Shrubsteppe Bird Response to Habitat and Landscape Variables in Eastern Washington, U.S.A.

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Abstract: *The landscape of the intermountain west has changed dramatically in the last 150 years, particularly in the state of Washington, where over half the native shrubsteppe ecosystem has been converted to agricultural lands, resulting in a fragmented landscape with few extensive tracts of shrubsteppe. We examined the historical and current distribution of shrubsteppe on different soil types in eastern Washington, and we censused bird communities at 78 sites in shrubsteppe from 1991 to 1993. We compared abundance of species among soil types and range conditions and developed models of species occurrence using site-specific vegetation and landscape variables. The pattern of shrubsteppe conversion has resulted in a disproportionate loss of deep soil communities. Eight bird species showed strong relationships with soil type and three with range condition. These associations likely resulted from the influence of soil type and range history on the vegetation of these communities. Brewer's Sparrows (*Spizella breweri*) and Sage Sparrows (*Amphispiza belli*) reached their highest abundances in deep, loamy soils, whereas Loggerhead Shrikes (*Lanius ludovicianus*) were most abundant in deep, sandy soils. Sage Sparrows occurred more frequently in landscapes dominated by shrubsteppe, indicating a negative relationship with fragmentation. Our results suggest that fragmentation of shrubsteppe and the pattern of agricultural conversion among soil types have had detrimental effects on numerous shrubsteppe species. The landscape for species with an affinity for deep, loamy soil communities has changed considerably more than the overall loss of shrubsteppe would indicate. Conservation practices that emphasize retention of shrubsteppe communities on deep soils and that reduce further fragmentation will be critical to the maintenance of avian biological diversity in this system.*

Respuesta de Aves de la Estepa Arbustiva a Variables del Hábitat y el Paisaje en la Región Este de Washington, E.U.A.

Resumen: *El paisaje del oeste intermontañoso ha cambiado dramáticamente en los últimos 150 años, particularmente en el estado de Washington donde más de la mitad del ecosistema de estepa arbustiva ha sido convertida a tierras agrícolas resultando en un paisaje fragmentado con pocas superficies extensas de estepa arbustiva. Examinamos la distribución histórica y actual de estepa arbustiva en diferentes tipos de suelo en la región este de Washington y monitoreamos comunidades de aves en 78 sitios de estepa arbustiva desde 1991 hasta 1993. Comparamos la abundancia de especies entre tipos de suelo y condiciones del rango y desarrollamos modelos de incidencia de especies usando vegetación sitio-específica y variables de paisaje. Los patrones de conversión de estepa arbustiva han resultado en una pérdida desproporcionada de comunidades de suelo profundo. Ocho especies de aves mostraron relaciones fuertes con el tipo de suelo y tres con la condición del rango. Estas asociaciones posiblemente resultaron de las influencias del tipo de suelo y la historia del rango en la vegetación de estas comunidades. El gorrión de Brewer (*Spizella breweri*) y el gorrión de salvia (*Amphispiza belli*) alcanzaron sus abundancias más altas en suelos arcillosos profundos, mientras que el alcaudón (*Lanius ludovicianus*) fue más abundante en suelos arenosos profundos. Los gorriones de salvia ocurrieron más frecuentemente en paisajes dominados por estepa arbustiva, indicando una relación negativa con la fragmentación. Nuestros resultados sugieren que la fragmentación de la estepa arbustiva y el patrón de conversión agrícola entre los tipos de suelos ha tenido efectos perjudiciales en numerosas especies de es-*

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tepa arbustiva. El paisaje para especies con afinidad por comunidades de suelos arcillosos profundos ha cambiado considerablemente más de lo que podría indicar la pérdida global de estepa arbustiva. Las prácticas de conservación que ponen énfasis en la retención de comunidades de estepa arbustiva en suelos profundos y que reducen aún más la fragmentación serán críticas para mantener la diversidad biológica de aves en este sistema.

Introduction

The landscape of the intermountain west has changed dramatically over the last 150 years, particularly within semiarid shrubsteppe ecosystems (Quigley & Arbelbide 1997). Anthropogenic changes in these shrub- and grass-dominated communities has been especially severe in the state of Washington, where over half the native shrubsteppe has been converted to agricultural lands (Dobler et al. 1996). Unlike forest communities that can regenerate after clearcutting, shrubsteppe that has been ploughed and that has grown agricultural crops is unlikely to return to its former native community. Furthermore, a long history of grazing, fire, and invasion by exotic vegetation has altered the composition of the plant community within much of the extant shrubsteppe in this region (Quigley & Arbelbide 1997; Knick 1999).

Conversion of shrubsteppe communities to agricultural fields in Washington has resulted in a fragmented landscape with few extensive tracts of shrubsteppe (Dobler et al. 1996). Fragmentation of previously extensive landscapes can influence the distribution and abundance of birds through redistribution of habitat types and through the pattern of habitat fragmentation, including characteristics such as decreased patch area and increased habitat edge (Ambuel & Temple 1983; Wilcove et al. 1986; Robbins et al. 1989; Bolger et al. 1991, 1997). Fragmentation also can reduce avian productivity through increased rates of nest predation (Gates & Gysel 1978; Wilcove 1985), increased nest parasitism (Brittingham & Temple 1983; Robinson et al. 1995), and reduced pairing success of males (Gibbs & Faaborg 1990; Villard et al. 1993; Hagan et al. 1996). Much of our knowledge of fragmentation effects on birds comes from studies in eastern and central regions of North America; little research has been conducted on western landscapes (Bolger et al. 1991, 1997; Knick & Rotenberry 1995; Tewksbury et al. 1998). We know little about the influence of fragmentation on shrubsteppe bird communities (Knick & Rotenberry 1995).

Disturbance plays an important role in determining successional pathways in shrubsteppe communities (Daubenmire 1970; Smith et al. 1995). Excessive grazing by livestock can reduce the abundance of some native plants while increasing that of others and can allow exotic species to enter and in some cases dominate communities (Branson 1985). Wildfire can promote the spread of annual grasses to the detriment of native plants (Whisenant 1990). The effects of livestock grazing on shrubsteppe vegetation can influence use of sites by birds, although the direction of influence (positive or negative) may vary (Saab et al. 1995). Invasion of exotic plants changes floristics and vegetation structure and can have adverse effects on site use by some birds (Knick & Rotenberry 1995).

The loss of once extensive shrubsteppe communities has reduced substantially the habitat available to a wide range of shrubsteppe-associated wildlife, including several birds found only in this community type (Quigley & Arbelbide 1997; Saab & Rich 1997). Sage Sparrows, Brewer's Sparrows, Sage Thrashers, and Sage Grouse are considered shrubsteppe obligates, and numerous other species are associated primarily with shrubsteppe at a regional scale. In a recent analysis of birds at risk within the interior Columbia Basin, the majority of species identified as of high management concern were shrubsteppe species. Moreover, over half these species have experienced long-term population declines according to the Breeding Bird Survey (Saab & Rich 1997).

Soils are a conspicuous component of shrubsteppe ecosystems and influence the composition of the vegetation community. The composition, texture, and depth of soils affect drainage, nutrient availability, and rooting depth and result in a variety of edaphic climax communities (Daubenmire 1970). Much of the interior Columbia Basin in eastern Washington is underlaid by basaltic flows, and the soils vary from deep accumulations of loess-derived loams to shallow lithosols in areas where glacial floods scoured the loess from underlying basalt. Sandy soils cover extensive areas in the westcentral and southern parts of the basin, the result of glacial outwash and alluvial and wind-blown deposition (Daubenmire 1970; Wildung & Garland 1988). Results of a previous census of shrubsteppe birds in eastern Washington suggested that the abundance of some species might vary with soil type of the vegetation community (Dobler et al. 1996). If it exists, this relationship might prove a valuable asset to management, because soils are a mapable component of the landscape and could be incorporated into spatially explicit models of resource use and availability.

