between the central bush and nearest bush in each quadrant using the vertical density pole technique of Robel et al. (1970). In all, the analyses included 14 measured and calculated (arithmetic mean and coefficient of variation) variables describing the central bush and the setting of that bush within a shrub patch (Table 1).

We used Mann-Whitney *U*-tests to compare vegetative characteristics of habitats of each species in Colorado and Nevada because data of some habitat variables were neither normally distributed nor homogeneous between areas (assumptions for parametric statistics). Probability of a Type I error was arbitrarily established at the  $\alpha \leq 0.05$  level. The crux of the approach involved the failure to reject statistical null hypotheses, and tests for Type II error were appropriate for comparisons where  $P > 0.05$ . However, statistical power ( $1 - \beta$ ; Toft and Shea 1983) tests are based upon known data distributions (Cohen 1988) and thereby not generally applied to distribution-free statistics such as the

TABLE 2. Numbers of sightings of Green-tailed Towhees and Brewer's Sparrows that were singing birds vs. sightings of birds in other activities in Colorado, Nevada, and Utah. The number of nest sites appears in parentheses.

	Brewer's Sparrow		Green-tailed Towhee	
	Singing	Other	Singing	Other
Colorado	23	27 (0)	13	37 (1)
Nevada	22	28 (0)	13	37 (0)
Utah	13	37 (2)	20	30 (3)

Mann-Whitney *U*-test. One approach available to us was to develop known data sets that we assumed represented the true distribution for each of our habitat variables, and then conduct power series analyses of that test on the known population. An alternative approach was to merely assume that data for habitat variables, for which we had failed to reject the null hypothesis, were normally distributed and then derive a power for the test based upon *n*,  $\alpha$ , and a predetermined effect size from power tables for paired *t*-tests available in Cohen (1988). Both approaches required an assumption about the distribution of the data. We chose the *t*-test approach for cases of equal variances and sample sizes (Cohen 1988, p. 27) because the normal distribution is well-known in biological sampling, and power (relative efficiency) of the Mann-Whitney *U*- and the *t*-test is similar for normally distributed data in cases of larger sample sizes (Snedecor and Cochran 1972, p. 132).

#### TESTS OF PREDICTIONS AT AN INDEPENDENT AREA

From 11 to 14 June 1984, we measured the same habitat variables within habitats of 50 sparrows and 50 towhees at five areas in northern Utah, near the center of the breeding range of each species. The vicinity was approximately 560 km west of the Colorado study areas and 630 km east of the Nevada study area. The areas included the Temple Fork (41°47'N, 111°36'W) and West Hodges Creek (41°53'N, 111°33'W) areas of Logan Canyon (2,000–2,300 m elevation) which were 27 km and 35 km, respectively, northeast of Logan, Cache County; an area (41°57'W, 112°4'W) 1 km west of Collinston (1,460 m elevation), Cache County; and two areas within 10 km northeast (41°49'N, 112°24'W) and northwest (41°49'N, 112°29'W) of Howell (1,390 m elevation), Box Elder County. The Logan Can-

yon areas were mixed-species shrub communities dominated by common chokecherry (*Prunus virginiana*), big sagebrush, true mountain mahogany, Utah juniper (*J. osteosperma*), snowberry (*Symphoricarpos* spp.), and serviceberry (*Amelanchier* spp.). Vegetation of other areas was predominantly big sagebrush, but included some mountain mahogany and rubber rabbitbrush (*Chrysothamnus nauseosus*). We observed both bird species at four of the five areas; most of the Green-tailed Towhees were at the Logan Canyon areas and most of the Brewer's Sparrows were at the Box Elder county areas.

Data from those vegetation variables identified as being similar between Colorado and Nevada areas in 1983 were pooled by species and tested against data for that species collected in Utah in 1984. The statistical probability of a Type I error remained at the  $\alpha \leq 0.05$  level. Observations of bird habitats were not paired in this comparison ( $n_1 = 50$ ,  $n_2 = 100$ ), and we calculated  $n' = 66$  (Cohen 1988, p. 130) to define the statistical power of these comparisons.

#### RESULTS

Although singing males were seen at greater distances than birds observed in other activities, singing activity generally declined rapidly after the first hour of our daily surveys. Thus, fewer than half of the 50 individuals recorded at each study area were singing males of either species (Table 2).

