

Grassland bird densities in seral stages of mixed-grass prairie

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Abstract

Birds associated with prairie ecosystems are declining and the ecological condition (seral stage) of remaining grassland communities may be a factor. Livestock grazing intensity influences the seral stage of grassland communities and resource managers lack information to assess how grassland birds are affected by these changes. We estimated bird density, species diversity, and species richness on 37 sites in 4 seral stages of western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Löve]-green needlegrass [*Nassella viridula* (Trin.) Barkworth] communities of the Fort Pierre National Grassland. Bird species richness did not differ among seral stages ($P = 0.57$), but bird species diversity was greater ($P < 0.10$) in early seral stages compared to late-intermediate seral stages. Grasshopper sparrow (*Ammodramus savannarum* Gmlin), bobolink (*Dolichonyx oryzivorus* Linnaeus), dickcissel (*Spiza americana* Gmlin), and brown-headed cowbird (*Molothrus ater* Boddaert) density increased ($P < 0.10$) from early to late seral stages. Burrowing owl (*Athene cunicularia* Molina), upland sandpiper (*Bartramia longicauda* Bechstein), chestnut-collared longspur (*Calcarius ornatus* Townsend), and horned lark (*Eremophila alpestris* Linnaeus) density decreased ($P < 0.10$) from early to late seral stages. Western meadowlarks (*Sturnella neglecta* Audubon) were more abundant in early ($P = 0.05$) and early-intermediate ($P = 0.01$) seral stages than late seral stages. Birds with habitat requirements including tall vegetation and residual cover were more abundant in later seral stages. Early seral stages were beneficial to birds that prefer short grass and sparse vegetative cover. Seral stage was an effective predictor of density for many bird species. A mosaic that includes all seral stages is necessary to maximize grassland bird species diversity and abundance across the landscape. Managers can assess the effects on grassland birds of management actions that alter the seral stage of the vegetation.

Key Words: Fort Pierre National Grassland, South Dakota, classification, range condition

Long-term data suggest that grassland bird populations are declining in the United States (Knopf 1994, Herkert 1995). Conversion of native grassland for agricultural purposes, invasion of alien plants, urban water development, and habitat fragmenta-

Resumen

Las aves asociadas a los ecosistemas de praderas están declinando y la condición ecológica (etapa seral) de las comunidades remanentes de pastizal puede ser un factor de esta disminución. La intensidad de apacentamiento del ganado influye en la etapa seral de las comunidades de pastizal y los manejadores de los recursos carecen de información para evaluar como las aves del pastizal son afectadas por estos cambios. Estimamos la densidad de aves, y la diversidad y la riqueza de especies en 37 sitios en 4 etapas serales de comunidades de “Western wheatgrass” [*Pascopyrum smithii* (Rydb.) A. Löve]-“Green needlegrass” [*Nassella viridula* (Trin.) Barkworth] situadas en el Pastizal Nacional Fort Pierre. La riqueza de especies de aves no difirió entre etapas serales ($P = 0.57$), pero la diversidad de especies fue mayor ($P < 0.10$) en las etapas serales iniciales comparada con las etapas intermedias y finales. La densidad de “Grasshopper sparrow” (*Ammodramus savannarum* Gmlin), “Bobolink” (*Dolichonyx oryzivorus* Linnaeus), “Dickcissel” (*Spiza americana* Gmlin) y “Brown-headed cowbird” (*Molothrus ater* Boddaert) se incrementó de ($P < 0.10$) de las etapas serales iniciales a las etapas serales finales. En cambio las densidades de “Burrowing owl” (*Athene cunicularia* Molina), “Upland sandpiper” (*Bartramia longicauda* Bechstein), “Chestnut-collared longspur” (*Calcarius ornatus* Townsend) y “Horned lark” (*Eremophila alpestris* Linnaeus) disminuyeron ($P < 0.10$) de las etapas serales iniciales a las etapas finales. Los “Western meadowlarks” (*Sturnella neglecta* Audubon) fueron más abundantes en las etapas serales inicial ($P = 0.05$) e inicial-intermedia ($P = 0.01$) que en las etapas serales finales. Las aves con requerimientos de hábitat de vegetación alta y cobertura residual fueron más abundantes en las etapas serales finales. Las etapas serales iniciales fueron benéficas para las aves que prefieren zacates cortos y vegetación dispersa. La etapa seral fue un predictor efectivo de la densidad de muchas especies de aves. Para maximizar la diversidad de especies de aves y la abundancia a través del paisaje se necesita un mosaico que incluya todas las etapas serales. Los manejadores pueden evaluar los efectos de las acciones de manejo que alteran la etapa seral de la vegetación sobre las aves del pastizal.