We examined the response of birds to local and landscape variables in shrubsteppe communities in eastern Washington. Our primary objective was to determine if bird abundance varied with soil type and range condition and to compare present and historic distribution of shrubsteppe among soil types to assess the potential effects of this pattern on shrubsteppe bird communities. Our second objective was to develop models of relationships between site-specific characteristics, including a simple index to habitat fragmentation, and the probability of specific species occurring at a site. By building such models and testing them against independent data from the study area, we sought to identify variables to help describe the distribution of shrubsteppe birds on the landscape.

Study Area

The study took place in eastern Washington (U.S.A.) within the geographic region known as the Columbia Basin (Fig. 1). The region is characterized by hot, dry summers and cold winters. Mean monthly air temperatures range from −5.5 to 24.5° C. Precipitation falls mainly during winter, with annual totals ranging from 15 to 55 cm, decreasing from north to south across the study area (Daubenmire 1970). The study area included seven counties with generally flat to rolling topography which occur on a basaltic plain that slopes from approximately 750 m elevation in the north to <250 m in some areas in the south (Daubenmire 1970).

Historically, most of the land in the study area that was not forested supported shrubsteppe vegetation communities (Daubenmire 1970). Large-scale clearing of land for agriculture began in the late 1800s and expanded when irrigation became widespread after the damming of the Columbia River in the 1930s (National Research Council 1995). A considerable portion of the study area is farmed; dryland wheat is the main crop in higher rainfall zones, whereas irrigated orchards, vineyards, and row crops prevail at lower elevations. Grazing by livestock began in the basin in the late 1800s and has continued to varying degrees (Quigley & Arbelbide 1997). Although livestock grazing likely occurred on most of our sites (presently or historically), we lacked a detailed grazing history for such a large area.

Most sites used in the study were characterized by a dominant overstory of sagebrush (*Artemesia* spp.) and an understory of bunch grasses and forbs. Common shrubs included big sagebrush (*A. tridentata*), three-tip sagebrush (*A. tripartita*), stiff sagebrush (*A. rigida*), gray rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*C. viscidiflorus)*, and antelope bitterbrush (*Purshia tridentata*). Bunch grasses included bluebunch wheatgrass (*Agropyron spicatum*), Sandberg's blue grass (*Poa secunda*), Idaho fescue (*Festica idahoensis*), and needle and thread grass (*Stipa* spp.). Common forbs on the sites included balsam root (*Balsamorhiza* spp.), lupin (*Lupinus* spp.), phlox (*Phlox* spp.), and desert buckwheat (*Eriogonum* spp.). Cheatgrass (*Bromus tectorum*), an introduced annual grass, was ubiquitous on the study area and was present at low densities in even the least-disturbed sites. Little shrubsteppe remained in presettlement condition (Daubenmire 1970).

Methods

Landcover Classification

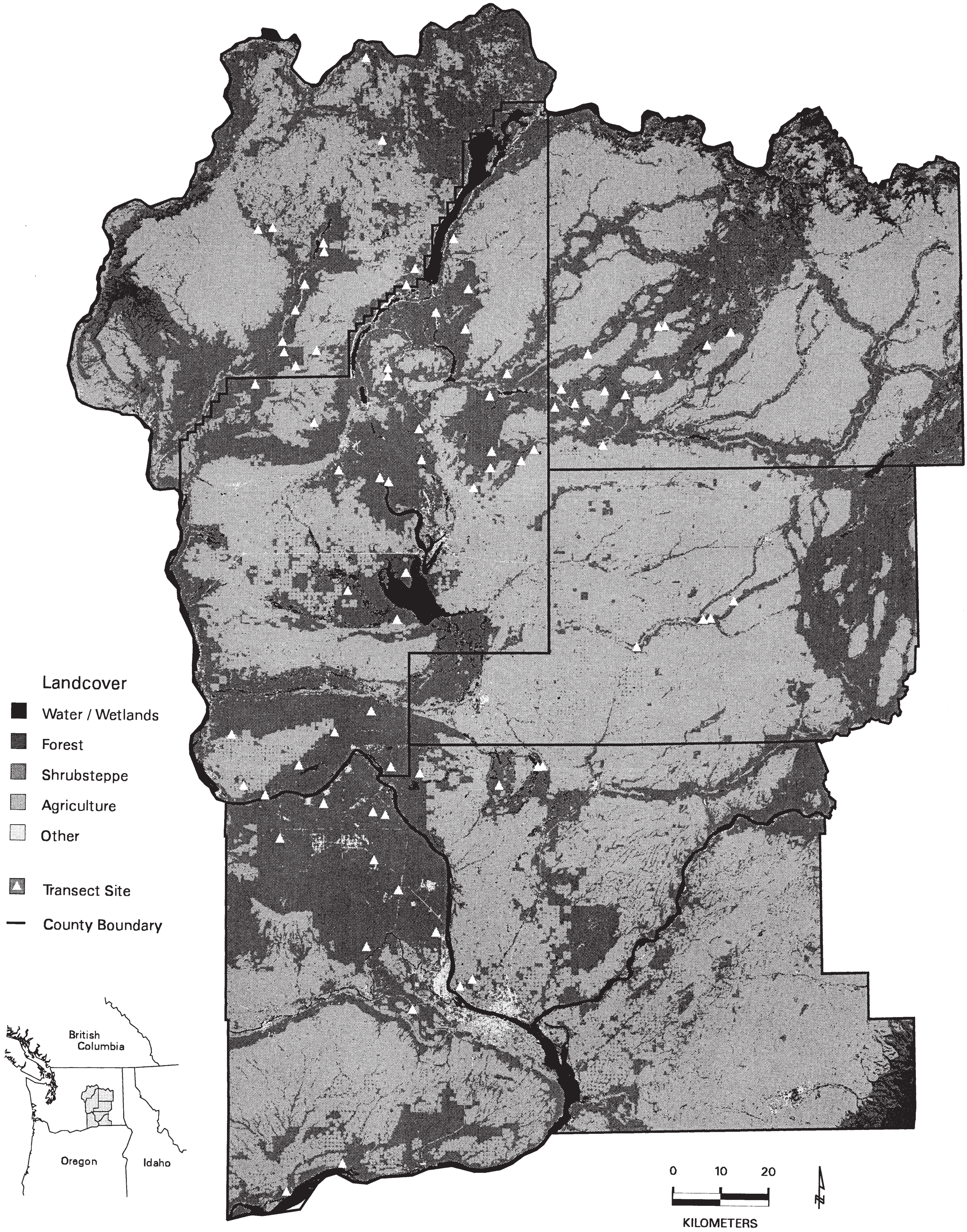
We used Landsat thematic mapper data (25-m spatial resolution) to develop landcover classes for the study area. Landsat scenes acquired in May 1993 and August 1994 were used as a multitemporal data set to increase discernability between vegetative landcover due to phenological differences. Landcover classes developed were (1) shrubsteppe, (2) agriculture, (3) woodland, (4) urban, (5) barren/shadow, and (6) open water. Landcover data were imported into ARCINFO (Environmental Systems Research Institute, Redlands, California) to establish a geographic information system (GIS) for the study area.

Digitized soil data were obtained from the Natural Resources Conservation Service and were incorporated into the GIS. We combined soils based on their published descriptions (Stockman 1981; Gentry 1984) into three broad classes: loamy (mostly loam and sandy loam with depths of >50.8 cm); sandy (mostly sand and loamy sand with depths of >50.8 cm); and shallow (thin, overlaying bedrock or hardpan with depths of < 50.8 cm). Soil complexes that included >35% shallow soils were included in the shallow soil class. We used the GIS to determine soil types for the current landcover classes in the two counties (Lincoln and Grant) for which digitized soil data were available. We also used the GIS to derive the historical distribution of shrubsteppe in the study area for the three soil classes. Land currently in agriculture was assumed to be historically shrubsteppe based on known soil-vegetation relationships and vegetation zones delineated in Daubenmire (1970).

Site Selection

We selected 78 study plots in patches of shrubsteppe large enough to contain a 500-m survey transect and a 100-m buffer. Sites were stratified by soil type and fell within one of the three soil classes described above. We established transects along a north-south axis and marked them with wooden stakes at 100-m intervals.

