GUILD STRUCTURE OF A RIPARIAN AVIFAUNA RELATIVE TO SEASONAL CATTLE GRAZING

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Abstract: The avifauna within the willow (*Salix* spp.) community on the Arapaho National Wildlife Refuge (NWR) was dominated (96% of all observations each year) by 11 species of passerine birds during the summers of 1980–81. Using 28 vegetation variables measured or calculated for randomly selected points and points where birds were sighted, we assigned the species to 3 distinct response guilds relative to historical patterns of seasonal grazing. A eurytopic response guild (habitat generalists) included yellow warblers (*Dendroica petechia*) (YEWA), savannah sparrows (*Passerculus sandwichensis*) (SASP), and song sparrows (*Melospiza melodia*) (SOSP). A stenotopic response guild (habitat specialists) included willow flycatchers (*Empidonax traillii*) (WIFL). Lincoln's sparrows (*Melospiza lincolnii*) (LISP), and white-crowned sparrows (*Zonotrichia leucophrys*) (WCSP). The intermediate, mesotopic response guild included American robins (*Turdus migratorius*) (AMRO), red-winged blackbirds (*Agelaius phoeniceus*) (RWBL), and brown-headed cowbirds (*Molothrus ater*) (BHCO). Population densities of the eurytopic response guild differed little between healthy (historically winter-grazed) and decadent (historically summer-grazed) willow communities within a year. Densities of species in the mesotopic response guild differed more dramatically, and stenotopic response-guild species were absent or accidental in decadent willows. Information on habitat use patterns of the individual species between years supported the definition of response guilds; vegetation structure was most variable in habitats of eurytopic species and least variable in habitats of stenotopic species. Comparisons between used and available vegetation features indicated that species in the stenotopic response guild used locations that differed from random on the basis of bush spacing. We hypothesize that the response-guild structure primarily reflects the impact of cattle upon the horizontal patterning of the vegetative community.

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Grazing by domestic cattle is the most common historical use of native rangelands in the western United States (Busby 1979). Ecologists have described the impacts of grazing upon breeding bird communities by comparing avian populations on adjacent sites that have been subjected to different levels of grazing (Kantrud 1981, Mosconi and Hutto 1982), on the same site before and after exclusion of grazing (Duff 1979), or both (Bock et al. 1984). Those studies generally have described patterns of species presence or abundance relative to grazing impacts upon vegetation.

Birds generally respond to changes in vegetation structure as a consequence of grazing rather than to the presence of cattle per se (Bock and Webb 1984). However, avian responses to vegetative changes are neither easily defined nor consistent among sites (Wiens and Dyer 1975). Ryder (1980) reviewed studies of grazing impacts upon avian communities and categorized species as either increasers or decreasers (in abundance) with the introduction of cattle into their habitats. Studies of grazing impacts, however, generally have not elaborated on the nature of avian behavior or population responses, especially relative to all bird species within a community.

Previous studies in northern Colorado have shown that seasonal grazing practices over a 75–100-year period may alter the horizontal and vertical structure of a shrub–willow community as potential habitats for birds (Knopf and Cannon 1982). Our objectives were to define avian guilds within the shrub–willow community which respond similarly to structural vegetation parameters, statistically test the validity of the response-guild structure with information on species densities and habitat use, and identify vegetation parameters that cattle alter that appear important to sensitive bird species.

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STUDY AREA

The study was conducted on the Arapaho NWR at an elevation of 2,500 m, approximately 10 km south of Walden, Colorado. The Arapaho NWR is in an intermountain glacial basin where the dominant native vegetation type is sagebrush (*Artemisia* spp.)–steppe (Kuchler 1964). The specific study site was the riparian floodplain along the Illinois River immediately north and south of the refuge headquarters, historically known as the Allard Ranch. The woody community included coyote willow (*Salix exigua*), Geyer willow (*S. geyeriana*), Wolf willow (*S. wolfii*), planeleaf willow (*S. planifolia*), Bebb willow (*S. bebbiana*), *S. monticola*, *S. caudata*, and *S. pseudocordata* (Cannon and Knopf 1984).

The study area included 4 historical pastures of 105–351 ha each. Since being homesteaded, pastures 1–3 had been maintained as ditch-irrigated hay meadows. Hay was stored on site at harvest and fed (as a supplement) to cattle, which annually were moved onto the pastures from late fall through early spring. Thus, we refer to these as winter-grazed pastures. In contrast, cattle were grazed on pasture 4 from late spring through early fall and we refer to this as the summer-grazed pasture.