tion are apparent factors in the decline of grassland avifauna (Knopf and Samson 1995). The ecological condition of remaining grassland ecosystems has been altered by changes in grazing patterns, wildfire suppression, soil disturbances, and competition with alien plant species. Vegetative conditions of nonfederal rangelands suggest a high degree of alteration (USDA 1987). Grazing intensity influences grassland bird abundance (Owens

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and Myres 1973, Kantrud 1981, Kantrud and Kologiski 1982, Bock and Webb 1984) and seral condition (Brown and Schuster 1969, Ryder 1980, Hart et al. 1988). Thus, seral stage may be a factor influencing grassland bird populations in Great Plains prairie landscapes.

The objectives of this study were to estimate grassland bird density, species richness, and species diversity in seral stages of western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Löve]-green needlegrass [*Nassella viridula* (Trin.) Barkworth] communities of the mixed-grass prairie. We also wanted to determine if seral stage was an adequate predictor of birds, or whether additional vegetative characteristics improved predictions of bird abundance. This information will enable managers to predict changes in grassland bird populations due to management actions that alter the seral stage of prairie vegetation.

Study Area and Methods

The study was conducted on the Fort Pierre National Grassland in central South Dakota (approx. 44° 15' north and 100° 30' west). The Fort Pierre National Grassland is 46,977 ha in size covering parts of Stanley, Lyman, and Jones counties. The area is situated within the Pierre Hills physiographic region (Johnson et al. 1995). Soils are primarily clays derived from Cretaceous Pierre Shale. Topography consists of flats cut by intermittent drainages and gently rolling hills. Elevation ranges from approximately 590 to 727 m above sea level. The climate is temperate with average temperatures ranging from -4° C in winter to 23° C in summer. Mean annual precipitation is 460 mm with 43% occurring between March and June.

The area is characterized as a wheat-grass-needlegrass community within the mixed-grass prairie region (Küchler 1975). Dominant grasses of the area include western wheatgrass, green needlegrass, buffalo grass [*Buchloe dactyloides* (Nutt.) Engelm.], big bluestem (*Andropogon gerardii* Vitman), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], and blue grama [*B. gracilis* (Willd. ex Kunth) Lag. ex Griffiths]. Common forbs include western yarrow (*Achillea millefolium* L.), scarlet globemallow [*Sphaeralcea coccinea* (Nutt.) Rydb.], bracted spiderwort (*Tradescantia bracteata* Small ex Britt), fringed sagewort (*Artemisia frigida*

Willd.), cudweed sagewort (*Artemisia ludoviciana* Nutt.), black samson (*Echinacea angustifolia* DC), and prairie coneflower [*Ratibida columnifera* (Nutt.) Woot & Standl.]. Scattered brush patches and trees occur mainly in drainages and include cherry (*Prunus* spp.), willows (*Salix* spp.), cottonwoods (*Populus* spp.), and western snowberry (*Symphoricarpos occidentalis* Hook).

During July and August of 1995, we identified 31 study sites that were representative of the 4 seral stages of wheat-grass-needlegrass communities on the Fort Pierre National Grassland. Six additional sites were selected during early spring 1996. At the time these sites were selected, we made a preliminary classification of seral stage on each using percent cover (Daubenmire 1959) multiplied by frequency of occurrence data for western wheatgrass, green needlegrass, and buffalo grass along 3 to 5 transects on the site. These data were then multiplied by the Fisher classification coefficients developed for wheatgrass-needlegrass communities of the Fort Pierre National Grassland using the methods developed by Uresk (1990) to classify seral stage on the site. We initially attempted to locate 10 sites in each seral stage. However, the distribution and area of early and late seral stages were limited and constrained our initial design. Each site was reclassified during late July to early August of 1996 and 1997 to make final seral stage assignments for the study (see below).

On each site, we established a transect that was positioned within the identified seral stage and made as long as possible (up to 400 m in length). Early and late seral stages were limited in size, abundance, and distribution, and thus, 4 transects in these seral stages were only 250 to 300 m. A transect served as the experimental unit for our study design. We attempted to position the transects more than 200 m from fence lines, wetlands, roads, and other edges to minimize bias associated with these areas when estimating bird populations (Reese and Ratti 1988), but this was not always possible.

