Response of Avian Communities to Historic Habitat Change in the Northern Chihuahuan Desert

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Abstract: *Throughout much of the northern Chihuahuan Desert, the grasslands that were widespread at the time of European settlement have been replaced by desert shrublands. Little is known about the effects of this change on avian communities. We analyzed historic U.S. Government Land Office records to assess large-scale changes in vegetation cover from the 1880s to the present day. We studied vegetation and avian communities in one grassland habitat type and four desert shrubland habitat types to examine (1) how breeding-bird communities may have changed in response to habitat conversion from grassland to desert shrubland and (2) whether breeding-bird communities differ among the four desert shrubland habitat types that compose Chihuahuan Desert scrub in this region. To estimate the characteristics of 1880s black grama (*Bouteloua eriopoda*) grassland, we focused on plots located within extensive patches of present-day black grama and compared the avian communities found there with those in desert shrubland. Species richness was higher in desert shrubland than grassland. Among the desert shrubland habitat types, species richness was consistently highest in mesquite. Avian abundance patterns differed among the four desert shrubland habitat types. At least 30% of the avian community in each habitat pair was distinct. Conversion of grassland to shrubland in south-central New Mexico has likely been accompanied by a major turnover in the avian community. Remaining tracts of black grama provide habitat for species that may be uniquely adapted to the northern Chihuahuan Desert and should be protected.*

Respuesta de las Comunidades de Aves a Cambios Históricos de Hábitat en el Norte del Desierto de Chihuahua

Resumen: *En la mayor parte del norte del Desierto de Chihuahua, los extensos pastizales presentes en el momento del asentamiento de los europeos han sido reemplazados por chaparrales de desierto. Se sabe poco de los efectos de este cambio sobre las comunidades de aves. Analizamos los registros históricos de la Oficina de Tierras del gobierno de E.U.A. para evaluar los cambios a gran escala en la cobertura de la vegetación desde la década de 1880 hasta nuestros días. Estudiamos la vegetación y las comunidades de aves en un tipo de hábitat de pastizal y en cuatro tipos de hábitat de chaparral de desierto para examinar 1) como pudieron cambiar las comunidades de aves debido a la conversión del hábitat de pastizal a chaparral y 2) si las comunidades de aves difieren entre los cuatro tipos de hábitat de chaparral que componen el Desierto de Chihuahua en esta región. Para estimar las características del pastizal de grama negra (*Bouteloua eriopoda*) en 1880, nos concentramos en parcelas localizadas dentro de extensos fragmentos de grama negra reciente y comparamos las comunidades de aves con las del chaparral del desierto. La riqueza de especies fue mayor en el chaparral que en el pastizal. Entre los tipos de hábitat de chaparral, la riqueza de especies fue consistentemente más alta en el mezquital. Los patrones de abundancia de aves difirieron entre los cuatro tipos de hábitat de chaparral. Por lo menos 30% de la comunidad de aves en cada par de hábitats fue diferente. Es muy probable que la conversión de pastizal a chaparral en el centro-sur de Nuevo México ha sido acompañada por un cambio en la comunidad de aves. Los fragmentos remanentes de grama negra proporcionan hábitat para especies que pudieran estar adaptadas especialmente al norte del desierto de Chihuahua y deben ser protegidos.*

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Introduction

Much of the northern Chihuahuan Desert has experienced an extreme shift in vegetation cover over the last 150 years. Prior to European settlement, black grama (*Bouteloua eriopoda*) grassland was the dominant habitat type (Dick-Peddie 1993). The extent of black grama grassland has declined sharply, whereas creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) shrublands have expanded (e.g., Buffington & Herbel 1965; Gross & Dick-Peddie 1979). Conversion of black grama to mesquite was recognized as early as 1922 (Jardine & Forsling 1922, cited in Campbell 1929), leading to concerns about the loss of high-quality grass and a concomitant increase in low-quality shrub forage (e.g., Leopold 1951; Hennessy et al. 1983; Warren et al. 1996).

The spatial extent of the vegetation shift across the northern Chihuahuan Desert was large. For example, 31 townships in southern New Mexico—which were predominantly grassland at the time of the original U.S. General Land Office survey (1858)—had <5% grass cover in 1969 (York & Dick-Peddie 1969). In 1858, abundant grass cover was present on >90% of the Jornada Experimental Range (58,000 ha) in southern New Mexico, but by 1963 <25% of the area had abundant grass cover and none of the remnant grassland was shrub-free (Buffington & Herbel 1965).

The shrubs that replaced grassland include several species. Mesquite and creosotebush have undergone extensive range expansion (Dick-Peddie 1993) and predominate among the current shrub communities. Sandsage (*Artemisia filifolia*), whitethorn acacia (*Acacia neovernicosa*), and tarbush (*Flourensia cernua*) have also likely undergone range expansion (W. A. Dick-Peddie, personal communication; R. Spellenberg, personal communication). Although it is generally assumed that patterns of vegetation change are consistent throughout southern New Mexico, there is little information specifically related to military lands in south-central New Mexico (127,940 km^2) (but see Kenmotsu 1977).