The different seasonal grazing practices over a 75–100-year period have not influenced the floristic composition of the willow community among pastures (Cannon and Knopf 1984). However, the different grazing histories dramatically influenced the structure of the willow community as habitat for migratory birds (Knopf and Cannon 1982). The winter-grazed pastures were structurally comparable to one another, containing bushes of similar mean height, radius, volume, vigor, and horizontal patterning. The summer-grazed pasture, however, differed from winter-grazed pastures in all structural variables measured. Bushes in this pasture were larger and notched (i.e., lower branches were missing), more widely spaced, contained a higher proportion of dead branches, and tended to be located closer to the streambank (Fig. 1). Knopf and Cannon (1982) concluded that the winter-grazed pastures contained a healthy riparian community, whereas the summer-grazed pasture was a decadent woody community.

Fig. 1. Historically winter-grazed (top) and summer-grazed (bottom) pastures containing shrub–willow communities along the Illinois River on the Arapaho National Wildlife Refuge, Colorado. The absence of lower, lateral branches on bushes in the lower photograph is indicative of excessive summer grazing of shrub–willow communities in the past.

METHODS

We surveyed avian communities in pastures during June 1980–81 using a point transect technique (Burnham et al. 1980:195) that incorporated a field methodology similar to that of Reynolds et al. (1980). In 1980, 120–125 survey stations were located in each of 3 pastures (2 grazed in winter, 1 grazed in summer) at measured 100-m intervals along the stream, and at random distances perpendicular to the streambank and out to the far edge of the willow community. Survey stations were located on the streambank at sites where the willow community was <20 m wide. Some stations were >100 m apart to avoid visual overlap between stations. An additional pasture was added in the 1981 field season and the number of stations was reduced to 100/pasture. Thus, we surveyed birds

Table 1. Measured and calculated vegetation variables used in preliminary analyses of patterns of habitat use by passerine birds in the shrub–willow community at Arapaho National Wildlife Refuge, 1980–81.

Variable	Description
Structural measures	
HT1	Ht of central bush
RANGHT	Range in ht among the 5 bushes
HTDIF	Sum of ht differences between central bush and nearest bush in each quadrant
HT2	$\bar{x}$ ht of nearest bush in each quadrant
SDNRBUSH	SD ht of the nearest bush in each quadrant
MHTRAD	$\bar{x}$ ht of max. radius for the 5 bushes
SDHTRAD	SD ht of max. radius for the 5 bushes
CANVOL1	Canopy vol for the central bush calculated as the vol of a spherical segment
MCANVOL	$\bar{x}$ canopy vol for all 5 bushes/site
SHRBVOL1	Shrub vol for the central bush calculated as vol of a spherical segment + the frustrum of a cone
MSHRBVOL	$\bar{x}$ shrub vol for all 5 bushes/site
MRAD	$\bar{x}$ radius for the 5 bushes
SDRAD	SD of radius for the 5 bushes
MINSEP	Distance to closest bush in a quadrant
MAXSEP	Distance to furthest bush in a quadrant
RANGSEP	Range in distance to nearest bush for 4 quadrants
MSEP	$\bar{x}$ distance to nearest bush in each quadrant
SDSEP	SD distance to bushes in 4 quadrants
OPEN	No. quadrants with no bush ≤100 m from central bush
MCANVLAR	MCANVOL × plant density (calculated from MSEP)
MSHRBVLAR	MSHRBVOL × plant density (calculated from MSEP)
Vigor measures	
STEML	No. live stems in central bush
STEMD	No. dead stems in central bush
ASPSTEML	% stems alive in central bush (arcsin transformed)
ASPSTEMD	% stems dead in central bush (arcsin transformed)
BUSHCMPT	Stem density within central bush
Herbaceous measures	
MROB	$\bar{x}$ standing biomass of herbaceous layer in 4 quadrants
SDROB	SD standing biomass of herbaceous layer in 4 quadrants

from 365 separate stations in 1980 and 400 stations in 1981.