We counted birds from 15 May to 30 June of 1996 and 1997 along these transects. Bird counts began 1/2 hr before sunrise, and were completed within 4 hours. While slowly (~1 km/hr⁻¹) walking the transects, we recorded the species, sex, and perpendicular distance (to the nearest m) to the transect of all birds seen or heard. Birds were counted on each site for 2 consecutive days constituting 1 count session. Two count sessions were com-

pleted during each year of the study on each site. Birds were not counted during periods of moderate to heavy rainfall (Manuwal and Carey 1991) or wind speed exceeding 5.5 m/sec⁻¹. (Erskine 1978, Mikol 1980). We used 2 observers during the bird counts. Observers were trained prior to bird counts to recognize birds in the area by site and sound. Observers counted different sites each count session to minimize bias from individual observers.

We combined data for both study years to obtain density estimates for breeding pairs of birds because we were interested in developing species habitat relations useful for rangeland managers in relation to long-term management objectives. Densities of breeding bird pairs (hereafter referred to as density) were estimated using the DISTANCE program (Laake et al. 1993). Perpendicular distance data were grouped in the DISTANCE program to minimize judgment errors (Buckland et al. 1993). We used the Akaike Information Criterion and Chi-Square goodness-of-fit tests to determine the most appropriate detection probability model for each species. Insufficient observations prevented development of detection probability functions for each bird species in each seral stage. Therefore, we developed a detection probability function for each species and assumed the shape of these functions were similar among all seral stages. We did not estimate density for birds with less than 30 observations or for species that this methodology is inappropriate (e.g., raptors, greater prairie chickens (*Tympanuchus cupido* Linnaeus), and sharp-tailed grouse (*Tympanuchus phasianellus* Linnaeus) were not included). Horned lark (*Eremophila alpestris* Linnaeus), grasshopper sparrow (*Ammodramus savannarum* Gmelin), chestnut-collared longspur (*Calcarius ornatus* Townsend), dickcissel (*Spiza americana* Gmelin), bobolink (*Dolichonyx oryzivorus* Linnaeus), western meadowlark (*Sturnella neglecta* Audubon), and red-winged blackbird (*Agelaius phoeniceus* Linnaeus) pair densities were estimated from the number of breeding males observed. Brown-headed cowbird density (*Molothrus ater* Boddaert) was estimated using the total number of all male birds observed regardless of whether the bird was singing or not. Because upland sandpipers (*Bartramia longicauda* Bechstein) are not sexually dimorphic, density was estimated by dividing the total number of birds observed by 2. Burrowing owl (*Athene cunicularia* Molina) density represents the density of indicated pairs, based on

observed behavior. The multiple response permutation procedure (MRPP, Mielke 1984) with Bonferroni corrections to the α -level to preserve experiment-wise error rates of multiple comparisons was used to test differences in bird densities, species richness, and species diversity among seral stages.

We characterized the vegetation structure of each site after completing daily bird counts. At 100-m intervals along the main transect on each site, we established 3 to 5 transects 60 m in length (hereafter referred to as vegetation transects) that were perpendicular to, and centered on, the main transect. Visual obstruction measurements (VOM, Robel et al. 1970), representing the height in which 100% of a pole was obstructed from view, were recorded at the endpoints and at points located at 5-m intervals along these vegetation transects. At each point, vegetation height was recorded as the height that vegetation contacted a 30-cm diameter plexiglass disc lowered over the pole (Higgins and Barker 1982), and litter depth was measured using a ruler lowered through the litter layer.

During July and August of each year, we characterized vegetation composition at each site. We estimated percent canopy cover (Daubenmire 1959) of total grasses, total forbs, bare ground, litter, western wheatgrass, green needlegrass, buffalo grass, and yellow sweet clover [*Melilotus officinalis* (L.) Lam.] in thirty, 0.10-m² quadrats spaced at 2-m intervals along the vegetation transects. We calculated an index of vegetation composition using percent canopy cover times frequency of occurrence for western wheatgrass, green needlegrass, and buffalo grass for each transect. The average values for these indices were applied to the discriminant function classification coefficients to determine seral stage (Uresk 1990; unpubl. rep., USDA For. Serv., Rocky Mtn. Res. Stn., Rapid City, S.D.). We calculated the coefficient of variation for VOM, vegetation height, and litter depth to characterize vegetation heterogeneity (Rotenberry and Wiens 1980) for each transect, and averaged these for each site.

Initial vegetation analyses suggested that vegetation variables were not independent among seral stages. Therefore, we used principal component analysis to identify the groups of vegetation variables that responded similarly among seral stages. We then used multivariate MRPP analyses using BLOSSOM statistical software (Slauson et al. 1991) to test for differences in groups of vegetation variables among

seral stages. We applied a step-down multiple comparison procedure that maintained the predetermined α -level for multiple comparisons among seral stages for these tests (Petronidas and Gabriel 1983).