Several previous researchers studying the avian community in the northern Chihuahuan Desert have applied the term *desert scrub* generally to all desert shrub–dominated upland areas without differentiating among shrub habitats (Dixon 1959; Raitt & Pimm 1976; Kozma & Mathews 1997). The bird community in one habitat type, creosotebush, has been portrayed as "representative of southern New Mexico desert communities" (Raitt & Maze 1968). This may be a simplification of the diversity of the northern Chihuahuan Desert ecosystem. At the Jornada Experimental Range in 1963, creosotebush-dominated communities made up only 14% of the desert shrubland communities (Buffington & Herbel 1965).

We studied vegetation characteristics and avian communities in five shrub- and grass-dominated habitat types in the northern Chihuahuan Desert. We analyzed historic vegetation data to assess large-scale habitat changes on a military reserve in south-central New Mexico from the 1880s to the present day. Specifically, we examined (1) how breeding-bird communities may have changed in response to habitat conversion from grassland to desert shrubland and (2) whether breeding-bird communities in desert-shrub ecosystems differ among different shrub types. We sought to improve understanding of present-day avian community structure and to predict the effects of future habitat alterations on avian communities in this region and perhaps the greater northern Chihuahuan Desert.

Study Area

We conducted this study from 1996 through 1998 on approximately 282,500 ha (2825 km^2) of the Ft. Bliss Military Reserve in New Mexico (Fig. 1). The study was confined to the Tularosa Basin and the western edge of Otero Mesa within McGregor Maneuver Range. This area lies within the arid basin-and-range physiographic region of south-central New Mexico (Hawley 1975) and is representative of the northern Chihuahuan Desert.

The climate is arid, and evapotranspiration exceeds rainfall (Pieper et al. 1983). Average maximum and minimum temperatures in July are 35.3° C and 18.6° C, respectively, and annual precipitation averages 25.8 cm (Western Regional Climate Center 1998). Rains are concentrated from July through September (Minnick & Coffin 1999), when about 50% of the annual total occurs as intense, highly localized thunderstorms of short duration (Hennessy et al. 1983). The nature of summer rainstorms results in much of the water being lost through rapid runoff and evaporation (Pieper et al. 1983). Frequent wind from the southwest further contributes to evaporation.

Habitat types included in this study were black grama grassland, sandsage, mesquite, creosotebush, and whitethorn. Although other distinct habitat types were present, they occurred in patches too small to meet our minimum requirements for plot size.

Black grama grasslands include black grama, scattered shrubs, cane cholla (*Opuntia imbricata*), and *Yucca* sp. In our study area they occur at about 1500 m of elevation, occupying level to gently rolling areas within the irregular terrain between the escarpment defining the western edge of Otero Mesa and the eastern edge of the Tularosa Valley. They occur on shallow, well-drained, gravelly alluvium of weathered limestone and carbonate fragments interspersed with small amounts of calcareous eolian sediment (Derr 1981).

Whitethorn acacia habitat intergrades with black grama and occurs at the same elevation. This open-desert shrubland type occupies limestone outcrops intermingled with shallow, well-drained soils (Derr 1981) and includes several species of shrub and cacti as subdominant elements. The most abundant shrub, whitethorn acacia, is a spines-

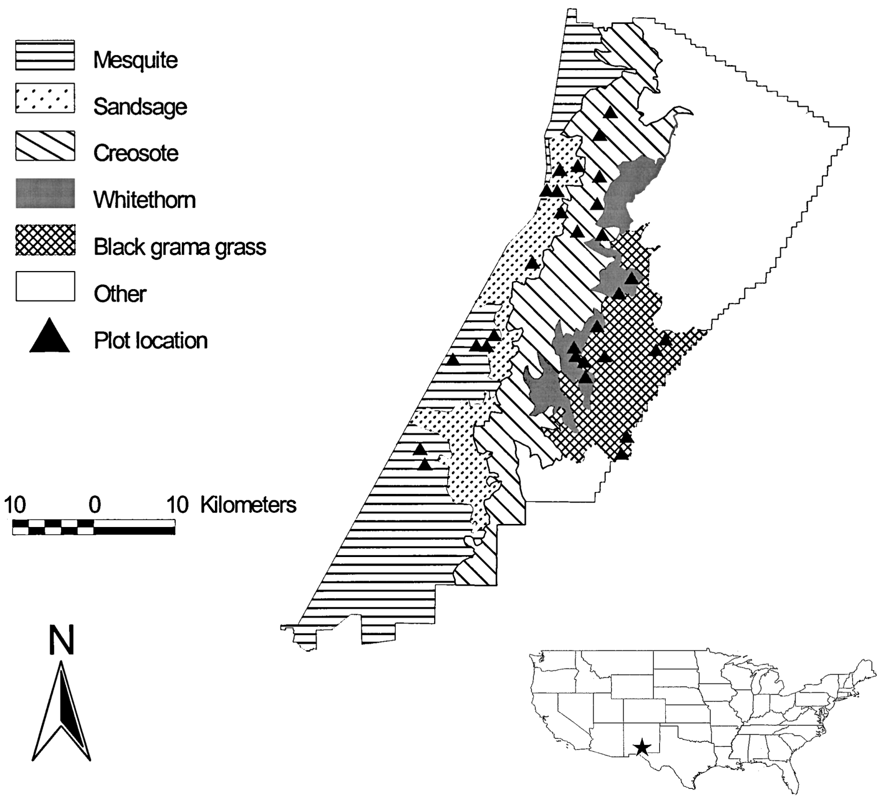

Figure 1. Map of study area in the McGregor Range, Ft. Bliss, New Mexico.

cent plant with relatively thin stems and an open-growth form.