We characterized the condition of the vegetation community at each site based on a modification of the Natural Resources Conservation Service's (1976) range-site index. Our index was based on the proportion of potential climax vegetation present on the site and was calculated from estimates of percent cover. We considered sites with >50% cover in climax species to be in good range condition, those with 25–50% cover in climax species to be in fair range condition; and those with <25%


Landcover
Water / Wetlands
Forest
Shrubsteppe
Agriculture
Other
Transect Site
County Boundary
British Columbia
Oregon
Idaho
0 10 20
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cover in climax vegetation to be in poor range condition. Distribution of sites among the nine combinations of soil type and range condition were as follows: loamy/good, 9 sites; loamy/fair, 11 sites; loamy/poor, 16 sites; sandy/good, 5 sites; sandy/fair, 5 sites; sandy/poor, 9 sites; shallow/good, 9 sites; shallow/fair, 9 sites; shallow/poor, 5 sites. Our range-condition index should be interpreted as a general indication of past disturbance, with grazing one of several likely factors.

Habitat Variables

We measured vegetation along each transect (Table 1) between 29 May and 25 June 1991. Transects were divided into 100-m segments, and measurements were taken within the first, third, and fifth segments. Shrub cover by species and shrub height was measured by means of a 100-m line intercept (Canfield 1941). Percent cover of herbaceous plants was measured by means of 0.1-m^2 micro-plots (Daubenmire 1959) placed at 5-m increments along the transect. Measurements were averaged across the three segments for each transect.

We used principal components analysis (SAS Institute, Inc. 1990) to identify trends in vegetation among soil and range classes. There was high correlation ($r > 0.48$) among percent cover of life forms (e.g., shrubs) and their major component species, so to simplify this descriptive analysis we used only percent cover of life forms and structural variables in the principal components analysis. Percentage data were arcsine–square root transformed to improve normality. We inspected bivariate plots of the first three principal components to look for differences among soil and range classes along the resulting vegetation gradients.

Landscape variables were derived for each site from the study area GIS. The extent of remaining shrubsteppe was calculated within circles of 1-, 3-, and 5-km radius extending from the center of each study transect. We used the percent shrubsteppe within each circle as an index of the degree of habitat fragmentation in the landscape around each transect at three different scales. We determined the latitudinal position of each site using global positioning system receivers, and we derived elevation from topographic maps. We estimated average annual rainfall for each study site from the PRISM model (Daly et al. 1994).

Bird Censuses and Abundance

We censused birds using line transect methods between sunrise and 0930 hours, except during periods of high winds or rain. During each census, one trained observer walked each transect, noting all birds seen or heard and their sighting distance and angle to the transect. Distance of each bird from the observer was estimated with an optical rangefinder. Each transect was surveyed three to six times per year in April and May 1991–1993. Censuses were conducted by three observers in 1991 and four observers in 1992 and 1993, with two observers present all 3 years. Within each year, observers alternated sites so that all transects were censused by each observer at least one time. Sighting distance and angle to the transect were converted to perpendicular distance for each observation. Analyses were limited to observations within 100 m perpendicular to the transect and included both stationary and flying birds.

We used the maximum number of individuals recorded on a single census as an estimate of the annual abundance of each species on each transect. Although the maximum value likely resulted in an optimistic estimate, this measure is more likely to give an accurate assessment of the number of territorial males on our plots than would the mean of all visits. Several of the more common species on our study area are known to sing less when paired or nesting, so detectability varies over the breeding season (Best & Petersen 1985; W.M.V., personal observation), and using the mean of all visits would underestimate the number of territorial males.

We compared the abundance of individuals among soil types and range conditions with analysis of deviance using Glim 4.0 (Francis et al. 1993). Count data are generally not normally distributed, so we used a Poisson distribution function in all models (Crawley 1993). Because our study design included, a priori, comparisons of the effects of soil type and range condition, we proceeded with a set of one-way models to test for differences among soil and range classes. First, we used cell means models (Searle 1987) developed for each species from the nine combinations of soil and range. We then tested for interaction between soil type and range condition using a full model with soil, range, and soil-range interaction. For species with significant soil-range interaction, we used Fisher's protected least-significant-difference test (Steel & Torrie 1980) to examine differences among soil-range combinations. In the absence of a significant interaction, we used one-way models to test for effects of soil and range. We further examined significant one-way models using Fisher's exact test (Sokal & Rohlf 1995) to test among-group differences. Year was included as a main effect in all models. We considered test results significant when $p < 0.05$.

Figure 1. Current landcover and location of study sites in the central Columbia Basin, Washington. Landcover classes were derived from Landsat Thematic Mapper data by means of multi-temporal analysis (scene dates: May 1993 and August 1994). "Other" landcover class includes urban areas and rock or other impervious surfaces.

Table 1. Vegetation and landscape variables measured at shrubsteppe sites in eastern Washington and used in logistic regression analysis of bird occurrence.[a]

	Loamy		*Sandy*		*Shallow*	
	mean	*SE*	*mean*	*SE*	*mean*	*SE*
Vegetation variables						
annual grass (% cover)	12.65	2.17	40.19	2.13	15.84	1.88
perennial grass (% cover)	42.38	2.76	17.42	2.59	22.52	0.96
annual forbs (% cover)	10.20	1.97	15.36	1.99	8.29	0.85
perennial forbs (% cover)	6.52	0.85	2.89	0.64	3.70	0.41
total herbaceous vegetation (% cover)	71.17	3.52	75.86	3.32	51.71	2.60
mean height of herbaceous vegetation (cm)	27.90	1.68	24.39	2.11	10.91	0.81
big sagebrush (% cover)	11.66	1.03	5.16	1.14	5.76	1.04
stiff sagebrush (% cover)	0.35	0.18	0.00	0.00	2.94	0.69
three-tip sagebrush (% cover)	0.23	0.10	0.00	0.00	0.43	0.26
antelope bitterbrush (% cover)	0.00	0.00	0.95	0.41	0.06	0.06
green rabbitbrush (% cover)	0.51	0.19	0.59	0.25	0.33	0.15
grey rabbitbrush (% cover)	0.54	0.15	1.01	0.33	0.10	0.03
total shrubs (% cover)	13.94	1.12	8.06	1.18	10.37	1.31
mean height of shrubs (m)	0.65	0.03	0.70	0.06	0.49	0.03
Landscape variables						
shrubsteppe within 1-km radius of site (%)	85.32	2.08	87.19	3.37	85.27	3.15
shrubsteppe within 3-km radius of site (%)	68.40	3.43	68.91	5.64	69.50	3.56
shrubsteppe within 5-km radius of site (%)	59.57	3.67	64.18	6.22	60.95	3.20
latitude[b]	232534	7442	158521	7735	262305	3848

[a] *Values are mean and SE for sites on loamy (n = 36), sandy (n = 19), and shallow (n = 23) soils.*
[b] *Measured in Universal Transverse Mercator.*

Regression Models

We used stepwise logistic regression (PROC LOGISTIC, SAS Institute, Inc. 1990) to examine the influence of local and landscape variables (Table 1) on species occurrence. We considered a species present at a site if it occurred on two or more surveys in any year. This selection criterion made us less likely to include species passing through a site but not breeding. Brown-headed Cowbirds were the single exception to this rule and were considered present at a site if they occurred on any census because their frequency of occurrence was biased highly to single events (W.M.V., unpublished data). Models were developed for species present at >25% of possible sites. We examined the Akaike information criterion (AIC) at each step of the modeling process to evaluate further the contribution of each variable to the overall model (Hosmer & Lemeshow 1989).