Multiple, linear regression was used to assess the effectiveness of seral stage versus vegetation characteristics as predictors of bird species density on these grassland sites. Independent variables with k categories can be modeled using $k-1$ dummy regressors (Fox 1997). We developed 3 dummy variables representing contrasts between the early and other seral stages. These dummy regressors were forced into the regression model while allowing vegetation variables to enter into the model using a step-wise technique. This procedure holds variation accounted for by seral stage regressors constant while allowing vegetation variables to enter the model when they significantly add to the reduction in the sum of squares due to regression. The model estimates different intercept coefficients for each seral stage but common slope coefficients for each continuous variable. Independent vegetation variables considered in these analyses included VOM, litter depth, percent forb cover, and percent bare ground cover. We applied log transformations to the density estimates of some bird species and vegetation variables to meet the assumption of normal distributions. Plots of residuals and

analysis diagnostics were examined to assess the assumptions of the regression analysis and to determine if any outliers were present in our analyses.

Scientific names of plants are from the USDA-NRCS (1999) and scientific names for birds are from the American Ornithologists' Union (1999). Statistical significance was determined at $\alpha = 0.10$ and all multiple range tests preserve experiment-wise error rates at that alpha level.

Results

Seral stage of some sites changed from our initial selection, and our final classification had 7 sites in the early, 6 in the early-intermediate, 18 in the late-intermediate, and 6 in the late seral stage. Percent composition and frequency of occurrence of western wheatgrass, buffalo grass, and green needlegrass differed among seral stages (Table 1). Percent canopy cover and frequency of buffalo grass were highest on early seral sites and declined as succession progressed toward the late seral stage. Frequency and cover of western wheatgrass increased as seral stage changed from early to late-intermediate, then declined slightly in the late seral stage. Frequency and cover of green needlegrass increased from early to late seral stages. Nonetheless, statistical patterns of differ-

Table 1. Mean ($\pm$ SE) of vegetation variables in seral stages of mixed-grass prairie on Fort Pierre National Grassland, South Dakota 1996 and 1997.¹

Vegetation Variable ^{2,3}	Seral Stage			
	Early $\bar{X} \pm \text{SE}$	Early-intermediate $\bar{X} \pm \text{SE}$	Late-intermediate $\bar{X} \pm \text{SE}$	Late $\bar{X} \pm \text{SE}$
Percent canopy cover				
Western wheatgrass	39.1 $\pm$ 2.8 A	44.0 $\pm$ 6.8 B	73.7 $\pm$ 2.0 C	42.9 $\pm$ 7.1 D
Buffalo grass	68.2 $\pm$ 2.2 A	25.4 $\pm$ 5.7 B	9.8 $\pm$ 2.0 C	6.9 $\pm$ 1.6 D
Green needlegrass	1.1 $\pm$ 0.5 A	6.5 $\pm$ 3.1 B	10.3 $\pm$ 1.7 C	57.4 $\pm$ 0.9 D
Total grasses	90.5 $\pm$ 1.0	85.7 $\pm$ 3.5	91.3 $\pm$ 0.5	91.6 $\pm$ 1.3
Forbs	18.0 $\pm$ 2.0	26.1 $\pm$ 4.6	19.3 $\pm$ 1.7	19.2 $\pm$ 2.5
Bare ground	10.7 $\pm$ 2.3	12.9 $\pm$ 6.6	7.1 $\pm$ 1.7	1.8 $\pm$ 0.4
Litter	80.7 $\pm$ 3.1	81.3 $\pm$ 7.1	87.2 $\pm$ 2.1	94.6 $\pm$ 0.6
Percent frequency of occurrence				
Western wheatgrass	91.3 $\pm$ 3.1 A	95.7 $\pm$ 4.0 B	98.0 $\pm$ 1.3 C	95.4 $\pm$ 1.7 C
Buffalo grass	84.1 $\pm$ 6.8 A	54.7 $\pm$ 12.28 B	30.3 $\pm$ 4.5 C	33.2 $\pm$ 6.4 C
Green needlegrass	3.0 $\pm$ 1.25 A	12.6 $\pm$ 3.7 B	38.8 $\pm$ 6.7 C	60.4 $\pm$ 15.4 C
Vegetation height (cm)	26.6 $\pm$ 2.3 A	35.3 $\pm$ 4.5 A	45.0 $\pm$ 1.5 B	51.8 $\pm$ 2.8 B
Vegetation height CV	39.1 $\pm$ 2.6 A	34.1 $\pm$ 2.6 A	26.6 $\pm$ 1.0 B	27.4 $\pm$ 2.4 B
Litter depth (cm)	0.9 $\pm$ 0.1 A	1.4 $\pm$ 0.3 A	2.5 $\pm$ 0.2 B	3.1 $\pm$ 0.1 B
Litter depth CV	96.4 $\pm$ 6.3 A	101.4 $\pm$ 11.0 A	67.0 $\pm$ 5.0 B	44.1 $\pm$ 5.0B
VOM(cm)	5.8 $\pm$ 1.0 A	8.6 $\pm$ 1.5 A	14.5 $\pm$ 1.0 B	17.0 $\pm$ 1.8 B
VOM CV	86.2 $\pm$ 7.3 A	72.2 $\pm$ 9.8 A	44.5 $\pm$ 2.2 B	41.2 $\pm$ 2.9 B