Creosotebush-dominated habitat is low in shrub-species richness and has a high component of bare ground. Creosotebush has an open-growth form and occurs frequently in stands of uniform height, occasionally punctuated by small groups of taller yucca or mesquite plants. It occurs on deep, well-drained, strongly calcareous, and moderately alkaline soils on the lower parts of alluvial fans, fringes of fans, and bottomlands (Derr 1981).

At its western edge creosotebush grades into sandsage habitat. Sandsage is a dominant species that usually occurs as a short shrub with a relatively dense life form. Soaptree yucca (*Yucca elata*), little leaf sumac (*Rhus microphylla*), and mesquite all occur as subdominants. The habitat type occurs on gently rolling land composed primarily of loose sand.

Mesquite habitat occurs at the lowest elevation in the center of the Tularosa Valley. On McGregor Range, mesquite occurs as two growth forms, tree and shrub. The multistemmed shrub, which entraps drifting sand, forming "coppice dunes" (Hennessy et al. 1983), is predominant. These dunes are typically 7 × 5 × 2 m in size but can attain sizes of 20 × 10 × 3.5 m. Slopes on the sides of dunes can be up to 80%. Soils are deep and well- to excessively drained (Derr 1981). Interdunal areas are sparsely vegetated with small shrubs and soaptree yucca. Cover of forbs and grasses is low.

Methods

Plot Selection and 1880s Landcover

We used a Landsat thematic-mapper landcover classification (Mehlhop et al. 1996) to identify sites with relatively homogeneous cover in the four desert shrubland habitats and one grassland habitat. Within each of these classes we randomly placed six 1200 × 900 m plots (108 ha each) with a surrounding buffer of at least 50 m of continuous habitat.

We used U.S. General Land Office territorial survey records (Bureau of Land Management, Santa Fe, New Mexico) to reconstruct the 1880s vegetation cover for our plots. New Mexico territorial survey records have been used to examine the degree of shrub encroachment at the Jornada Experimental Range (Buffington & Herbel 1965), to reconstruct vegetation patterns of the 1880s across New Mexico (Gross & Dick-Peddie 1979), and to examine landcover change in two townships on McGregor range (Kenmotsu 1977). The original land surveyors provided a vegetation description of each section line (1.6-km interval) they traversed and described each township's general character, including grass cover, shrubs, and soils. The surveyors' vegetation description evaluated the land's potential for growing hay and grazing livestock. The plant names they used were fairly consistent but differed somewhat from current nomenclature. We followed York and Dick-Peddie (1969) and used expert opinion (W.A. Dick-Peddie, personal communication; R. Spellenberg, personal communication). We examined 1880s landcover descriptions of section lines that traversed or were immediately adjacent to our study plots, and summaries written by the surveyors for those townships in which our plots were located. We qualitatively compared these reconstructions with current vegetation measurements from the plots, making a direct comparison of landcover in the 1880s with that of the present day in the same geographic location. We assumed that present-day black grama patches do not differ qualitatively from those in the 1880s and that use of black grama grassland by the avian community has not changed since the 1880s.

Habitat Surveys

We used data gathered at each of 12 points on a 3 × 4 sampling grid to determine vegetation characteristics on each plot. Gridpoints were located 300 m apart to ensure even coverage across the plot. At each gridpoint we established four vegetation subsampling points. We centered the first on the grid point and the remaining points 30 m away. The direction of the second subsample was random, whereas the third and fourth were at an angle of 120° from the preceding subsample. We sampled vegetation once in either 1997 or 1998.

For each gridpoint at each of the four subsampling points, we estimated percent cover of seven groundcover categories at five sites (four randomly located sites plus the center). The resulting 20 values were averaged to obtain a mean sample-point cover value, and the 12 sample-point values were averaged to obtain a mean plot-cover value. We used the three outer subsampling points at each grid point to estimate the density of shrubs and *Yucca* sp., employing a modification of the point-center quarter method in which the search radius is truncated (Warde & Petranka 1981). Foliage height diversity (FHD) was estimated (Wiens & Rotenberry 1981; Mills et al. 1991) at four randomly located sites at each subsampling point and averaged as described above for groundcover.

We assumed that average cover of vegetation was consistent between years. This assumption is probably valid for shrubs and perennial grasses (Rotenberry & Wiens 1980) but may not be true for forbs and annual grasses. In deserts, however, plant growth responds most strongly to precipitation (Polis 1991), and precipitation was minimal before 7 June during the 3 years of the study, by which time approximately 90% of vegetation sampling was completed.

Bird Surveys

Using point counts, we surveyed breeding birds on the 12-point (3 × 4) grid on each plot between 1 May and 7 June, 1996 through 1998 (Martin et al. 1997). All birds heard or observed ≤150 m from each point were recorded by species. We surveyed on mornings with low wind (<12 km/hour) and no rain, beginning within 0.25 hours of sunrise and ending within 3.5 hours after sunrise. Counts lasted 10 minutes at each point. We sampled each site every 6–10 days four to five times each year. We surveyed all plots in each habitat once, before the next survey round began. Observers followed a different path each time they surveyed a plot to minimize potential bias at particular points resulting from bird activity correlated with time of day.