Surveys were conducted from 30 minutes before sunrise until approximately 1000 hours daily. A motionless observer waited for 1 minute at each station and then recorded all perched birds seen within a 10-minute period. Birds heard, but not seen, were not recorded to minimize the likelihood of recording an individual twice, and to avoid potential biases due to variable vocalization rates among species (Mayfield 1981), variability in estimation of distances to a vocalizing bird (Scott et al. 1981), and differences in observer ability to identify vocalizations (Kepler and Scott 1981). We felt confident that all individuals that vocalized within the species-specific range of visibility were also seen (effective sighting distance was frequently <5 m at many stations). After each counting period, the investigator flagged the bushes that birds were in, or the bushes nearest to the point where birds were seen on the ground. Each afternoon, observers returned to those stations where birds were seen and measured station-to-bird distances to the nearest 0.1 m.

Densities of common (>15 sightings) bird species were calculated using program Transect (Burnham et al. 1980) modified for point data (K. P. Burnham, North Carolina State Univ., pers. commun.). We first plotted histograms of distances to individuals for all sightings of each species. The data were truncated by as much as 5% to enhance the accuracy of $f(0)$ estimators (Burnham et al. 1980:181). The data from each species were used to calculate densities using each of the 5 estimators (Fourier ser., exponential power series, exponential polynomial, negative exponential, and half-normal) available with this program and the function curve was plotted over distance histograms. A 3-parameter Fourier series estimator best fitted the sighting-distance distributions for each species and was used to estimate densities from ungrouped data (Burnham et al. 1980:141).

Vegetation measurements followed Knopf and Cannon (1982) and were recorded at flagged

Table 2. Densities ($\hat{D}$) of the most common birds in shrub–willow vegetation at Arapaho National Wildlife Refuge, Colorado, in 1980 and 1981.

Year Species	Birds/ha		
	$\hat{D}$	SE	95% CI
1980			
Savannah sparrow	2.22	0.21	1.81–2.63
Yellow warbler	1.88	0.17	1.55–2.21
Song sparrow	1.46	0.14	0.97–1.42
Brown-headed cowbird	0.92	0.14	0.65–1.18
Red-winged blackbird	0.83	0.16	0.52–1.14
Lincoln's sparrow	0.48	0.19	0.09–0.88
White-crowned sparrow	0.28	0.14	−0.02–0.58
American robin	0.27	0.07	0.12–0.41
Willow flycatcher	0.13	0.04	0.04–0.22
1981			
Yellow warbler	2.51	0.18	2.16–2.87
Song sparrow	1.11	0.12	0.88–1.34
Brown-headed cowbird	0.92	0.11	0.71–1.14
Savannah sparrow	0.84	0.08	0.68–1.00
Red-winged blackbird	0.32	0.06	0.20–0.43
American robin	0.18	0.04	0.11–0.26
Willow flycatcher	0.16	0.04	0.08–0.25
Lincoln's sparrow	0.14	0.06	0.01–0.27
White-crowned sparrow	0.08	0.03	0.02–0.14

sites where each bird was seen and at sites (also at 100-m intervals) determined by measuring random distances perpendicular to the streambank. At each site we recorded the width of the riparian tract as 0–25, 26–50, 51–75, 76–100 or >200 m, and the distance to the nearest bush (an index of density). The height and radius of the central bush and the number of 0.1-m intervals hit by live and dead branches on horizontal intercept lines along the north–south and east–west cardinal directions at half-bush height were recorded. For each quadrant delineated by cardinal directions, we measured distance from the outer edge of the central bush to the outer edge of the nearest bush. We also measured the height and radius of those 4 nearest bushes. At a distance midway between the central bush and outlying bush in each quadrant, we obtained an index to herbaceous biomass using a visual obstruction pole (Robel et al. 1970). In all, we measured or calculated 28 variables (Table 1) to ordinate the avian community along dimensions of the vegetative community.

The random data for each vegetation variable were summarized by pasture and tested relative to assumptions for analysis of variance. We examined residual plots (Draper and Smith 1966: 90–91) for homogeneity of variances and half-normal probability plots of residuals (Zahn 1975) for normality. Most vegetation variables for the summer-grazed pasture violated both of these assumptions of parametric statistics, so we used nonparametric Kruskal-Wallis distribution-free tests to compare variable means between grazing histories. Vegetation data from the winter-grazed pastures were normally distributed, so we used parametric analysis of variance to compare used versus available habitats of selected species in these pastures. We also employed stepwise discriminant (stepwise routine) and canonical discriminant analyses (SAS Inst., Inc. 1982) as exploratory techniques from which to develop predictions for evaluation (D. H. Johnson 1981, Williams 1981) rather than as tools for statistical interpretation.