¹Rows of means followed by different letters are significantly different ($P < 0.10$) using multivariate MRPP with step-down tests (Petronidas and Gabriel 1983).

²CV = coefficient of variation; VOM = visual obstruction measurement.

³Groups of variable separated by lines were analyzed together in MRPP.

ences for frequency and canopy cover among seral stages for these 3 species were slightly different. Percent canopy cover of total grasses, total forbs, bare ground, and litter were similar among seral stages. Late-intermediate and late seral stages had taller, more dense vegetation, and greater litter layers than early and early-intermediate seral stages. Vegetation patchiness (CV's) was greater in early and early-intermediate seral stages compared to late-intermediate and late seral stages. Six of the early sites and 2 of the early-intermediate sites were black-tailed prairie dog (*Cynomys ludovicianus* Ord) towns, possibly confounding some relations between plants and birds. Prairie dogs seem to be an important factor in maintaining the dominance of buffalo grass that delineates the early seral stage. Because prairie dog towns are an integral part of the prairie ecosystem and essentially represent the largest areas of early seral stage conditions on the Fort Pierre National Grassland, they were included in all analyses as the seral stage in which they were classified.

Thirty-eight bird species were counted on transects during the study. Grasshopper sparrows, western meadowlarks, brown-headed cowbirds, and chestnut-collared longspurs were the most abundant bird species, composing 76% of the birds. Other common species included the red-winged blackbird, bobolink, upland sandpiper, horned lark, lark bunting (*Calamospiza melanocorys* Stejneger), and marbled godwit (*Limosa fedoa* Linnaeus). Bird species richness did not differ among seral stages (Table 2). Bird species diversity was greater in the early seral stage compared to the late-intermediate seral stage.

Grasshopper sparrows, dickcissels, bobolinks, and brown-headed cowbirds were generally more abundant in the later seral stages than in the earlier seral stages. Horned lark, chestnut-collared longspur, upland sandpiper, and burrowing owl densities tended to be greater in the earlier seral stages than in the later seral stages (Table 2). Western meadowlarks were common in all seral stages, but were more abundant in the early and early-intermediate seral stages than on late seral sites.

Grasshopper sparrow, brown-headed cowbird, burrowing owl, and upland sandpiper densities were best predicted using seral stages in our study (Table 3). Coefficients of multiple determination (R^2) ranged from 0.13 to 0.43 and no vegetation variables entered the regression models for these species. Regression mod-

Table 2. Mean ($\pm$ SE) density of male birds per 10 ha in seral stages of mixed-grass prairie on Fort Pierre National Grassland, South Dakota 1996 and 1997.¹

Bird Species	Seral Stage			
	Early $\bar{X} \pm \text{SE}$	Early-intermediate $\bar{X} \pm \text{SE}$	Late-intermediate $\bar{X} \pm \text{SE}$	Late $\bar{X} \pm \text{SE}$
Species richness	14.70 $\pm$ 1.57	13.0 $\pm$ 1.32	12.4 $\pm$ 0.75	14.5 $\pm$ 1.43
Species diversity	0.88 $\pm$ 0.05A	0.80 $\pm$ 0.02AB	0.73 $\pm$ 0.02B	0.73 $\pm$ 0.04AB
Horned lark	1.41 $\pm$ 0.53A	0.88 $\pm$ 0.53A	0.03 $\pm$ 0.02B	0.0 $\pm$ 0.0AB
Grasshopper sparrow	1.57 $\pm$ 0.59A	4.26 $\pm$ 1.14AB	6.26 $\pm$ 0.59B	7.97 $\pm$ 0.84B
Chestnut-collared longspur	5.02 $\pm$ 1.84A	4.88 $\pm$ 1.63A	1.10 $\pm$ 0.54B	0.20 $\pm$ 0.11AB
Dickcissel	0.04 $\pm$ 0.04AB	0.0 $\pm$ 0.0A	0.06 $\pm$ 0.03A	0.61 $\pm$ 0.30B
Bobolink	0.04 $\pm$ 0.04A	0.09 $\pm$ 0.07A	0.86 $\pm$ 0.16B	0.43 $\pm$ 0.10B
Western meadowlark	4.74 $\pm$ 0.50A	4.95 $\pm$ 0.79A	4.07 $\pm$ 0.27AB	3.38 $\pm$ 0.14B
Red-winged blackbird	0.78 $\pm$ 0.26	0.43 $\pm$ 0.22	0.66 $\pm$ 0.20	0.20 $\pm$ 0.08
Brown-headed cowbird	1.55 $\pm$ 0.54A	1.82 $\pm$ 0.39AB	3.24 $\pm$ 0.30B	2.58 $\pm$ 0.30AB
Upland sandpiper	1.37 $\pm$ 0.81AB	0.63 $\pm$ 0.29A	0.22 $\pm$ 0.07AB	0.03 $\pm$ 0.03B
Burrowing owl	0.75 $\pm$ 0.22A	0.19 $\pm$ 0.19AC	0.03 $\pm$ 0.02BC	0.0 $\pm$ 0.0AB