We controlled for individual bias by having multiple observers conduct counts at each plot. We placed flags every 50 m throughout the plot to facilitate distance estimation during point counts. In the week prior to sampling, one or more practice point counts from each individual was compared with the count of an experienced observer and was rated on its precision, bias, and accuracy.

For each sampling day, the counts from the 12 points on each plot were summed. From the four or five counts each season, the average of the highest two counts of each species on each plot was used as the annual estimate of abundance. This method compensates for the general underestimation of individuals by point counts (DeSante 1981) and for asynchrony in the nesting cycle in the avian community. Some long-distance migrant species were still arriving at the time that some resident and short-distance migrants had already begun nesting. At the time of the surveys, various species were at different stages in their nesting cycle, with concomitant differences in detectability. For example, unmated males of some species sing more frequently than mated males (Hayes et al. 1985). Taking the average of the two highest counts also mitigated the effects of migrant pulses that briefly but spectacularly augmented the counts of breeding species (Redmond et al. 1981).

Classification of Habitats

The initial selection of plots within each habitat was based on visual classification during ground reconnaissance. Using *K*-means partitioning to assign plots to habitat types based on measured vegetation variables, we conducted a second classification of the desert shrubland habitats subsequent to field sampling. The analysis was conducted among all grid points in all desert shrubland plots. The *K*-means partitioning could not be conducted directly because the matrix of vegetation measurements contained too many double zeros, indicating the absence of a plant species at both grid points being compared (Legendre & Vaudor 1991). To overcome this problem we assessed the resemblance of abundance patterns of 20 plant species among the grid points by calculating a matrix of association using the coefficient of divergence (Legendre & Legendre 1998). The matrix was then used in principal coordinate analysis (PCO), which reorganizes, in reduced space, the position of every sample point (Legendre & Vaudor 1991). Following PCO, *K*-means partitioning grouped plots into four clusters, corresponding to whitethorn, creosotebush, sandsage, and mesquite habitat.

This analysis corroborated the visual classification of 23 of the 24 desert shrubland plots. One plot was reclassified from sandsage to mesquite, resulting in decreased variance within habitats and stronger differentiation between habitats for several vegetation and bird variables. We present the results of analyses performed on five sandsage plots and seven mesquite plots. Remaining habitat-plot sample sizes remained unchanged.

Data Analysis

We conducted one-way analyses of variance (ANOVAs; SAS Institute 1999) on transformed variables, with the protected least-squares differences (LSD) method, to understand how individual habitat components varied among desert shrubland habitats and to assess the degree of similarity between the two plot-classification methods. The level of significance was set at alpha = 0.05; trends were assessed at 0.10.

We limited analyses of absolute and relative abundance to avian species for which we detected at least 150 individuals over 3 years. We also excluded species for which point-count surveys on 108-ha plots are inappropriate because they forage over much greater areas.

To examine whether a change from grassland to desert shrubland affects the bird community, we tested for differences in species richness, total number of breeding species detected, and species diversity as defined by the Shannon index, H' (Magurran 1988):

$$H' = -\sum p_i \ln p_i, \qquad (1)$$

where p_i is the proportional abundance of a species. We used the Kruskal-Wallis test to compare these indices and absolute abundance between black grama habitat and desert shrubland habitat.

To examine whether the relative extent of the four shrub habitats affects the bird community, we compared differences in species richness and diversity, absolute abundance, and relative abundance (number of individuals detected, by species, divided by the total of all individuals of all species detected) among habitat types. We used ANOVAs (protected LSD method) on transformed variables or the Kruskal-Wallis test if normal distributions could not be achieved through transformation. The degree of similarity of the bird communities between pairs of desert shrubland habitat types was estimated through two versions of the community coefficient (CC). In the first we used presence/absence data only: CC = $2S_s/(S_j + S_k)$, where S_s is the number of species shared by two plots, S_j is the number in the first, and S_k is the number in the second (Whittaker 1972; Magurran 1988). We used quantitative data in the second version: CC = $2N_t/(N_j + N_k)$, where N_t is the sum of the lower of the two abundances of those species that occur in both sites, Nj is the number of individuals (of all species) that occur at site j, and N_k is the number of individuals (of all species) that occur at site k (Magurran 1988; Legendre & Legendre 1998).

Results

Landcover of the 1880s

The amount of change in vegetation from the 1880s to the 1990s varied among habitat types and specific plots, but overall there was strong evidence for landcover change (Table 1). Phrases in quotes, below, are excerpts from the original survey notes.

Black grama habitat grass cover in the 1880s was considered "first rate" or "prairie" in the context of a grazing standard. From 1996 to 1998, grass-cover values in these plots ranged from 31% to 45% (mean 40%; Table 2). For black grama grasslands, 45% cover is considered dense and of high quality by modern plant ecologists (W. A. Dick-Peddie, personal communication). Making the assumption that 45% cover would have been considered first-rate by 1880s surveyors, we infer that present-day black grama plots approximate 1880s black grama conditions at the local scale of the plot. Shrub cover in the 1880s ranged from nonexistent to "scattering," descriptions that also apply to the 1990s.