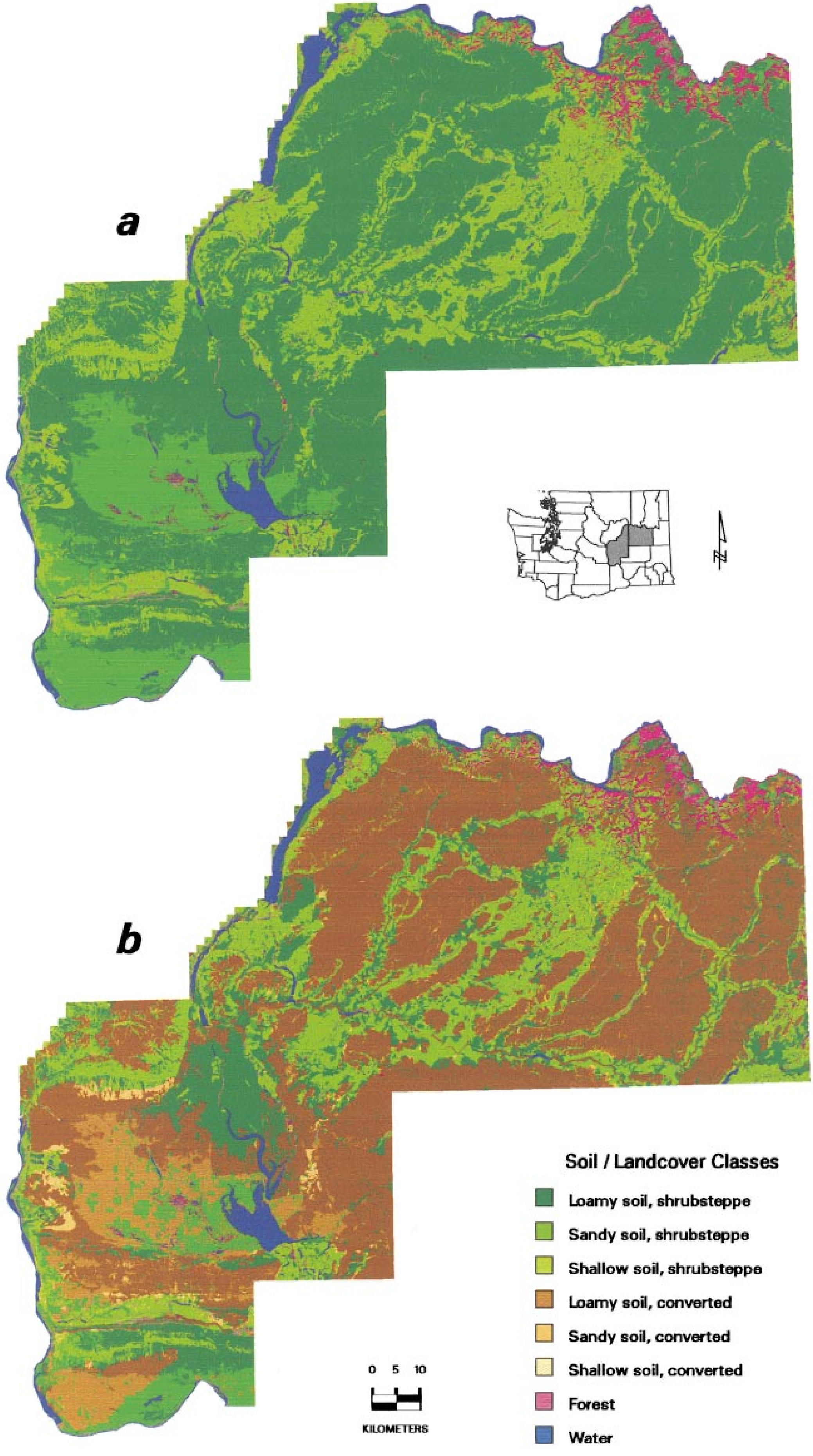
We tested the validity of the final logistic regression models using an independent data set from within the study area. This data set comprised survey results from 45 500-m transects sampled for ≥2 years between 1988 and 1990 by methods identical to those we employed in our census. Sites selected in the earlier census were not stratified by soil class, and 12 of the 45 transects included two soil classes. We applied the same criteria for species presence to the independent data set and used habitat and landscape data from each transect to model the predicted outcome. We used the proportion of correct outcomes from the 45 independent transects as an indication of each model's validity for the study area (Capen et al. 1986). Prior probabilities of group membership were set at 0.5. Model predictions for each transect were classified as either correct, in that the outcome matched that observed in the field; false negative, in that the outcome erroneously predicted absence; or false positive, in that the outcome erroneously predicted presence. We compared the proportion of independent sites correctly classified by each model to that expected by a chance model (Morrison 1969) using chi-square analysis with Yates's correction for continuity.

Results

Soil and Landcover Relationships

Overlaying GIS soil and landcover layers for the study site revealed a striking difference between the historic and the current distribution of shrubsteppe among soil classes (Fig. 2). Historically, most of the shrubsteppe in the analysis area was on deep soils (62.8% on loamy soils, 12.4% on sandy soils), whereas 24.8% was on shallow soils. We found that extant shrubsteppe occurred

Figure 2. The (a) historical and (b) present distribution of shrubsteppe communities among three soil classes in Lincoln and Grant Counties, Washington. Converted landcover classes are primarily agricultural fields.


a
b
Soil / Landcover Classes
Loamy soil, shrubsteppe
Sandy soil, shrubsteppe
Shallow soil, shrubsteppe
Loamy soil, converted
Sandy soil, converted
Shallow soil, converted
Forest
Water
0 5 10
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predominantly on shallow soils (49.6%), that loamy soil communities made up 36.5% of the shrubsteppe, and that the proportion on sandy soils had remained relatively unchanged (12.8%). Seventy-five percent of loamy-soil shrubsteppe in the analysis area had been converted to agriculture or other land uses. The only large area of loamy-soil shrubsteppe remaining (Fig. 2b) was generally unsuitable for cropland (Gentry 1984). Over half the sandy-soil communities had been converted (55.5%), whereas shallow soils were the least converted (13.9%). Although digital soils data were not available for other counties at the time of our analysis, this pattern likely holds for most of the study area. Moreover, the percent loss of loamy-soil shrubsteppe in parts of the study area probably exceeded values reported here.

Site Characteristics

The first three axes of the principal components analysis explained 78% of the variation in vegetation variables among survey sites. Principal component one (PC1) had high positive loadings for percent cover in annual forbs, percent cover in perennial grass, total cover of herbaceous vegetation, and mean height of herbaceous vegetation (Table 2). Principal component two (PC2) had high positive loadings for percent cover in perennial grass, percent cover in perennial forbs, and total shrub cover, and high negative loadings for percent cover in annual grass and percent cover in annual forbs (Table 2). Principal component three (PC3) represented a gradient for shrub height and total shrub cover. Percent cover in shrubs was correlated with cover of sagebrush ($r = 0.96$) and particularly with cover of big sagebrush ($r = 0.89$).

Trends in vegetation physiognomy among the three soil classes were evident in the bivariate plot of PC1 and PC2 (Fig. 3). Loamy sites generally scored high on both axes, indicating sites with more shrub cover and an herbaceous layer with overall greater height and cover, more perennial grasses and forbs, and fewer annual grasses. Sandy sites generally were lower on PC2 than were loamy and shallow sites, indicating lower percent cover in shrubs and perennial grasses and more cover of annual grasses. Shallow sites generally were lower on PC1 than loamy or sandy sites, indicating lower cover of perennial grasses and an herbaceous layer shorter in height and lower in percent cover. There was no distinction among soil classes in bivariate plots including PC3. Range condition did not show any obvious patterns in bivariate plots based on combinations of the first three principal components.

Bird Censuses and Abundance

We counted 93 species and 20,410 individuals over 3 years of censusing (Appendix). Most birds (85%) were detected within 100 m perpendicular to the transect. Brewer's Sparrows, Western Meadowlarks, and Horned Larks were the three most common species and made up over 50% of the total observations (Appendix; Table 3). We limited our analyses to the 15 most common species, achieving an abundance rating of ≥0.5 in one or more of the nine soil-range classes.

Comparison of abundances among the soil types and range conditions revealed significant main effects for 6 of the 15 species tested (Table 3). Brewer's Sparrows and Sage Sparrows were most abundant in loamy soils. Loggerhead Shrikes were most abundant in sandy soils, and Mourning Doves were most abundant in shallow soils. Western Meadowlarks and Sage Thrashers both were equally abundant in loamy and shallow soils and less abundant in sandy soils.

Abundance among range conditions was different for three species (Table 3). Sage Thrashers were least abundant in range of poor condition and were equally abundant in good and fair range conditions. The abundance of Brewer's Sparrows was significantly lower at sites in poor condition than at sites in fair condition, but it did not differ between fair and good sites and between good and poor sites. Sage Sparrows were most abundant in poor sites.