¹ Rows of densities followed by different letters are significantly different ($P < 0.10$) using MRPP tests.

els for bobolinks, dickcissels, chestnut-collared longspurs, and horned larks included both seral stage regressors and vegetation variables. When vegetation variables entered the regression models for bobolinks, chestnut-collared longspurs, and horned larks, the seral stage regressors lost significance. For example, bobolink density was initially modeled using seral stage contrast variables early versus early-intermediate (D2) and early versus late-intermediate (D3) having significant P -values of $P = 0.01$ and $P = 0.06$, respectively. When the vegetation variables litter depth and bare ground entered the regression equation (Final Model, Table 3), these variables became nonsignificant $P = 0.32$ and $P = 0.71$ for early versus early-intermediate and early versus late-intermediate, respectively. Seral stage regressors were not effective in modeling densities for western meadowlarks or red-winged blackbirds.

Discussion

The concept that wildlife densities are related to plant succession and recognizable seral stages is fundamental to wildlife management (Robinson and Bolen 1984, Christensen and Davis 1986). Both vegetation structure and composition differed among seral stages of wheatgrass-needlegrass communities on the Fort Pierre National Grassland. Later seral stages provided habitat conditions favorable to species that require taller and more dense cover with deeper litter layers. Grasshopper sparrows preferred late-intermediate and late seral stages and were nearly absent on early seral sites. Wheatgrass and needlegrass areas provide

suitable grasshopper sparrow habitat in the Great Plains (Kantrud and Kologiski 1982). Grasshopper sparrows are positively associated with vegetation height and density in short to mixed-grass prairie (Rotenberry and Wiens 1980).

Bobolink and dickcissel densities on the Fort Pierre National Grassland were lower than reported in other prairie areas (Bollinger and Gavin 1992, Rotenberry and Wiens 1980, Wiens 1969). On the Fort Pierre National Grassland, bobolinks had greatest densities in later seral stages. Bobolinks are associated with tall, dense vegetation (Wiens 1969, Renken and Dinsmore 1987) and with increased litter (Tester and Marshall 1961). Dense nesting cover for waterfowl (Renken and Dinsmore 1987), hayfields, and tame grass pastures (Kendeigh 1941, Kantrud 1981, Bollinger and Gavin 1992) are also considered favorable habitats for bobolinks. Madden (1996) suggested that the preference of bobolinks for exotic grasses and hayfields in the northern Great Plains may be due to their affinity for tall grass prairie. Dickcissels were most abundant on late seral sites. Dickcissels are more common in eastern tall grass prairie compared to western prairies in South Dakota (South Dakota Ornithologists' Union 1991). Density of dickcissels was notably high on 2 study sites in 1996, presumably due to the abundance of yellow sweet clover, which may have been important for nesting (Overmire 1962, Harmeson 1974, Wiens 1969). Regionally, the Fort Pierre National Grassland does not support large populations of bobolinks or dickcissels, but locally late-intermediate and late seral stages are important habitats for these species.

Table 3. Multiple regression models generated to assess the relative effectiveness of seral stage versus vegetation characteristics as predictors of bird species density on Fort Pierre National Grassland, SD 1996 and 1997. D1, D2, and D3 are dummy-coded variables which represent the categorical variable seral stage. Dummy variables were forced into the model and multiple models are reported when vegetation variables enter the model using a step-wise technique. If the dummy variables did not generate a significant model then only vegetation variables were used in the regression analysis.