Vegetation on the plots in whitethorn habitat appeared not to have changed appreciably in the last century. In the 1880s, grass cover was described as "second rate" in five of six of these plots and "third rate" in one. Shrub cover ranged from scattering to dense. In 1996–1998, mean grass cover was 14% and the average density of shrubs was high, 0.25/m^2 (Table 2).

Creosotebush habitat has undergone substantial change from grassland to desert shrubland in the areas represented by our plots. The territory surveyor recorded dense grass cover on four of the six plots, using phrases like "very fine grass," first-rate grass, and "rolling prairie." Using the same phrases, surveyor L. M. Lampton described the grass cover in the 1880s on both creosotebush and black grama plots, supporting the equivalence of this qualitative description in both habitat types. By the 1990s, mean grass cover was 22% on creosotebush plots compared with 40% on black grama plots (Table 2). Total shrub density in 1996–1998 was high at 0.26/m^2 (Table 2), compared with the sparse shrubs in most plots in the 1880s.

It is unclear how plots in sandsage habitat have changed over the last century. In the 1880s these plots were on level to gently rolling land, which "produce[d]

Table 1. A comparison of 1880s landcover with 1990s grass and shrub cover on study plots in McGregor Range, Ft. Bliss, New Mexico.

Habitat type and plot no.	*1880s original land survey (section line traversing plot)*	*Present-day cover values*	
		grass cover (%)	*shrub cover (%)*
Black grama grassland			
1	good grass/prairie/land rolling[a]	39.83	0.95
2	good grass/third-rate soil/high-level prairie/ no mention of undergrowth[b]	44.52	1.67
3	grass first-rate/soil sandy second-rate/land broken/scattered undergrowth	44.67	3.40
4	grass first-rate/soil sandy second-rate/land rolling/no mention of undergrowth	34.92	6.43
5	grass first-rate/soil sandy second-rate/land rolling/no mention of undergrowth[b]	41.82	2.67
6	grass first-rate/soil sandy second-rate/land rolling/no mention of undergrowth	31.55	1.42
Whitethorn			
1	grass second-rate/soil sandy/land rolling-broken/scattered undergrowth	11.26	14.83
2	grass first- or second-rate/soil sandy/land rolling	13.48	12.77
3	grass second- or third-rate/soil sandy-rocky/land rolling-broken/dense undergrowth[b]	13.66	13.47
4	grass second-rate/soil sandy/land rolling-broken/dense undergrowth[b]	16.80	14.45
5	grass second-rate/soil sandy-rocky/land rolling, sandstone ridges/dense undergrowth	13.43	17.29
6	grass first- or second-rate/soil sandy/land rolling/dense undergrowth	14.71	12.53
Creosotebush			
1	grass first-rate/soil sandy/scattered undergrowth[b]	36.26	9.47
2	grass second-rate/soil sandy/land level/ scattered undergrowth	20.12	8.81
3	grass first-rate/soil sandy/land rough, rolling/scattered undergrowth	33.08	12.37
4	grass first- or second-rate/soil sandy/land rolling/dense undergrowth[b]	12.85	8.60
5	grass second-rate/soil sandy/rolling rocky prairie/scattered scrub[b]	9.19	5.96
6	very fine grass/soil sandy/rolling prairie	18.74	5.52
Sandsage			
1	very fine grass/soil sandy/gently rolling prairie/scattered undergrowth[b]	16.04	11.31
2	grass first-rate/soil sandy/land rolling/no mention of undergrowth	8.50	7.50
3	very fine grass/soil sandy/gently rolling prairie/dense to scattered undergrowth[b]	18.00	8.91
4	grass second- or third-rate/soil sandy/land rolling/no mention of undergrowth	17.37	11.15
5	grass second-rate/soil sandy/land rolling/ scattered undergrowth[b]	25.96	13.86
Mesquite			
1	grass second-rate/soil sandy/land level/scattered mesquite brush[c]	2.71	13.89
2	grass second-rate/soil sandy/land level/scattered mesquite brush[b]	0.13	15.47
3	grass second-rate/soil sandy/land rolling/ dense to scattered undergrowth[b]	4.43	10.10
4	grass second-rate/soil sandy/land gently rolling/scattering undergrowth	1.08	6.22
5	grass second-rate/soil sandy/land gently rolling/dense undergrowth[b]	1.09	10.97
6	grass second-rate/soil sandy/land rolling/scattered undergrowth[c]	6.62	20.42
7	grass second-rate/soil sandy/scattered undergrowth	1.92	8.21

[a]*The words used in 1880s descriptions are direct quotes from original notes by U.S. General Land Office surveyors.*
[b]*No section line traversed the plot, so the next closest section line was used. Description was for section lines within 0.8 km (1/2 mile) of plot.*
[c]*Description was never recorded for section line traversing plot, so the next closest description was used. Description was for section lines within 3.2 km (2 miles) of plot.*

Table 2. Mean (SD) of local habitat variables in four shrubland habitat types separately, all shrubland plots combined, and black grama grassland in the northern Chihuahuan Desert.[a]