We used simple correlation matrices among habitat variables from the three study areas combined ( $n = 150$ /species) to identify redundancies in the habitat information. Only height and diameter of the central bush were strongly correlated (Brewer's Sparrow:  $r = 0.89$ ,  $P = 0.001$ ; Green-tailed Towhee:  $r = 0.73$ ;  $P = 0.001$ ), and we dropped diameter of the central bush from the analyses.

#### SPARROW/TOWHEE HABITAT PERSPECTIVES

Before examining habitat selection within species, we compared sparrow habitats to towhee habitats across all areas. Habitats of Brewer's Sparrows included 14 species of shrubs, although birds were most strongly associated with sagebrush (Table 3). Habitats of Green-tailed Towhees included 23 shrub species, with the two species of mountain mahogany being most dominant; sagebrush and common chokecherry also occurred

TABLE 3. Percentage dominance of major shrubs (>10% species frequency/bird species) within habitats of Brewer's Sparrows vs. Green-tailed Towhees in Colorado, Nevada, and Utah. Shrub species were recorded as the perch site of the bird when sighted (center shrub) and for the nearest shrub in each of four quadrants delineated by the cardinal directions (shrub patch).

	Brewer's Sparrow		Green-tailed Towhee	
	Center <sup>a</sup>	Patch <sup>b</sup>	Center	Patch
<i>Artemisia</i> spp.	74.7	81.8	5.3	26.0
<i>Cercocarpus ledifolius</i>	14.7	0.5	29.3	1.3
<i>C. montanus</i>	3.3	1.2	28.7	25.7
<i>Prunus virginiana</i>	0.0	0.0	10.0	7.0
Others <sup>c</sup>	7.3	16.5	26.7	40.0

<sup>a</sup>  $n = 150$ .

<sup>b</sup>  $n = 600$ .

<sup>c</sup> Number of additional woody species recorded: Brewer's Sparrow = 11, Green-tailed Towhee = 19.

regularly (>10%) in the plots. Simple community coefficient ( $CC$ ) comparisons (Whittaker 1975, p. 118) of floristic similarity across the geographic range of sparrows and towhees revealed that the birds were more similar ( $CC = 0.471$ ) in their selection of a central bush than in their selection of a shrub patch ( $CC = 0.270$ ). The two species showed differential use of sagebrush ( $\chi^2 = 92.3$ ;  $P < 0.001$ ) with sparrows frequenting sagebrush in proportion to its occurrence within patches and towhees selecting other shrub species in sagebrush-dominated patches.

Vegetative parameters differed significantly ( $P < 0.05$ ) between sparrows and towhees for eight of the 13 remaining descriptors of individual shrub (Table 4). Sparrows occurred in more open (MSEP) and less regularly spaced (CVSEP) shrub patches than towhees. Sparrows also tended to occur in patches of more variable bush vigor (CVVIG). Towhees were in taller central bushes (HTC) located within taller (MHT) and more uniformly vigorous (MVIG, CVVIG) patches than sparrows. However, towhee habitats were more variable than sparrow habitats relative to physical bush dimensions (CVHT and CVDIA). The preference of towhees for sites with greater variability in herbaceous biomass (CVHB) appeared biologically significant considering the power of these tests.

Brewer's Sparrows and Green-tailed Towhees were similar in their selection of individual shrubs based upon vigor of the central bush (VIGC) and its proximity to the next bush (DNB). Both species selected shrub patches of similar mean bush di-

TABLE 4. Comparisons (Mann-Whitney  $U$ -test) of vegetation descriptors measured in Brewer's Sparrow vs. Green-tailed Towhee habitats ( $n = 150$ /species) in Colorado, Nevada, and Utah, 1983-1984. Power of the paired tests for  $\alpha_2$  of 0.05 and a posited effect size of 0.5 is 0.99.