RESULTS

Avian Community Structure

Eleven species represented 96% of the entire bird community in 1980 and 1981. These species included the WIFL, black-billed magpie (*Pica pica*), AMRO, YEWA, SASP, SOSP, LISP, WCSP, RWBL, Brewer's blackbird (*Euphagus cyanocephalus*), and BHCO in 1980. The western meadowlark (*Sturnella neglecta*) was among the dominant species in 1981, replacing the black-billed magpie. Savannah sparrows were the most abundant species (26% of all individuals) in 1980, and yellow warblers were the most abundant (28%) in 1981. Densities of the 9 species that were among the most dominant in 1980

Table 3. Vegetative variables identified by stepwise discriminant analysis as significantly ($P \leq 0.0001$) important in the separation of random points and points used by 9 bird species in a shrub–willow community.

Variable[a]	Partial r^2	F
HT1	0.28	63.50
OPEN	0.09	15.86
SDNRBUSH	0.06	9.73
STEML	0.04	7.39
HT2	0.04	5.85
MROB	0.03	5.24
MSEP	0.03	4.46
STEMD	0.02	3.87

[a] HT1 = ht of central bush, OPEN = no. quadrants with no bushes ≤100 m from central bush, SDNRBUSH = SD of nearest bush in each quadrant, STEML = no. live stems in central bush, HT2 = $\bar{x}$ ht of nearest bush in each quadrant, MROB = $\bar{x}$ standing biomass of herbaceous layer in 4 quadrants, MSEP = $\bar{x}$ distance to nearest bush in each quadrant, STEMD = no dead stems in central bush.

and 1981 varied from 0.13 ± 0.04 (SE) to 2.51 ± 0.18 birds/ha (Table 2).

Patterns of Avian Response to the Grazing Histories

The stepwise discriminant analysis (n = 1,442) identified 10 of 28 vegetation variables as having the power ($P < 0.15$) to discriminate among random sites and sites used by the 9 species of birds. We used the 8 vegetation measurements significant at $P \leq 0.0001$ in a canonical discriminant analysis (Table 3). Function/variable correlation coefficients indicated that the first canonical variable was dominated by central-bush height (i.e., vertical structure) and the second variable was codominated by the number of quadrants without willows and the standard deviation of the height of the nearest bush (i.e., horizontal patchiness). Plotting the means of the first and second canonical variables for each class (bird species or random site by grazing history) provided a graphical technique (Fig. 2) for tentatively assembling the 9 species into 3 response guilds (groups of species that respond similarly to vegetation changes induced by the grazing practices within the pastures).

Habitats of YEWA, SASP, and SOSP on winter- and summer-grazed pastures shifted in multivariate space parallel to, and a similar distance as, the random vegetation information. We tentatively proposed that YEWA, SASP, and SOSP represented a eurytopic response guild when selecting habitats within the riparian community.

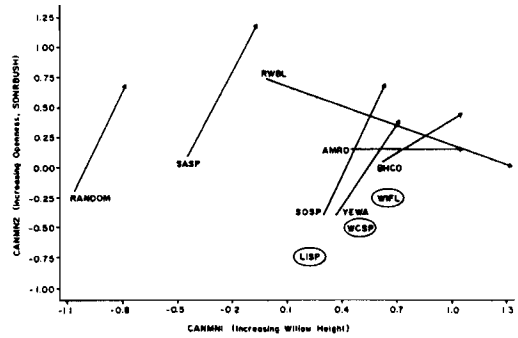

Fig. 2. Patterns of change surrounding random points versus bird observation points within a shrub–willow community subjected to different historical grazing practices at Arapaho National Wildlife Refuge, Colorado, 1981. Figure represents a plot of the first and second canonical means moving from winter-grazed into summer-grazed pastures. Circled bird species abbreviations (YEWA = yellow warbler, SASP = savannah sparrow, SOSP = song sparrow, AMRO = American robin, RWBL = red-winged blackbird, BHCO = brown-headed cowbird, WIFL = willow flycatcher, LISP = Lincoln's sparrow, WCSP = white-crowned sparrow) represent species present in historically winter-grazed pastures but absent in summer-grazed pastures.

Willow flycatchers, LISP, and WCSP were present on winter-grazed pastures but were virtually absent in the summer-grazed pasture. No WIFL were recorded in the summer-grazed pasture, and only 1 LISP and 2 WCSP were observed there. These species composed a stenotopic response guild in that they appeared intolerant of the changes in the vegetation structure resulting from the influence of summer grazing.