Habitat variable	*Desert shrubland, habitats separate* sandsage	mesquite	creosote	whitethorn	*Desert shrubland, habitats combined*	*Black grama grassland*
Shrubs (number per m^2)						
short shrubs	0.15(0.10) b	0.06(0.06) c	0.23(0.13) a	0.21(0.13) a	0.16(0.13) x[b]	0.02(0.03) y[b]
tall sparse shrubs	<0.01(0.01) c	<0.01(0.01) c	0.02(0.02) b	0.03(0.03) a	0.01(0.02) x[b]	<0.01(0.01) y[b]
tall dense shrubs	0.01(0.02) b	0.02(0.02) a	0.01(<0.01) b	0.01(0.01) b	0.01(0.01) x[b]	<0.01(0.01) y[b]
yucca species	<0.01(<0.01)	<0.01(<0.01)	<0.01(0.01)	<0.01(<0.01)	<0.01(<0.01)	<0.01(0.01)
total shrubs	0.16(0.10) b	0.08(0.06) c	0.26(0.13) a	0.25(0.14) a	0.18(0.13) x[b]	0.03(0.04) y[b]
Foliage height diversity	1.11(0.34)	1.13(0.34)	1.17(0.30)	1.17(0.30)	1.15(0.32) x[b]	0.46(0.24) y[b]
Ground cover (%)						
cactus	0.03(0.24) b[b]	0.04(0.34) b[b]	0.38(0.72) a[b]	0.22(0.51) a[b]	0.17(0.51)	0.14(0.41)
forb	3.47(4.45)	0.50(1.25)	1.52(2.79)	0.81(1.31)	1.45(2.85)	1.57(2.18)
grass	17.17(10.47) a	2.57(4.79) b	21.71(15.23) a	13.89(10.74) a	13.23(13.03) y[b]	39.56(10.66) x[b]
bare ground	62.32(12.83)	74.88(10.59)	65.99(13.53)	70.04(10.08)	68.83(12.60) x[b]	57.02(10.41) y[b]
litter	21.45(10.62) a	13.60(9.40) b	8.95(8.03) bc	6.73(4.23) c	12.35(9.88) x[b]	6.18(5.48) y[b]
shrub & cholla	10.54(6.83) ab	12.18(7.83) ab	8.45(5.97) b	14.22(7.05) a	11.42(7.28) x[b]	2.76(3.23) y[b]

[a]*Within rows and organizational level, means with different letters are significantly different (*p *> 0.05).*
[b]*Kruskal-Wallis test used because of non-normality of data. All other results are from analysis of variance.*

a fine growth of grass"; but the plots also had "dense undergrowth" (i.e., dense shrubs). In the 1990s, grass cover averaged 17%, forb and litter cover were high, and the density of shrubs, 0.16/m^2, was moderate (Table 2).

Some of the plots in mesquite habitat underwent the greatest cover change from the 1880s to 1998. In 1884, "generally level" or "gently rolling" land with second-rate grass cover, "sandy soil," and a "scattering of undergrowth" were by the time of the 1924 re-survey "sand hummocks 10 ft. high, undergrowth of mesquite and yucca," and there was no mention of grass cover. In 1996–1998 these plots had <5% grass cover and were dominated by shrub-covered dunes with average density of 0.08/m^2 (Table 2).

Habitat

Black grama grassland had significantly higher grass cover and significantly lower shrub density and foliage height diversity than the pooled desert shrubland habitats (Table 2). Of 1300 shrubs recorded in black grama plots, only 41 were mesquite and 399 were creosotebush, of which 292 were <0.5 m tall.

Within the shrub habitats, both the density of shrubs of <0.5 m and total shrub density were significantly higher in creosotebush and whitethorn habitats than in sandsage and mesquite (Table 2). Despite low shrub density in mesquite, the percent cover of shrubs and cholla was high because of the large area covered by individual mesquite shrubs. The density of shrubs with tall (>1.4 m), open life forms was significantly higher in whitethorn, and the density of shrubs with tall, impenetrable life forms was significantly higher in mesquite than in other habitat types. The cover of grass was significantly lower in mesquite than in other habitat types, and bare ground was highest in mesquite and whitethorn. Litter cover was highest in sandsage.

Birds

Bird species-year interactions occurred for most species, so years were treated separately in all analyses of birds. Species richness was consistently higher in desert shrubland than in black grama grassland (Table 3). Diversity was higher in desert shrubland in 2 years.

Among desert-shrub habitat types, avian species richness differed significantly in all 3 years, with richness highest in mesquite (Table 3). Mean richness peaked at 33.4 in mesquite and bottomed out at 19.6 in sandsage. There was a trend toward higher diversity in whitethorn in 2 of the 3 years.

There was a significant difference in the abundance of 14 bird species between desert shrubland and black grama habitat in at least 2 years, whereas the abundance of 7 species was never significantly different (Appendix). Ten species were more abundant in desert shrub- land, and 4 species were more abundant in black grama grassland. Among desert-shrub habitat types, 9 species exhibited significant differences in all 3 years, and 2 species exhibited differences in 2 of the 3 years (Appendix).