Dependent variable	Model Summary			Independent ¹ variables	Coefficient Summary	
	Adjusted R ²	SE of estimate	Significance		B (±SE)	Significance
Horned lark (seral stages only)	0.41	0.71	< 0.01	D1	-0.30 (0.40)	0.46
				D2	-1.37 (0.32)	<0.01
				D3	-1.57 (0.40)	<0.01
Horned lark (final model)	0.50	0.66	<0.01	D1	-0.08 (0.38)	0.84
				D2	-0.70 (0.39)	0.09
				D3	-0.68 (0.50)	0.18
				Litter Depth	-2.16 (0.82)	0.01
Grasshopper sparrow (final model)	0.43	0.24	< 0.01	D1	0.27 (0.13)	0.05
				D2	0.47 (0.02)	< 0.01
				D3	0.64 (0.13)	< 0.01
Chestnut-collared longspur (seral stages only)	0.21	0.81	0.01	D1	0.03 (0.45)	0.94
				D2	-0.92 (0.36)	0.02
				D3	-1.12 (0.45)	0.02
Chestnut-collared longspur (final model)	0.45	0.68	< 0.01	D1	0.40 (0.39)	0.31
				D2	-0.60 (0.32)	0.07
				D3	-0.41 (0.44)	0.36
				Bare Ground	0.99 (0.33)	0.01
				% Forbs	-2.15 (0.72)	0.01
Dickcissel (seral stages only)	0.13	0.67	0.06	D1	-0.21 (0.37)	0.57
				D2	0.10 (0.30)	0.75
				D3	0.82 (0.37)	0.03
Dickcissel (final model)	0.22	0.63	0.02	D1	-0.42 (0.36)	0.26
				D2	0.08 (0.28)	0.79
				D3	0.78 (0.35)	0.04
				% Forbs	1.45 (0.67)	0.04
Bobolink (seral stages only)	0.36	0.13	< 0.01	D1	0.02 (0.07)	0.79
				D2	0.23 (0.06)	< 0.01
				D3	0.14 (0.07)	0.06
Bobolink (final model)	0.58	0.10	< 0.01	D1	-0.04 (0.06)	0.47
				D2	0.06 (0.06)	0.32
				D3	-0.03 (0.08)	0.71
				Litter Dept	0.397 (0.16)	< 0.01
				Bare Ground	0.020 (0.06)	< 0.01
Western meadowlark (final model)	0.15	0.12	0.01	Litter Depth	-0.27 (0.10)	0.01
Red-winged Blackbird (final model)	-----	-----	NS	-----	-----	NS
Brown-headed cowbird (final model)	0.22	0.12	0.01	D1	0.03 (0.07)	0.68
				D2	0.17 (0.05)	< 0.01
				D3	0.10 (0.07)	0.13
Upland sandpiper (final model)	0.13	0.46	0.05	D1	-0.04 (0.26)	0.87
				D2	-0.37 (0.21)	0.08
				D3	-0.64 (0.26)	0.02
Burrowing owl (final model)	0.49	0.57	< 0.01	D1	-1.26 (0.32)	< 0.01
				D2	-1.44 (0.25)	< 0.01
				D3	-1.60 (0.32)	< 0.01

¹D1 = contrast between early and early-intermediate seral stage; D2 = contrast between early and late-intermediate seral stage; D3 = contrast between early and late seral stage.

Early and early-intermediate seral stages supported species that require shorter and more sparse vegetative conditions. Chestnut-collared longspur and horned lark habitat typically consists of short, less dense vegetation (Owens and Myres 1973, Kantrud 1981, Wyckoff 1986, Wiens 1973). This helps explain why chestnut-collared longspur density was 25 times greater in the early seral stage compared to the late seral stage ($P = 0.12$). Considering the magnitude of the difference in density

and its effect on breeding potential, the difference is most likely biologically important (e.g., Stiedl et al. 1997).

Burrowing owls in the Great Plains region are associated with prairie dog towns (Agnew et al. 1986) and we assume the differences in density estimates of burrowing owls among seral stages were due to the presence of prairie dog burrows on early and early-intermediate seral sites. Prairie dog burrows provide nest sites and escape corridors for burrowing owls

(MacCracken et al. 1985). Burrowing owls will use areas of low grass cover and burrows of other mammals (Bue 1955, Martin 1973). On the Fort Pierre National Grassland, prairie dog towns comprised 10 of the 13 early and early-intermediate seral sites. Prairie dog towns are probably required for maintaining burrowing owl populations on the Fort Pierre National Grassland.