	Brewer's Sparrow mean rank	Green-tailed Towhee mean rank	$P$
<b>Shrub variables<sup>a</sup></b>			
HTC	109.0	192.0	0.000
VIGC	149.1	152.0	0.729
DNB	148.0	153.0	0.153
<b>Shrub patch variables</b>			
MSEP	168.9	132.1	0.000
CVSEP	166.8	134.2	0.000
MHT	131.9	169.1	0.000
CVHT	137.6	163.4	0.010
MDIA	144.0	157.0	0.192
CVDIA	128.8	172.2	0.000
MVIG	117.6	183.4	0.000
CVVIG	175.7	125.3	0.000
MHB	143.3	157.7	0.148
CVHB	141.2	159.8	0.062

<sup>a</sup> Vegetation descriptors are defined in Table 1.

ameter (MDIA) and herbaceous biomass (MHB). Of those comparisons, the similarity in central bush vigor was especially dramatic ( $P = 0.729$ ) with both species selecting a central bush of comparable vigor (sparrow:  $\bar{x} = 1.81 \pm 0.05$  (SE); towhee:  $\bar{x} = 1.80 \pm 0.06$ ) within a patch even though populations of the two species were only allopatric at the Colorado and Utah study areas.

#### CORRESPONDENCE WITHIN SPECIES' HABITATS

Brewer's Sparrow habitats differed in nine of 13 vegetation descriptors between Colorado and Nevada (Table 5), so those nine descriptors were discarded from further consideration. Sparrows at both locations perched in bushes of similar vigor (VIGC) and within shrub patches that showed similarities in both mean vigor (MVIG) and vigor variability (CVVIG). Sparrows also used sites marginally similar in mean herbaceous biomass (MHB) at the two areas.

Green-tailed Towhee habitats differed in seven of the 13 vegetation descriptors between Colorado and Nevada (Table 5). Towhees showed similar preferences for shrub spacing between the central bush and nearest adjacent shrub (DNB) at both areas. Towhee patterns of shrub-patch selection between the two states were similar to those of the sparrow: patches were selected based

TABLE 5. Probability levels (Mann-Whitney *U*-test) for Colorado vs. Nevada comparisons of vegetation descriptors measured in Brewer's Sparrow and Green-tailed Towhee habitats ( $n = 50/\text{species}/\text{state}$ ), 1983. Power of the paired tests for  $\alpha_2$  of 0.05 and a posited effect size of 0.5 is 0.70.

	Brewer's Sparrow	Green-tailed Towhee
<b>Shrub variables<sup>a</sup></b>		
HTC	0.000	0.000
VIGC	0.251	0.004
DNB	0.042	0.648
<b>Shrub patch variables</b>		
MSEP	0.000	0.000
CVSEP	0.000	0.003
MHT	0.000	0.000
CVHT	0.016	0.958
MDIA	0.003	0.000
CVDIA	0.007	0.154
MVIG	0.549	0.584
CVVIG	0.734	0.848
MHB	0.061	0.075
CVHB	0.012	0.004

<sup>a</sup> Vegetation descriptors are defined in Table 1.

on shrub vigor parameters (MVIG, CVVIG) and marginally on herbaceous biomass (MHB). Unlike sparrows, towhees also selected shrub patches of similar variability in shrub dimensions (CVHT, CVDIA) within patches.

#### TESTS OF PREDICTIONS

Vegetation predictors of species' habitats in Colorado and Nevada were pooled and tested for validity against independent data from Utah (Table 6). For Brewer's Sparrows, measurements for all four descriptors at the Utah study area were similar to the combined Colorado/Nevada data although evidence supporting CVVIG and MHB as common predictors was marginal ( $0.05 < P < 0.10$ , power = 0.81). Thus, we could support all four variables as valid regionwide descriptors of sparrow habitats. For Green-tailed Towhees, only three of the vegetation descriptors (DNB, CVDIA, and MVIG) were similar between the Utah and the Colorado/Nevada data and supported as valid predictors regionally. Towhee habitats differed significantly between the Utah and Colorado/Nevada data for the remaining descriptors (CVHT, CVVIG, MHB).

#### DISCUSSION

##### SPARROW/TOWHEE HABITAT COMPARISONS

The Brewer's Sparrow is the dominant bird species of sagebrush landscapes in western North

TABLE 6. Probability levels for comparisons (Mann-Whitney *U*-test) of vegetation descriptors identified as being similar within Brewer's Sparrow or Green-tailed Towhee habitats in Colorado and Nevada, 1983 ( $n = 100/\text{species}$ ) vs. independent data from Utah, 1984 ( $n = 50/\text{species}$ ). Power of these paired tests for  $\alpha_2$  of 0.05,  $n' = 66$  and a posited effect size of 0.5 is 0.81.