Interaction between soil type and range condition was significant for six species. Comparison of abundances among the nine combinations of soil type and range condition revealed distinct patterns for several species (Table 4). Abundances of Vesper Sparrows and Horned Larks were significantly lower in sandy soils than in loamy or shallow soils. Abundances of Savannah Sparrow and Horned Lark were greatest in shallow/poor sites, and Vesper Sparrows were most abundant in shallow/poor and in loamy/good sites.

Regression Models

Occurrence of seven species of breeding birds was significantly related to landscape and/or habitat variables measured at each site (Table 5). No model was attempted for the Western Meadowlark because it occurred on every census in every year. Latitudinal position of the site occurred in models for four species and was positively correlated with both elevation ($r = 0.90$) and annual precipitation ($r = 0.82$). Increasing latitude had a positive effect on the presence of all four species, indicating greater occurrence in the wetter, more productive sites. Percent cover of shrubsteppe within 5 km of the transect was the only landscape variable that occurred in a model. All three landscape variables were correlated ($r > 0.73$), and percent shrubsteppe within 5 km exhibited the greatest range and variability among sites. Higher means and lower ranges of values for the other two landscape variables (percent shrubsteppe

Table 2. Variable loadings on principal components for variables measured on 78 transects in shrubsteppe communities in eastern Washington.

Variable	*PC1*	*PC2*	*PC3*
Annual grass (% cover)	0.023901	−0.612929	0.073657
Annual forb (% cover)	0.353835	−0.385298	0.154115
Perennial grass (% cover)	0.405519	0.434833	−0.044597
Perennial forb (% cover)	0.253112	0.316057	−0.356396
Herbaceous vegetation (% cover)	0.577760	−0.214293	0.038745
Herbaceous vegetation (mean height)	0.545541	0.102373	0.106916
Shrub (% cover)	−0.109834	0.358718	0.567639
Shrub (mean height)	0.047253	0.042562	0.711808
Variance explained (%)	31	27	20

within 1 km and percent shrubsteppe within 3 km) likely were a function of the minimum area required to contain the census transect and the associated buffer of shrubsteppe. Percent shrubsteppe within 5 km was positively associated with occurrence of one species and negatively associated with occurrence of two species.

Sage Sparrows were more likely to occur at sites with more shrub cover and in landscapes with more shrubsteppe (Table 5; Fig. 4a). Shrub cover was more important than landscape in determining site use by Sage Sparrows, as indicated by its greater standardized parameter estimate (Table 5). Brewer's Sparrows occurred more frequently in the northern part of the study area and on sites with greater shrub cover (Table 5; Fig. 4b). Vesper Sparrows occurred more frequently in the northern part of the study area, on sites with greater shrub cover, and on sites with less cover of annual grasses (Table 5; Fig. 4c). Grasshopper Sparrows were more likely to be present at sites with greater cover in perennial grasses (Table 5).

As was the case with other shrubsteppe obligates, the regression model for Sage Thrashers contained a positive parameter for shrub cover (Table 5). The presence of Sage Thrashers was positively related to increasing latitude and negatively related to the proportion of shrubsteppe in the landscape (Fig. 4d). Horned Larks were more likely to occur at sites with lower shrub height and greater cover of perennial grasses (Table 5; Fig. 4e). The

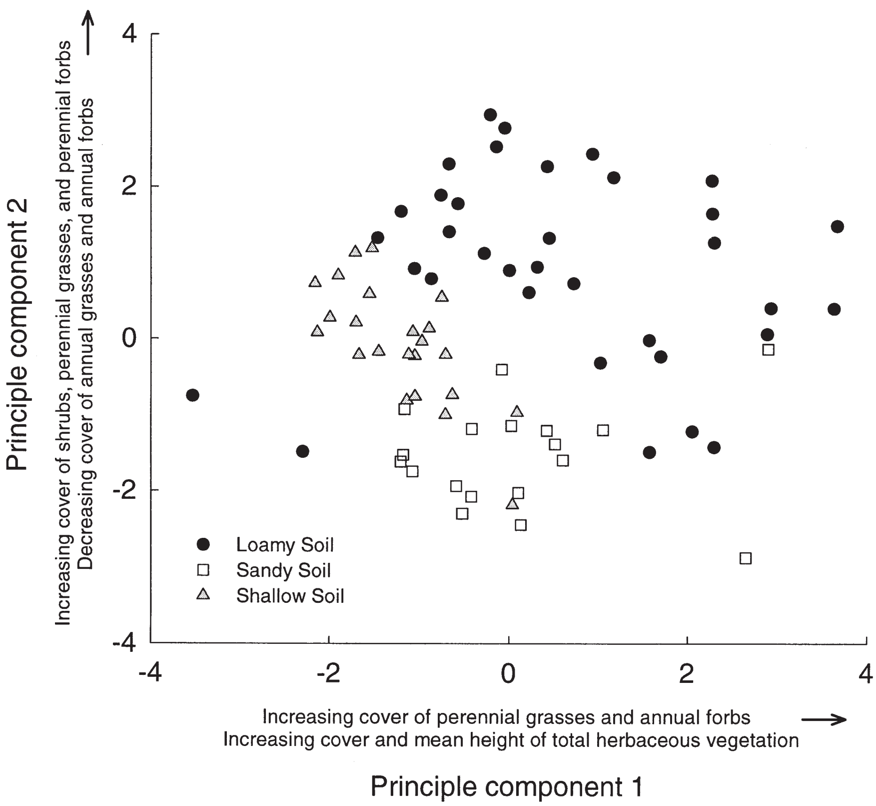


Figure 3. Principal components ordination of 78 sites stratified by soil type in shrubsteppe communities of eastern Washington. Ordination derived from vegetation data measured at each site.

Table 3. Mean abundance (SE) by soil type and range condition of the 15 most abundant species of breeding birds counted on transect surveys in shrubsteppe communities, eastern Washington, 1991–1993.[a]

	Soil type			Range condition		
Species[b]	loamy	sandy	shallow	good	fair	poor
Brewer's Sparrow	8.48 (0.59)A	1.70 (0.32)B	4.94 (0.38)C	6.09 (0.57)AB	6.61 (0.69)A	4.87 (0.56)B
Western Meadowlark	4.94 (0.37)A	4.14 (0.30)B	5.10 (0.32)A	4.92 (0.32)A	5.00 (0.29)A	4.50 (0.35)A
Horned Lark[c]	4.13 (0.31)	1.94 (0.31)	5.42 (0.54)	4.23 (0.41)	3.83 (0.49)	3.92 (0.36)
Vesper Sparrow[c]	3.02 (0.25)	0.42 (0.10)	3.51 (0.25)	3.10 (0.26)	2.59 (0.30)	2.04 (0.26)
Sage Sparrow	2.04 (0.25)A	1.18 (0.21)B	0.88 (0.15)B	1.01 (0.16)A	1.40 (0.20)A	1.93 (0.30)B
Sage Thrasher	1.78 (0.20)A	0.14 (0.05)B	1.37 (0.19)A	1.78 (0.28)A	1.37 (0.19)A	0.77 (0.13)B
Red-winged Blackbird[c]	1.19 (0.33)	0.77 (0.18)	0.73 (0.18)	1.27 (0.46)	1.09 (0.25)	0.59 (0.16)
Brewer's Blackbird	0.79 (0.22)	0.60 (0.17)	1.06 (0.29)	0.78 (0.16)	1.15 (0.36)	0.58 (0.14)
Grasshopper Sparrow[c]	1.01 (0.15)	0.49 (0.15)	0.75 (0.17)	0.73 (0.15)	0.96 (0.21)	0.74 (0.13)
Brown-headed Cowbird[c]	0.92 (0.12)	0.35 (0.14)	0.88 (0.17)	1.12 (0.19)	0.69 (0.14)	0.57 (0.11)
Savannah Sparrow[c]	0.52 (0.09)	0.70 (0.19)	1.16 (0.29)	0.74 (0.13)	0.73 (0.15)	0.78 (0.23)
Mourning Dove	0.56 (0.08)A	0.54 (0.18)A	0.91 (0.14)B	0.77 (0.13)A	0.63 (0.11)A	0.60 (0.13)A
Common Raven	0.56 (0.15)	0.40 (0.11)	0.39 (0.08)	0.30 (0.09)	0.31 (0.07)	0.73 (0.17)
Lark Sparrow	0.49 (0.11)	0.33 (0.09)	0.48 (0.14)	0.52 (0.14)	0.25 (0.08)	0.56 (0.12)
Loggerhead Shrike	0.29 (0.05)A	0.63 (0.11) B	0.39 (0.08)A	0.33 (0.07)A	0.51 (0.09)A	0.37 (0.06)A