There were few differences in relative abundance among shrub habitat types. Relative abundance was significantly different for only three species in all 3 years (Common Nighthawk, Pyrrhuloxia, and Crissal Thrasher; scientific names of birds are provided in the Appendix). The variability of relative abundance was much higher than that of absolute abundance, which accounts for the finding of fewer differences. Fourteen species showed no significant differences in at least 2 of the 3 years. Although statistical significance was not achieved, the relationships among relative abundance values in different

Table 3. Mean richness and mean diversity of birds in black grama grassland and shrubland habitat and among four shrubland habitat types.[a]

Habitat type[a]	*Richness[b]*	*Shannon Diversity[b]*
	1996	
Black grama grassland	18.80 y	2.06
Desert shrubland	25.90 x	2.18
p^c	<0.001	0.759
Sandsage	22.40 b	1.97
Mesquite	33.43 a	2.22
Creosote	21.33 b	2.10
Whitethorn	24.50 b	2.38
p	0.001	0.074
	1997	
Black grama grassland	17.20 y	2.05
Desert shrubland	26.00 x	2.32
p^c	0.001	0.053
Sandsage	20.20 c	2.14
Mesquite	32.29 a	2.27
Creosote	23.16 bc	2.37
Whitethorn	26.33 b	2.47
p	0.008	0.117
	1998	
Black grama grassland	18.00 y	2.06 y
Desert shrubland	26.70 x	2.37 x
p^c	0.001	0.023
Sandsage	19.60 c	2.27
Mesquite	32.86 a	2.31
Creosote	26.66 b	2.30
Whitethorn	25.50 b	2.59
p	0.002	0.065

[a]There were six black grama plots and 24 desert shrubland plots.
[b]Within columns (within year), means with different letters are significantly different.
[c]p indicates values from Kruskal-Wallis test; all other p values are from analysis of variance.

Table 4. Mean and SD of community coefficients of breeding birds among habitat types in the northern Chihuahuan Desert, calculated from bird presence/absence and abundance data.

	Presence/ absence[a]		*Abundance[b]*	
Habitat type	*mean*	*SD*	*mean*	*SD*
		1996		
Sandsage-mesquite	0.63	0.07	0.70	0.07
Sandsage-creosote	0.65	0.06	0.68	0.07
Sandsage-whitethorn	0.62	0.07	0.63	0.05
Mesquite-creosote	0.62	0.07	0.63	0.06
Mesquite-whitethorn	0.62	0.07	0.64	0.06
Creosote-whitethorn	0.64	0.07	0.65	0.07
		1997		
Sandsage-mesquite	0.65	0.07	0.66	0.09
Sandsage-creosote	0.71	0.08	0.61	0.06
Sandsage-whitethorn	0.63	0.08	0.59	0.06
Mesquite-creosote	0.67	0.04	0.56	0.08
Mesquite-whitethorn	0.62	0.06	0.59	0.05
Creosote-whitethorn	0.68	0.08	0.60	0.06
		1998		
Sandsage-mesquite	0.69	0.07	0.58	0.08
Sandsage-creosote	0.68	0.06	0.63	0.07
Sandsage-whitethorn	0.67	0.06	0.62	0.05
Mesquite-creosote	0.65	0.09	0.59	0.07
Mesquite-whitethorn	0.65	0.08	0.60	0.06
Creosote-whitethorn	0.68	0.06	0.65	0.06

[a]Community coefficient = $2S_s/(S_j + S_k)$, where S_s is the number of species shared by two plots, S_j is the number in the first plot, and S_k is the number in the second plot.
[b]Community coefficient = $2N_s/(N_j + N_k)$, where N_j is the number of individuals of all species that occur at site j, N_k is the number of individuals of all species that occur at site k, and N_s is the sum of the lower of the two abundance values of those species that occur at both sites.

habitats were similar to those among absolute abundance values.

Community coefficients between black grama grassland and the four desert-shrub habitat types resulted in 46–59% similarity in each of the 3 years. The four desert-shrub habitat types differed in their avian communities by at least 30% in each pair-wise comparison (Table 4). Coefficients ranged from 0.58 to 0.71. Slightly more differentiation among habitat types was achieved by the quantitative method, with a separation of 7–10% each year.

Discussion

We found strong differences in avian communities among habitat types. Species richness and diversity were higher in desert shrubland than in grassland. Some species were strongly associated with grassland, whereas others were strongly associated with shrubs. Within desert shrubland, bird-assemblage patterns were distinct, reflecting the distinct assemblages of plant species.

We conducted many statistical tests, and by definition approximately 5% of the null hypotheses will be rejected by chance alone ($\alpha = 0.05$). We rejected well over 5% of the hypotheses tested and are therefore confident that our results indicate real differences.

Black Grama Grassland Conversion to Desert Shrubland

Desertification in the Chihuahuan Desert, resulting in the replacement of grassland by shrubland, may be caused by overgrazing (Yool 1998), the combined effects of grazing and fire suppression (Brown & Archer 1989), the dispersal and establishment abilities of plant species (Hennessy et al. 1983; Lopez-Portillo & Montana 1999), drought (Connin et al. 1997), and increasing climatic carbon-dioxide concentrations (Fredrickson et al. 1998). The successional pathways and stability of desert shrubland are strongly influenced by grazing and climate (Gibbens et al.1992; Warren et al.1996). Desert shrubland, a "lower successional state" than grassland (Laycock 1991), occurs when an ecological threshold is crossed to the shrub-dominant state (Archer 1989; Friedel 1991). Once that occurs, it is difficult to return to grassland and the change may be irreversible (Laycock 1991; Whitford et al. 1998).