Early and early-intermediate seral stages on the Fort Pierre National Grassland are

important upland sandpiper feeding habitats, whereas late-intermediate and late seral conditions are likely important for nesting activities. Upland sandpipers nest in dense vegetative cover < 20.5 cm tall (Higgins et al. 1969), but feed in short, sparse grass vegetation (Ailes 1976). Our bird counts were conducted in the morning when our observations indicated the upland sandpipers were feeding. Thus, we suspect upland sandpipers used early seral stage sites mainly for feeding. Upland sandpipers were uncommon on the early seral sites during the afternoon when vegetation structure measurements were being collected. We found 2 upland sandpiper nests and both were in late-intermediate or late seral stage sites.

Western meadowlarks are habitat generalists with a tolerance to a wide range of grassland habitats (Owens and Myres 1973, Rotenberry and Wiens 1980, Agnew et al. 1986). Grazing had little effect on western meadowlark abundance in North Dakota grasslands (Kantrud 1981). However, western meadowlarks are less abundant in areas where the vegetation becomes too tall and dense (Wiens 1969, Madden 1996). On the Fort Pierre National Grassland, tall dense vegetation, characteristic of late seral sites, was less occupied by western meadowlarks. Red-winged blackbirds are typically considered a wetland or wet meadow associated species that often nests in shrubs over dry land (South Dakota Ornithologists' Union 1991). Red-winged blackbird density was low in all seral stages and field observations suggest that density was most likely influenced by the proximity of the nearest wetland area rather than the seral stage of prairie vegetation.

Density of grasshopper sparrows, brown-headed cowbirds, burrowing owls, and upland sandpipers on the Fort Pierre National Grassland were predicted using only seral stage regressors. The step-wise addition of vegetation variables did not improve predictive ability of the regression models. Bobolinks, dickcissels, chestnut-collared longspurs, and horned larks were best predicted by including some vegetation variables in the regression models. With the exceptions of meadowlarks and red-winged blackbirds, each of the bird species above exhibited significant rank correlations to variables that reflected vegetation. Of those species that exhibited rank correlations to vegetation height, dickcissels alone lacked significant correlations to measures of patchiness in vegetation height. Nonetheless, when seral stage was entered into the regression equa-

tions, none of the species we evaluated showed significant correlations to measures of vegetation height or patchiness suggesting that for these species in needle-grass-wheatgrass communities of central South Dakota, seral stage was an adequate predictor of their habitat conditions. For those birds that vegetation variables entered the regression models after seral stage, the seral stage regressors often lost significance, demonstrating that there were confounding effects between vegetation variables and seral stage regressors. As a result, for some bird species it is difficult to determine whether seral stage was an adequate predictor of bird species density.

Numerous factors need to be considered when developing habitat models to facilitate management decisions. A large amount of the variability in bird densities remained unexplained regardless of the variables included. Territoriality, available nest sites, foraging opportunities, site tenacity, predation, or landscape features may be important determinants of the unexplained variation for these models. Managers must weigh the increased costs of measuring additional variables included in a model against the benefits of increased predictive ability. Models are satisfactory when they allow managers to make informed decisions. Habitat models do not need to depict reality, but rather simplify it (Starfield 1997). Managing rangelands with seral stages provides the manager with a unit of measure to determine objectives and to evaluate the effects of management (Dyksterhuis 1985, Uresk 1990). On a coarse scale, seral stage models may provide enough information about bird densities to facilitate management decisions, but specific vegetation measurements may be needed when making more finite habitat decisions for individual species.

Conclusions

On the Fort Pierre National Grassland, each of the 4 seral stages was important for grassland birds. A mosaic of seral stages should be maintained across the Fort Pierre National Grassland landscape to provide habitat for all grassland birds. Landscape issues such as fragmentation should be better investigated to determine appropriate seral stage patch size and distribution. Seral stage was an effective predictor of density for many grassland birds in this study. Seral stages provide an ecological framework for developing management plans and predicting effects of management decisions on grassland bird popu-

lations. We are not suggesting that vegetation structure and composition are unimportant in describing bird habitat relations. Vegetation structure (Wiens 1973, Rotenberry and Wiens 1980) and plant taxonomic composition (Wiens and Rotenberry 1981, Rotenberry 1985, Knopf et al. 1990) are important determinants for grassland birds. The concepts of seral stage versus vegetation structure or vegetation composition as predictors of grassland bird density are not mutually exclusive. Floristic composition was used to determine seral stage in our study. Additionally, plant forms and growth strategies provided inherent differences in vegetation structure among seral stages. Vegetation measurements are often tedious, time consuming, and costly to collect. Seral stages may provide managers with an efficient and functional tool from which multiple use management decisions can be made, including the development and monitoring of grassland bird management objectives.

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