[a] *Results of tests for significance among soil types and range conditions are presented only for species for which main effects were significant. Means followed by the same letter within either soil type or range condition were not significantly different (Fisher's exact test,* $p < 0.05$*). For example, the abundance of Brewer's Sparrow differed significantly among all three soil classes, whereas the abundance of Western Meadowlarks differed between loamy and sandy soils and between sandy and shallow soils but not between loamy and shallow soils.*
[b] *Species are listed in order of overall abundance across all sites.*
[c] *Significant interaction occurred between soil type and range condition (see Table 4).*

probability of encountering Brown-headed Cowbirds increased with latitude and decreased with percent shrubsteppe in the landscape (Fig. 4f). The model also indicated a positive relationship between the presence of cowbirds and cover of perennial grasses (Table 5).

Overall, the models performed well when applied to independent data from the study area. Five of six models correctly predicted occurrence of the species at ≥78% of 45 test transects (Table 5). The model for the Grasshopper Sparrow was built with data from the fewest number of used sites and did not classify sites correctly more than expected by chance (Table 5). Errors in assignment of used sites (false positive) by the Sage Sparrow model were relatively high at 50%; given that Sage Sparrows were present at only 20% of the independent sites, however, 50% correct classification is considerably greater than the 20% expected if assignment was based on chance (Morrison 1969). No test for model validity was possible for the Horned Lark because one of the variables in the model (shrub height) was not measured for the independent data set.

Discussion

Species Abundance

The abundance of numerous shrubsteppe birds in eastern Washington showed strong relationships with soil type and range condition, which likely resulted from the influence of soil characteristics and range history on the vegetation of these communities. Sage Sparrows and Brewer's Sparrows are strongly associated with big sagebrush (Wiens & Rotenberry 1981; Knick & Rotenberry 1995), and this shrub was most closely associated with loamy soils on our study sites. A suite of shrubsteppe birds (Brewer's Sparrow, Vesper Sparrow, Sage Thrasher) that commonly occur together in northern parts of the study area were largely absent from sandy sites, even those with adequate cover of big sagebrush. Most of the sandy sites were located in the southern portion of our study area and at low elevations where annual rainfall is lowest for the region. All three species occurred at higher elevations at this latitude in the study area (Rogers et al. 1988; W.M.V., unpublished data), locations where rainfall and plant productivity are more similar to those of sites in the north. These higher-elevation communities also generally have loamy or shallow soils (Wildung & Garland 1988), confounding any comparison. The lower occurrence of Vesper Sparrows on sandy sites may be related to their greater cover of annual grasses. Why Sage Thrashers and Brewer's Sparrows occurred infrequently on sandy sites remains unclear.

The abundance of only three species varied with range condition, all of them shrubsteppe obligates. Sage Thrashers and Brewer's Sparrows were least abundant on sites in poor condition, suggesting that they do best in less disturbed communities that approach climax conditions. In contrast, Sage Sparrows were most abundant on poor sites, but the amount of shrubsteppe in the landscape also was greatest at poor-condition sites. Because of its positive influence on the presence of Sage

Table 4. Mean abundance of breeding birds by soil-type and range-condition group for species with significant interactions between soil type and range condition derived from transect surveys in shrubsteppe communities, eastern Washington, 1991–1993.[a]

Species	*Code*[b] *and mean (SE)*								
Vesper Sparrow	SHP	LG	SHG	LF	SHF	LP	SF	SP	SG
	4.87 (0.74)A	4.56 (0.36)A	3.15 (0.27)B	3.12 (0.55)B	3.11 (0.35)B	2.08 (0.30)C	0.47 (0.19)D	0.41 (0.16)D	0.40 (0.19)D
Savannah Sparrow	SHP	SG	SHF	SHG	LF	SF	LG	SP	LP
	2.33 (1.23)A	1.07 (0.45)B	0.96 (0.23)B	0.70 (0.16)B	0.61 (0.20)B	0.6 (0.47)B	0.59 (0.15)B	0.56 (0.17)B	0.42 (0.12)B
Grasshopper Sparrow	LF	SHP	SG	LG	LP	SHF	SHG	SP	SF
	1.60 (0.41)A	1.53 (0.55)AB	1.00 (0.47)ABC	0.82 (0.20)ABC	0.71 (0.14)BC	0.59 (0.21)BC	0.48 (0.18)BC	0.37 (0.13)C	0.20 (0.15)C
Brown-headed Cowbird	SHG	LG	LP	SG	SHF	LF	SF	SHP	SP
	1.25 (0.33)A	1.11 (0.33)A	0.96 (0.18)A	0.87 (0.35)AB	0.82 (0.27)AB	0.70 (0.17)AB	0.47 (0.35)AB	0.33 (0.16)AB	0 (0)AB
Horned Lark	SHP	LG	SHF	SHG	LF	LP	SP	SG	SF
	7.73 (1.10)A	5.33 (0.71)B	5.03 (1.05)B	4.51 (0.58)B	4.30 (0.58)BC	3.35 (0.41)CD	2.82 (0.44)DE	1.73 (0.67)EF	0.60 (0.31)F
Red-winged Blackbird	LG	SF	SG	SHF	LF	LP	SHP	SHG	SP
	2.04 (1.12)A	1.53 (0.48)AB	1.27 (0.35)ABC	1.00 (0.39)ABC	0.97 (0.43)ABC	0.88 (0.28)BC	0.60 (0.26)BC	0.52 (0.22)BC	0.07 (0.05)C

[a]*Means followed by the same letter were not significantly different (Fisher's protected LSD test,* $p < 0.05$*). For example, the abundance of Vesper Sparrows in SHP did not differ significantly from their abundance in LG, but abundance in these two groups differed significantly from those in all other groups.*
[b]*LG, loamy soil/good condition; LF, loamy soil/ fair condition; LP, loamy soil/poor condition; SG, sandy soil/good condition; SF, sandy soil/fair condition; SP, sandy soil/poor condition; SHG, shallow soil/good condition; SHF, shallow soil/fair condition; SHP, shallow soil/poor condition.*

Sparrows, amount of Shrubsteppe in the landscape represents a possible confounding factor.

Regression Models

Although soil type and range condition influenced the abundance of some shrubsteppe birds, species occurrence was related mainly to vegetation structure, latitude, and characteristics of the landscape. Shrub cover was an important variable in the models for three shrubsteppe obligates, a relationship that has been documented in studies of both species abundance (Wiens & Rotenberry 1981) and species occurrence (Knick & Rotenberry 1995). Big sagebrush was the dominant shrub on most of our sites and was highly correlated with shrub cover, likely driving this relationship. Other shrub species occurred at lower abundance on our sites and failed to enter the models as separate variables, suggesting that they were of relatively little importance to the birds we considered. Vesper Sparrows also were positively associated with shrub cover on our study area and were frequently seen using shrubs as singing posts, although they are generally considered a grassland species. Wiens and Rotenberry (1981) also reported a positive association between shrub cover and the abundance of Vesper Sparrows.