	Brewer's Sparrow	Green-tailed Towhee
<b>Shrub variables</b>		
VIGC	0.302	NA <sup>a</sup>
DNB	NA	0.510
<b>Shrub patch variables</b>		
CVHT	NA	0.018
CVDIA	NA	0.247
MVIG	0.387	0.156
CVVIG	0.058	0.040
MHB	0.062	0.002

<sup>a</sup> Not applicable. Descriptor differed significantly in Colorado vs. Nevada comparison.

America, and dominance of Brewer's Sparrow habitats by sagebrush is well documented (Best 1972, Rich 1980). Our study confirms that Brewer's Sparrows occur in areas of rather homogeneous sagebrush cover. Sparrow use of mountain mahogany in Nevada surely reflected preferences of males to select elevated perches when singing.

In contrast to Brewer's Sparrows, habitats of Green-tailed Towhees are less well-known. Towhees occur in areas of: (1) increased shrub species diversity associated with rocky outcrops in sagebrush-dominated vegetative communities (Wiens and Rotenberry 1981; Rotenberry, pers. comm.), (2) enhanced shrub species richness within piñon (*Pinus edulis*)-juniper (*Juniperus osteosperma*) forests (Sedgwick 1987), and (3) enhanced shrub densities in the Sierra Nevada of California (Verner and Boss 1980). Across the biogeographic region that we sampled, towhees were only found in appreciable numbers in areas that included a component of mountain mahogany, *C. montanus*, in Colorado and Utah and *C. ledifolius* in Nevada. Thus, these congeneric shrub/small tree species were "typical" (but assuredly not exclusively so) of towhee habitats from a regional perspective. The presence of both sagebrush (within shrub patches) and mountain mahogany (central bushes) reflected the tendency for towhees to use vegetative ecotones where mountain mahogany and other shrub species encroach into sagebrush communities. However, because three of four towhee nests in our samples were in sagebrush and one was on the ground within a plot con-

taining mountain mahogany but no sagebrush, mountain mahogany may not provide satisfactory support for a nest despite being indicative of sites containing most other life requisites of towhees.

Brewer's Sparrows occurred in areas with smaller central shrub and surrounding shrub physical dimensions, whereas Green-tailed Towhees were located in taller shrubs occurring in larger, denser, and more homogeneously spaced shrub patches. Generally, these structural differences appeared to be related to floristic differences of habitats of the two species. Structural differences between sparrow and towhee habitats reflected the relative dominance of the smaller sagebrush (sparrow sites) and larger mountain mahogany (towhee sites) within shrub patches.

Both Brewer's Sparrows and Green-tailed Towhees tended to occur in shrubs of similar distance to neighboring shrubs and within patches containing bushes of similar diameter. Both species also were found at sites of comparable herbaceous coverage. The major commonality between species, however, was that birds selected vigorous central bushes.

#### CORRESPONDENCE WITHIN SPECIES' HABITATS

Avian habitats generally have been described by quantitative measures of vegetation structure. Recent studies within the northern Great Basin indicated that densities (Wiens and Rotenberry 1981; Wiens et al. 1986, 1987) and territory size (Wiens et al. 1985) within sparrow populations were independent of local plant species composition and structure. In our study, habitats of Brewer's Sparrows also appeared to be independent of the structural patterning of sagebrush patches. Green-tailed Towhees appeared to be somewhat dependent on vegetation cover; they occurred at sites of comparable nearest interbush distance and variability in bush diameter within patches (both descriptors of woody cover) among the three study areas.

Wiens and Rotenberry (1981) documented correlations between the abundances of both Brewer's Sparrows and Green-tailed Towhees and habitat physiognomy at a regional scale, and density and coverage of shrub species at a more local scale. They suggested a gestalt response (James 1971) by these birds to the general habitat configuration, such response being subject to floristic considerations at a local scale (Rotenberry 1986).

Our analyses represent a second line of evidence supporting their conclusions about the role of cover at the regional level for the Green-tailed Towhee especially, and for floristics at the local level. In addition, we emphasize the importance of floristics as predictors of Green-tailed Towhee habitats because biogeographic patterns revealed that preferred habitats of this species are sagebrush ecotones, rather than monotypic sagebrush stands.