The remaining common species (AMRO, RWBL, BHCO) were present at sites subjected to both grazing histories. However, measures of vegetation structure at sites used by these species did not change in a manner similar to those at random sites, especially along the second canonical variable. Thus, we considered birds in this guild to be mesotopic in habitat selection within the avian community.

Population Evidence Supporting the Response-Guild Structure

The inductive/deductive classification of dominant species within the avian community into 3 separate response guilds was stated as a research hypothesis (Romesburg 1981) for indirect, statistical testing. We already knew from the community ordination that species within the stenotopic response guild only occurred as stragglers within the historically summer-grazed

Table 4. Density ($\hat{D}$ = individuals/ha) comparisons for bird species occurring within 3 major response guilds between historically summer-grazed and winter-grazed shrub–willow communities on the Arapaho National Wildlife Refuge, Colorado, in 1980 and 1981.

Year and response guild Species	Winter-grazed $\hat{D}$	Winter-grazed SE	Summer-grazed $\hat{D}$	Summer-grazed SE	t	P
1980						
Eurytopic						
Yellow warbler	2.08	0.21	2.00	0.41	0.17	0.44
Savannah sparrow	2.42	0.28	1.91	0.32	1.20	0.12
Song sparrow	1.42	0.18	1.80	0.32	1.03	0.16
Mesotopic						
American robin	0.33	0.10	0.11	0.04	2.04	0.03
Red-winged blackbird	0.98	0.22	0.32	0.22	2.12	0.02
Brown-headed cowbird	0.81	0.18	1.30	0.27	1.51	0.07
Stenotopic						
Willow flycatcher	0.20	0.07				
Lincoln's sparrow	0.42	0.15	—[a]			
White-crowned sparrow	0.30	0.11	—			
1981						
Eurytopic						
Yellow warbler	2.41	0.18	3.10	0.51	1.28	0.11
Savannah sparrow	0.79	0.09	0.75	0.27	0.14	0.45
Song sparrow	1.14	0.14	1.21	0.31	0.20	0.43
Mesotopic						
American robin	0.17	0.04	0.44	0.18	1.46	0.09
Red-winged blackbird	0.37	0.07	0.17	0.08	1.88	0.04
Brown-headed cowbird	0.85	0.12	1.33	0.33	1.37	0.09
Stenotopic						
Willow flycatcher	0.22	0.05				
Lincoln's sparrow	0.14	0.07	—			
White-crowned sparrow	0.13	0.05	—			

[a] Densities were not calculated when <10 individuals were detected.

pasture. Using population information gathered on the other species, we predicted that species within the eurytopic response guild would occur in similar densities in summer-grazed and winter-grazed pastures within years whereas species within the mesotopic response guild would occur at variable densities between summer- and winter-grazed pastures.

We tested the statistical hypothesis that, for a given year, the population density of each species was similar between winter- and summer-grazed pastures. Results of the density tests supported the research hypothesis (Table 4). Densities of each species in the eurytopic response guild were similar ($P > 0.05$) between winter- and summer-grazed pastures. Density comparisons between winter- and summer-grazed pastures varied among species of the mesotopic response guild. Red-winged blackbird densities were higher in historically winter-grazed pastures (both years) whereas BHCO densities were only marginally higher in the summer-grazed pasture. American robin densities were higher in winter-grazed pastures in 1980 and in the summer-grazed pasture in 1981. Differences in species densities within this guild were of greater statistical significance than those within the eurytopic response guild.

Habitat Evidence Supporting the Response-Guild Structure

As a second approach to indirect testing of the response-guild structure, we predicted that univariate tests of vegetative features within habitats of individual species would show that:

1. The greatest number of vegetation variables would be significantly different between years in habitats of eurytopic species (i.e., less specific habitat selection).

Table 5. Kruskal-Wallis Chi-square approximation test statistics for between-year (1980 vs. 1981) comparisons of vegetation variables surrounding points used by birds in a shrub–willow community at Arapaho National Wildlife Refuge, Colorado.