Characteristics of the landscape surrounding a survey site can influence species presence or absence (Knick & Rotenberry 1995; Bolger et al. 1997). On our study area, percent cover of shrubsteppe within 5 km was related significantly to the occurrence of three species. Sage Sparrows occurred more frequently on sites embedded in a matrix dominated by shrubsteppe, indicating a negative relationship with fragmentation. A similar relationship was reported in Idaho, where the occurrence of Sage Sparrows increased with increasing area of sagebrush patches and decreasing fragmentation (Knick & Rotenberry 1995). Recent research in Washington suggests that Sage Sparrows are area-limited and nest only in relatively large blocks of shrubsteppe; with territories averaging <2 ha, however, the reasons for this are not clear (W.M.V., unpublished data). Sage Thrashers on our study area exhibited a positive relationship with fragmentation, occurring more frequently when shrubsteppe made up less of the landscape around the study plot. Sage Thrashers in Washington showed no indication of being area-limited and frequently were found nesting on small shrubsteppe fragments (<10 ha) in an agricultural matrix (W.M.V., unpublished data). In contrast, Sage Thrashers in extensive shrubsteppe in Idaho, where big sage communities were fragmented by fire and subsequent cheatgrass invasion, occurred more frequently in sites with less fragmentation of sagebrush (Knick & Rotenberry 1995). The different responses of Sage Thrashers to fragmentation may be related to differences in the land-

Table 5. Parameters for logistic regression models of species occurrence derived from vegetation and landscape variables at shrubsteppe sites, and results of model validation at independent sites, eastern Washington.

				Occurrence on sites (%)[a]		*Classification results (%)*[b]		
Species and variable	*Wald* χ^2	p	*Standardized estimate*	*model*	*independent*	*correct*	*false negative*	*false positive*
Horned Lark				87	91	—	—	—
perennial grass	7.35	0.0067	1.387					
shrub height	4.72	0.0298	−0.626					
Sage Thrasher				47	36	82	28	11
latitude	14.03	0.0002	1.745			$p < 0.005$		
shrubsteppe (5 km)	8.57	0.0034	−0.868					
shrub cover	6.9	0.0086	0.782					
Brewer's Sparrow				85	60	84	18	14
latitude	8.49	0.0036	1.951			$p < 0.005$		
shrub cover	4.02	0.0447	1.164					
Vesper Sparrow				73	62	80	25	17
annual grass	7.86	0.005	−0.898			$p < 0.005$		
latitude	8.52	0.0035	0.869					
shrub cover	3.15	0.076	0.517					
Sage Sparrow				49	20	82	9	50
shrub cover	12.56	0.0004	0.611			$p < 0.1$		
shrubsteppe (5 km)	5.19	0.0226	0.349					
Grasshopper Sparrow				37	49	60	43	30
perennial grass	7.78	0.0053	0.405			$p < 0.25$		
Brown-headed Cowbird				73	62	78	18	23
latitude	12.84	0.0003	0.674			$p < 0.005$		
perennial grass	4.75	0.0292	0.502					
shrubsteppe (5 km)	5.46	0.0194	−0.456					

[a] *Percentage of sites with species present on model development (*n *= 78) and independent (*n *= 45) sites.*
[b] *Percentage of independent sites correctly classified by model and false negative (predicted to occur by model but not present on independent site) and false positive (predicted not to occur by model but present on independent site) classification errors. Probability (*p*) values indicate probability that a chance model would produce equal or better classification rates on the independent data set. Dash indicates classification test not performed; variable in model (shrub height) not measured in independent data set.*

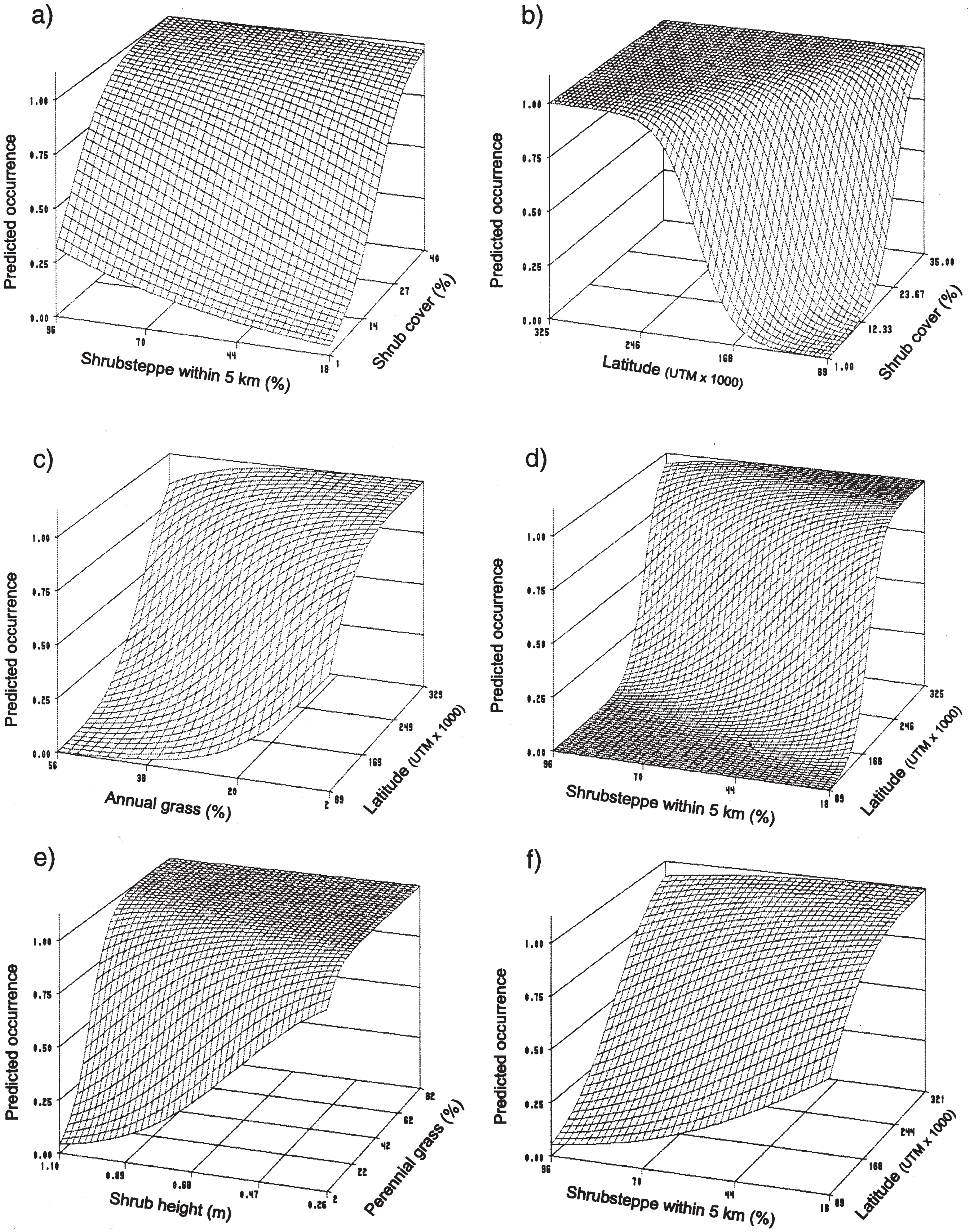
scape matrix between these two areas and warrant further investigation.

Brown-headed Cowbirds on our study area were associated with more fragmented landscapes, a result similar to findings from forest communities (Gates & Gysel 1978; Brittingham & Temple 1983; Robinson et al. 1995) and grassland communities (Johnson & Temple 1990). More frequent occurrences of Brown-headed Cowbirds suggest that birds nesting in fragmented shrubsteppe landscapes are exposed to greater potential rates of parasitism (Brittingham & Temple 1983). The model also indicates that cowbirds occur more frequently in communities with greater cover of perennial grass and in the northern, more productive sites. This may be related to the greater availability of potential hosts: Sage Sparrows, Brewer's Sparrows, and Vesper Sparrows were the most frequently parasitized species in Washington's shrubsteppe (Vander Haegen & Walker 1999), and the latter two species occurred more frequently in northern parts of the study area.