The study of floristics improved our understanding of habitat relationships beyond what we could have learned based solely upon a study of structural aspects of the vegetation. However, even floristic and structural information may be inadequate to identify meaningful habitat elements for a wide-ranging species. For example, the Black-throated Green Warbler (*Dendroica virens*) is a habitat generalist both locally within an avian assemblage (Sherry and Holmes 1985) and regionally as it inhabits five different forest communities varying from monotypic pine, through mixed-conifer/deciduous, to purely deciduous forests (Collins 1983). The floristic variability across habitat areas for this warbler suggests a wide range of associated structures acceptable to birds and precludes defining common structural components among areas (Collins 1983).

We found that the vigor of the shrub patch was the best vegetative descriptor of habitats of both Brewer's Sparrows and Green-tailed Towhees across our study areas. Vigor of the central bush was an additional common component in sparrow habitats, possibly reflecting a greater tendency for foliage-gleaning by the sparrow. The other descriptors of vegetation vigor (CVVIG, MHB) were more variable on a regional scale (i.e., Utah vs. Colorado/Nevada) for both species. Comparatively, the sparrow was recorded in highly vigorous bushes within vigorous stands whereas the towhee was in less vigorous bushes within vigorous stands. We hypothesize that both species select healthy patches within a shrub community. This conclusion is highly consistent with unpublished observations of patch use by foraging Brewer's Sparrows in other locations (Rotenberry, pers. comm.).

Selecting healthy shrubs and shrub patches likely provides birds with better cover for protection and concealment of nests (Petersen and Best 1985) and cover for individual birds when foraging. The primary significance of vigor as a

habitat descriptor, however, probably relates to its value as a predictor of food productivity (both insects and seeds) within a patch. Availability of food resources is elementary to discussions of habitat selection, but has been virtually ignored in studies of temperate species (Terborgh 1985). Arthropod abundance has been shown to be a better predictor of total bird populations than estimates of foliage volume or structural diversity (Brush and Stiles 1986), and is inversely correlated with territory size in some species (Stenger 1959, Cody and Cody 1972, Smith and Shugart 1987). Although shrubsteppe bird communities do not seem to be limited by insect biomass (Rotenberry 1980) Brewer's Sparrows and Green-tailed Towhees both eat seeds and insects in comparable proportions during the breeding season (Beaver 1976) and vigor may relate to the seed resource as much as it does to the insect resource. Presumably, preferred food items of these birds are not uniformly dispersed either spatially or temporally within shrub communities, and sparrows and towhees select the most productive/vigorous stands.

#### IMPLICATIONS FOR STUDIES OF HABITAT SELECTION

Studies of habitat selection by passerine birds have traditionally evaluated habitat of a species through comparison to random or unused sites. The resulting ordinations weight the most important variables and discard those where no differences occur. Investigators assume that the most heavily weighted variables are, in fact, selected by the birds. This underlying assumption that the variables proposed as proximate cues contain biological meaning sine dubia (Morse 1985) during the selection process has haunted field biologists.

Identifying commonalities among habitats of a species at distant areas followed by independent testing of the resulting predictions should facilitate the objective definition of key descriptors of bird habitats. This study, in conjunction with the findings of Tomoff (1974), Wiens and Rotenberry (1981), Collins (1983), and Rotenberry (1985), suggests that the role of vegetation structure as a descriptor of passerine habitats has been overemphasized. If birds initially select an area based upon gestalt floristic features, field measurements of structure in most studies are of so fine a resolution that statistical differences between species or sites can easily reflect inherent

patterns within the vegetative stand and lack biological meaning to the birds. Collins (1983) keenly noted that similarities in structuring of forest bird habitats at distant sites may require only the presence of trees, further suggesting that the sole use of measures of vegetation structure may be inadequate or inappropriate.

The accuracy of habitat descriptions should improve with the inclusion of data on floristic composition and vegetation vigor. The importance of vegetation vigor within a floristic association is biologically intuitive as it relates to potential availability of cover and food and thus to the spatial and temporal dispersion of individuals within populations. Substantial support for these conclusions can be inferred from earlier studies of forest bird assemblages relative to forest site quality (Smith 1977, Swift et al. 1984).

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