Habitat variable[b]	Response guild and species[a]								
	Eurytopic			Mesotopic			Stenotopic		
	YEWA	SASP	SOSP	AMRO	RWBL	BHCO	WIFL	LISP	WCSP
HT1	0.0	0.5	18.2**	0.0	12.9**	7.9**	1.9	2.1	0.4
OPEN	6.0*[c]	2.9	1.4	0.2	0.2	21.6**	0.7	1.1	1.8
SDNRBUSH	2.9	4.0*	2.5	2.0	3.4	0.2	2.9	0.5	1.2
STEML	4.1*	17.3**	1.3	0.3	0.4	6.6*	0.2	0.6	1.0
HT2	1.0	0.1	0.0	2.9	9.6**	1.7	0.0	1.6	0.1
MROB	61.8**	19.8**	14.9**	0.5	1.0	16.8**	8.9**	4.9*	1.0
MSEP	0.0	18.6**	0.0	0.2	0.8	0.3	0.0	0.4	0.0
STEMD	0.1	12.6**	4.3*	5.5*	2.8	7.8**	0.8	5.8*	2.4

[a] YEWA = yellow warbler, SASP = savannah sparrow, SOSP = song sparrow, AMRO = American robin, RWBL = red-winged blackbird, BHCO = brown-headed cowbird, WIFL = willow flycatcher, LISP = Lincoln's sparrow, WCSP = white-crowned sparrow.
[b] HT1 = ht of central bush, OPEN = no. quadrants with no bushes ≤100 m from central bush, SDNRBUSH = SD of nearest bush in each quadrant, STEML = no. live stems in central bush, HT2 = $\bar{x}$ ht of nearest bush in each quadrant, MROB = $\bar{x}$ standing biomass of herbaceous layer in 4 quadrants, MSEP = $\bar{x}$ distance to nearest bush in each quadrant, STEMD = no. dead stems in central bush.
[c] * = $P < 0.05$, ** = $P < 0.01$.

2. The fewest number of vegetation variables would be significantly different between years in habitats of stenotopic species (i.e., more specific habitat selection).
3. An intermediate number of variables would be significantly different between years in habitats of mesotopic species.

The 3 response-guild predictions were supported. Eleven of 24 tests of between-year differences were significant within a species' habitat for the eurytopic response guild (Table 5). In contrast, 8 of 24 vegetation variables differed between years within the mesotopic response guild and only 3 of 24 within the stenotopic response guild. Thus, habitats of species within the stenotopic response guild were most consistent between years, indicating greatest specificity in habitat requirements for these birds; and, the univariate between-year comparisons supported the response-guild predictions.

Habitat Use within the Stenotopic Response Guild

We compared habitat use by species within the stenotopic response guild to identify those vegetation parameters altered by long-term cattle grazing that appear to influence habitat selection by these species. All 3 species within the stenotopic response guild were seen in willows that were taller (ht of central bush [HT1]: $P = 0.00$) than those at random sites in 1980 and 1981 (Table 6). In addition, each species tended to use willows with greater ($P = 0.00$–0.11) numbers of dead stems (STEMD) than occurred in randomly located bushes. The 2 sparrow species showed a predictable pattern in their occurrence in stands of bushes with lower ($P < 0.05$) mean distances between bushes (MSEP) and reduced ($P = 0.01$–0.07) variability in those distances (SDSEP). The WIFL also appeared to use sites where bushes were more clumped, but without the emphasis on reduced variability in bush dispersion (i.e., more open surroundings). Clear relationships or patterns of vegetation use were not observed between habitat and random sites for the remaining variables.

DISCUSSION

The Response-Guild Structure

Guilds have been defined by Root (1967) as groups of species with similar resource-use patterns. For example, birds are often classified relative to their foraging or nesting habits (e.g., Franzreb and Ohmart 1978). Avian guilds have been proposed as an approach to evaluating impacts of land-management programs on public lands (R. A. Johnson 1981, Severinghaus 1981), especially from cost-effective perspectives (Verner 1984). Szaro (1986) summarized current approaches to guild delineation that were based upon either functional or structural criteria, and argued that both approaches are arbitrary for management applications and should be replaced by similarities among species' responses to a given perturbation. Our study provides information on the response of summer birds to grazing of shrub–willow vegetation at Arapaho NWR.

Species within the eurytopic response guild were the most flexible in selecting habitats with-

Table 6. Habitat-use patterns of bird species within the stenotopic response guild in historically winter-grazed shrub–willow vegetation at Arapaho National Wildlife Refuge, Colorado, 1980–81. Parametric *F*-tests compared habitat variables at random sites and sites within habitats of each of the species.