Implications for Bird Conservation in Shrubsteppe

The pattern of shrubsteppe conversion to agriculture in Washington has resulted in a disproportionate loss of deep-soil communities and a fragmented landscape with few extensive tracts of shrubsteppe. Our results suggest that both these changes in the historic landscape have had detrimental effects on numerous shrubsteppe species. Moreover, they indicate that habitat loss as measured for shrubsteppe ecosystems as a whole might not reflect the full loss to shrubsteppe species: the landscape for area-sensitive species and for species with an affinity for loamy-soil communities has changed considerably more than the overall loss of shrubsteppe would indicate. Sage Sparrow populations in particular, with

Figure 4. Influence of local and landscape variables on the predicted occurrence of shrubsteppe birds in eastern Washington. Data derived from logistic regression models for (a) Sage Sparrow, (b) Brewer's Sparrow, (c) Vesper Sparrow, (d) Sage Thrasher, (e) Horned Lark, and (f) Brown-headed Cowbird. Values on the horizontal axes were limited to the range observed on the survey sites. Latitude was measured as Universal Transverse Mercator.


a)
Predicted occurrence
1.00
0.75
0.50
0.25
0.00
Shrubsteppe within 5 km (%)
96
70
44
18
Shrub cover (%)
1
14
27
40
b)
Predicted occurrence
Latitude (UTM x 1000)
325
246
168
89
Shrub cover (%)
1.00
12.33
23.67
35.00
c)
Predicted occurrence
Annual grass (%)
56
38
20
2
Latitude (UTM x 1000)
89
169
249
329
d)
Predicted occurrence
Shrubsteppe within 5 km (%)
96
70
44
18
Latitude (UTM x 1000)
89
168
246
325
e)
Predicted occurrence
Shrub height (m)
1.10
0.89
0.68
0.47
0.26
Perennial grass (%)
2
22
42
62
82
f)
Predicted occurrence
Shrubsteppe within 5 km (%)
96
70
44
18
Latitude (UTM x 1000)
89
166
244
321

both an affinity for loamy-soil communities and an adverse response to fragmentation, likely have experienced considerable declines attributable to these changes in the landscape.

Although the species we considered are likely associated with soil communities by the vegetation that these soils support, other species are tied to deep-soil communities by the structure provided by the soil itself. Burrowing Owls, badgers (*Taxidea taxus*), and pygmy rabbits (*Brachylagus idahoensis*) depend on deep soils for their burrows. These species and others that depend on deep soil shrubsteppe communities also are at risk from the historic and current trends in land conversion.

Changes to the vegetation of extant shrubsteppe have resulted from excessive livestock grazing, introduced exotic vegetation (Branson 1985), and changes in the fire regime following invasion by cheatgrass (Mack 1981; Whisenant 1990). Our results suggest that, as grazing and invasion by exotics reduces the cover of perennial grasses, bird species associated with this element of the plant community will decline. Similarly, as sites become dominated by cheatgrass and shrubs are eliminated by increasing fire frequency (Whisenant 1990), birds associated with the shrub component of the community will decline. Exclusion of shrubsteppe obligates from fire-created annual grasslands has been documented for former sagebrush communities on Idaho's Snake River Plain (Knick & Rotenberry 1995). Our results are based on measures of species occurrence and abundance, and such measures do not necessarily reflect the reproductive value of the habitat or landscape (Van Horne 1983; Vickery et al. 1992). Research is needed on the effects of habitat and landscape variables on the productivity of birds in shrubsteppe ecosystems.

Shrubsteppe communities on deep soils in Washington continue to be converted to agricultural fields and orchards, and vegetation on extant shrubsteppe continues to change as a result of excessive livestock grazing and invasion by exotic plants. Furthermore, much of Washington's shrubsteppe, particularly low-elevation sites on the Columbia River Plain, are at risk of conversion to annual grasslands through an accelerated fire cycle (Quigley & Arbelbide 1997). Because these factors act to further fragment and alter the character of the remaining shrubsteppe, species dependent on this community will be limited to fewer and more fragmented sites. In the short term, conservation practices that emphasize retention of deep-soil shrubsteppe communities and that reduce further fragmentation will be critical to the maintenance of avian biological diversity in this system. If fragmentation is to be reversed and the extent of deep-soil shrubsteppe communities increased on the landscape, restoration of annual grasslands and low-productivity agricultural lands will be necessary.

In the state of Washington, the Conservation Reserve Program (CRP) currently represents the only extensive effort to restore shrubsteppe communities. Under the CRP, agricultural fields of marginal productivity are removed from production for 10 years and planted to tame bunch grasses, with sagebrush frequently seeding in from adjacent native habitat. There are over 475,000 ha of CRP–enrolled land in Washington (R. Hamilton, personal communication). Several grassland-associated passerines nest in CRP fields (Berthelsen & Smith 1995; Patterson & Best 1996), as do Sage Grouse (M. A. Schroeder, personal communication) and Sharp-tailed Grouse (McDonald 1998). Expansion of the CRP with an emphasis on planting native species has the potential to restore continuity to large blocks of shrubsteppe, at least in the short term. More permanent means of restoring deep-soil communities should be pursued.

Because of their inherent poor value for farming, shallow-soil communities are in less danger of conversion but are susceptible to changes in vegetation that result from overgrazing. Conservation practices that prevent overgrazing, reduce or eliminate the spread of exotic plants, and encourage restoration of degraded range on shallow soils likely will help maintain or improve their value to shrubsteppe birds.

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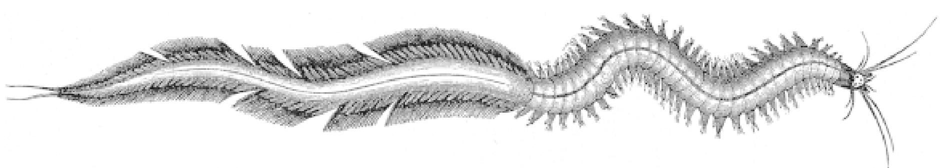

Appendix

Birds counted on surveys in shrubsteppe communities, eastern Washington, 1991–1993.[a]

Common name	*Scientific name*	*Total count*
Brewer's Sparrow	*Spizella breweri*	3720
Western Meadowlark	*Sturnella neglecta*	2872
Horned Lark	*Eremophila alpestris*	2274
White-crowned Sparrow[b]	*Zonotrichia leucophrys*	1763
Vesper Sparrow	*Pooecetes gramineus*	1357
Sage Sparrow	*Amphispiza belli*	783
Sage Thrasher	*Oreoscoptes montanus*	600
Cliff Swallow	*Hirundo pyrrhonota*	333
Red-winged Blackbird	*Agelaius phoeniceus*	312
Grasshopper Sparrow	*Ammodramus savannarum*	271
Brown-headed Cowbird	*Molothrus ater*	223
Brewer's Blackbird	*Euphagus cyanocephalus*	211
Savannah Sparrow	*Passerculus sandwichensis*	201
Mourning Dove	*Zenaida macroura*	184
European Starling	*Sturnus vulgaris*	139
Loggerhead Shrike	*Lanius ludovicianus*	134
Common Raven	*Corvus corax*	122
Lark Sparrow	*Chondestes grammacus*	119
American Pipit[b]	*Anthus rubescens*	105
Long-billed Curlew	*Numenius americanus*	94
Violet-green Swallow	*Tachycineta thalassina*	54
Black-billed Magpie	*Pica pica*	50
American Robin	*Turdus migratorius*	50
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	48
Rock Dove	*Columba livia*	41
Northern Harrier	*Circus cyaneus*	40
Barn Swallow	*Hirundo rustica*	36
Killdeer	*Charadrius vociferus*	35
Chukar	*Alctoris chukar*	34
Ring-necked Pheasant	*Phasianus colchicus*	27
California Quail	*Callipepla californica*	26
Rock Wren	*Salpinctes obscoletus*	21
Gray Partridge	*Perdix perdix*	19
Sage Grouse	*Centrocercus urophasianus*	12
Western Kingbird	*Tyrannus verticalis*	12
Red-tailed Hawk	*Buteo jamaicensis*	10
Burrowing Owl	*Athene cunicularia*	9
Sharp-tailed Grouse	*Tympanuchus phasianellus*	7
Say's Phoebe	*Sayornis saya*	5
Ferruginous Hawk	*Buteo regalis*	4

[a] *Only landbirds that occurred more than one time on one or more transects in any year are listed.*
[b] *Nonbreeding migrant.*