Year Species	HT1[a]	OPEN	SDSEP	STEML	HT2	MROB	MSEP	STEMD
1980								
Random (n = 244)								
$\bar{x}$	2.7	0.2	4.7	18.7	2.6	2.6	3.9	4.9
SE	0.1	0.0	0.4	0.6	0.1	0.1	0.3	0.3
Willow flycatcher (n = 20)								
$\bar{x}$	5.0	0.1	3.3	16.0	3.0	2.6	2.2	10.5
SE	0.3	0.1	1.4	1.7	0.1	0.4	0.7	1.0
P	0.00	0.24	0.33	0.20	0.11	0.95	0.09	0.00
Lincoln's sparrow (n = 19)								
$\bar{x}$	3.7	0.2	1.0	18.7	2.4	2.6	0.8	7.3
SE	0.2	0.1	0.3	1.6	0.1	0.4	0.3	0.9
P	0.00	0.52	0.01	0.97	0.28	0.87	0.00	0.03
White-crowned sparrow (n = 16)								
$\bar{x}$	4.7	0.1	2.0	23.1	2.8	2.3	1.5	7.9
SE	0.3	0.1	0.7	2.8	0.2	0.3	0.6	1.7
P	0.00	0.39	0.07	0.07	0.39	0.45	0.04	0.01
1981								
Random (n = 299)								
$\bar{x}$	2.7	0.1	6.3	14.2	2.5	1.7	5.0	7.4
SE	0.1	0.0	0.5	0.6	0.1	0.1	0.4	0.3
Willow flycatcher (n = 30)								
$\bar{x}$	4.6	0.1	3.7	16.5	3.0	1.3	2.5	9.7
SE	0.2	0.1	1.0	1.6	0.2	0.2	0.7	1.1
P	0.00	0.36	0.12	0.23	0.01	0.03	0.04	0.03
Lincoln's sparrow (n = 19)								
$\bar{x}$	4.1	0.1	2.3	22.7	2.7	1.3	1.6	10.8
SE	0.2	0.1	0.9	2.4	0.2	0.2	0.5	1.0
P	0.00	0.37	0.06	0.00	0.34	0.16	0.03	0.01
White-crowned sparrow (n = 14)								
$\bar{x}$	4.4	0.0	1.8	18.7	2.8	1.8	1.3	9.8
SE	0.4	0.0	0.7	1.8	0.3	0.4	0.5	1.5
P	0.00	0.20	0.06	0.10	0.32	0.58	0.04	0.11

[a] HT1 = ht of central bush, OPEN = no. quadrants with no bushes ≤100 m from central bush, SDSEP = SD distance to bushes in 4 quadrants, STEML = no. live stems in central bush, HT2 = $\bar{x}$ ht of nearest bush in each quadrant, MROB = $\bar{x}$ standing biomass of herbaceous layer in 4 quadrants, MSEP = $\bar{x}$ distance to nearest bush in each quadrant, STEMD = no. dead stems in central bush.

in the shrub–willow community. These species might be considered riparian generalists in the sense that they also occupied a variety of other floodplain communities within the region. Avifaunal surveys in 12 vegetative communities (Knopf 1985) across a 1,800-m elevational gradient from the Arapaho NWR east to the Crook, Colorado, vicinity indicated that YEWA and SOSP occurred in riparian areas across the entire continuum with the exception that YEWA were not present at the highest (2,747 m) study area. Those communities varied from shrub–willow stands in a glacial moraine to a plains cottonwood (*Populus sargentii*) savannah. Both species occurred at maximum densities at the Arapaho NWR, and neither species was observed in upland vegetation. In contrast, SASP occurred only at the Arapaho site. This species is apparently least flexible of these 3 species in its selection of habitats although it also occurs in saltgrass (*Distichlis* spp.) and other moist-grassland communities in Colorado (Bailey and Niedrach 1965).

Similar altitudinal patterns were observed among species within the mesotopic response guild with RWBL and BHCO occurring across the altitudinal gradient but at greatest densities at the Arapaho NWR. American robins tended

to reach maximum abundance in shrub–willow communities at slightly lower elevations, in areas of pine uplands. The BHCO and AMRO, however, also were common in upland vegetation throughout northern Colorado. We considered these species to represent regional (vs. riparian-specific) habitat generalists.

Species within the stenotopic response guild were only seen in areas of shrub–willow communities at study sites ≥2,293 m elevation. None were recorded in upland vegetation.

Migratory Bird Response to Historical Grazing Practices

Willow communities in pastures that have been historically grazed in the winter can be characterized as healthy stands with vigorous vegetative production and regeneration. Historically summer-grazed pastures are comparatively decadent (Knopf and Cannon 1982). Riparian areas appear more resilient to grazing impacts when cattle are introduced during fall or winter (Sedgwick and Knopf 1987) due, in part, to drier soils and dormancy of the vegetation. Continuous or growing-season grazing of riparian areas seem particularly damaging to vegetation within floodplains (Kauffman and Krueger 1984).

Whereas avian species may be thought of as either increasing or decreasing in numbers with the introduction of cattle into their habitats (Ryder 1980), responses to changes in plant communities that have been historically altered are more complex. The most abundant species at Arapaho NWR were the 3 members of the eurytopic response guild, and their densities were comparable between the healthy and decadent willow communities. The BHCO showed the greatest tendency to increase in numbers in decadent, summer-grazed pastures; locally high densities (at least in northern Colorado) would indicate a historically damaged willow community. Alternatively, high local densities of species within the stenotopic response guild (and perhaps the RWBL) would indicate a healthy riparian community relative to historical grazing practices.

The Arapaho NWR is managed primarily for waterfowl production. In general, grazing by domestic cattle has a negative effect on waterfowl production on wildlife refuges (Braun et al. 1978). The avian community on our study pastures included low (≤8 sightings) numbers of green-winged teal (*Anas crecca*), mallards (*A. platyrhynchos*), cinnamon teal (*A. cyanoptera*), gadwall (*A. strepera*), and lesser scaup (*Aythya affinis*). Seventeen of the 18 observations of ducks on the area were in the historically summer-grazed pasture. No water-control structures or other habitat-enhancement programs have been implemented on the pastures and we attribute greater duck use of that pasture to the narrower woody community with a more open canopy (Knopf and Cannon 1982). The limited waterfowl use of the area was inadequate to enable us to elaborate further on the nature of waterfowl responses to changes in the vegetative community. However, management of the riparian zone for waterfowl (creating more open areas within the floodplain) would appear to conflict with practices that enhance breeding habitats for passerine birds, especially those within the stenotopic response guild.

Grazing Impacts Upon Bird Habitats

Birds within a vegetative association may respond to the species of vegetation as well as to structural variables when selecting habitats (Franzreb 1978, Holmes and Robinson 1981, Rice et al. 1984, Rotenberry 1985). Distribution of the 8 willow species varied among pastures, but in no meaningful pattern relative to the grazing histories (Cannon and Knopf 1984). Dispersion of willows appear to reflect patterns of historical water management rather than grazing practices. We did not collect data on specific use of willows by the bird species.

Diversity and species composition of avian communities are generally correlated with the vertical diversity of structure within the woody vegetation (MacArthur and MacArthur 1961) although the relationship does not hold for all communities (Willson 1974, Balda 1975). In our study, the importance of taller bushes within habitats appeared biased because singing male WIFL and WCSP selected prominent sites for song posts. The importance of taller bushes as key habitat structures was diminished further by the observation that the mean height of the nearest bush in each quadrant (HT2) was similar ($P > 0.05$) between random sites and bird sites in all but 1 comparison, thus indicating that individual birds of these species were moving to the tallest bush to sing, but were not selecting patches of taller bushes specifically.

The importance of dead stems to birds within the stenotopic response guild was more apparent. Willow flycatchers use such stems as sub-

strates from which to locate and catch flying insects. We speculate that a greater number of dead stems within a bush also creates additional foraging opportunities for LISP and WCSP by facilitating exploitation of food items near the ground and within the bush interior. Under summer-grazing programs, cattle tend to rub on dead branches when seeking shade, thereby reducing the number of dead branches available for foraging sites.

Strong relationships between bird species diversity and horizontal patterning of the vegetation have been reported in tropical forests (Karr and Roth 1971) and temperate brushlands (Roth 1976). Our observations of habitat use relative to structural variables within the stenotopic response guild imply that species within this guild, and species richness, were influenced most by horizontal patterning of bushes within the community. We speculate, likewise, that the influence of cattle grazing upon clumping of bushes (or some correlate thereof) was the primary impact that precluded use of the summer-grazed pasture by species within the stenotopic response guild. We caution, however, that these conclusions are based upon pattern detection rather than process explanation (Wiens 1983) and assume rapid recovery of food resources of the birds in both summer- and winter-grazed pastures once cattle are removed.

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