Whether the cause of landcover change was overgrazing, drought, or some combination of factors, we need to understand the consequences of this change for the avian community. Population trends are apparent, yet their causes are unknown. A very different avian community is associated with black grama grassland than with desert shrubland. Further, habitat types within shrubland have had different trajectories in the last 150 years. Some are relatively well documented, as is the case for mesquite and creosotebush, whereas the history of others, including whitethorn and sandsage, is less clear. Regardless history, the avian community does not respond to all desert shrubland equally.

We are limited in our understanding of avian population trends by the lack of information about 1880s bird communities in this region and about the similarities and differences between black grama grasslands in the 1880s and the 1990s. The assumption that 1880s black grama and present-day black grama are equivalent in their role as habitat for grassland bird species may be false. Landscape structure may well have changed; smaller average patch size and greater patch isolation in 1990s black grama grasslands are likely differences. Smaller patch size would have a direct effect on area-sensitive grassland bird species.

It is unclear why the remaining areas of black grama are located where they are, when all former grasslands at lower elevations have been converted to shrubland. Cornelius et al. (1991) demonstrated significant associations between landscape-level patterns of environmental heterogeneity and the distribution patterns of black grama at the Jornada Long-term Ecological Research Site. Both available water and nitrogen were more abundant in areas covered by black grama than at the lower-elevation sites adjacent to black grama. The authors suggest that these patterns arise in part from differences in soil texture that affect infiltration, water-holding capacity, and moisture release. McAuliffe (1995) demonstrated the relationship between the age of soils, their water-storage capacity, and their dominant vegetation in southeast Arizona. Landscape evolution and soil development may be key to the distribution of grasses.

Historical differences may have created these patterns; grazing, in particular, is likely to have changed local site conditions. Areas that have remained in black grama are unlikely to have been heavily grazed, but the remains of an early homestead within 2 km of two of our black grama plots make it likely that some grazing occurred in the vicinity of our study plots. It is possible that creosote and mesquite are not as competitive as whitethorn in this combination of elevation and soil type. Furthermore, whitethorn may be a less-aggressive invader into black grama, allowing the grassland to recover from bouts of grazing and to maintain its extent.

On Ft. Bliss, black grama areas are protected as the McGregor Black Grama Grassland Area of Critical Environmental Concern. Livestock is excluded from these areas, activities that disturb the vegetative cover are discouraged, and the primary goal is "the continuation of ecosystem processes without undue disturbances" (U.S. Bureau of Land Management 1990).

Local Bird-Habitat Associations

Availability of food, relative risk of nest predation, suitable nest substrate, and microclimate conditions all influence the abundance patterns of breeding birds among habitat types. Both species richness and diversity were lower in black grama than in desert shrubland, which may be associated with a low diversity of foliage height, which creates fewer available nest substrates (MacArthur & MacArthur 1961).

General life-history trends for different avian nesting guilds may explain observed patterns of abundance. Ground nesters included Horned Larks and Common Nighthawks, which prefer an open landscape (Ehrlich et al. 1988). Horned Larks were rarely detected in desert shrubland, and Common Nighthawks were least abundant in mesquite and sandsage. Mesquite dunes may change the character of the landscape from the perspective of a ground-nesting bird, so that it is no longer perceived as "open." Eastern Meadowlarks and Cassin's Sparrows, species that require grasses as material for their nests, which are on or near the ground, were least abundant in mesquite, where grass cover was lowest.

In the northern Chihuahuan desert in general, shrubs with a tall, dense life form are a limiting resource as nesting substrates for several open-cup nesters (Kozma & Mathews 1997). If these shrub forms were the only limiting factor, one would expect to find many nest substrate–limited species in mesquite, where tall, dense shrubs predominate. Yet of the many open-cup nesters present, only the Pyrrhuloxia had highest abundance in mesquite exclusively, suggesting that availability of nest sites is only one factor influencing distribution patterns of desert birds among habitat types. Western Kingbirds, which nest almost exclusively in *Yucca* sp. in this ecosystem (personal observation), were most abundant in mesquite and sandsage, where the density of *Yucca* sp. is highest. Verdins, which use spinescent twigs to make their nests, were most abundant in whitethorn and mesquite, where spinescent shrubs were most abundant.

Implications of Habitat Change for Birds

Habitat change can have a considerable effect on bird populations (Dolman & Sutherland 1995) and has been accompanied by vertebrate community change in heathland

(Blackstock et al. 1995), tall-grass prairie, short-grass prairie (Telfer 1992), interior temperate forest (Hansen & Urban 1992), and mature tropical forest (Sader et al. 1991).

The implications of habitat change for the northern Chihuahuan Desert bird community are significant. Avian species richness was consistently lower in black grama than desert shrubland, which agrees with Whitford's (1997) findings. Although we cannot quantify 1880s species richness, we can speculate that one or more additional species could have been present as breeding populations in the 1880s. Breeding populations of the Grasshopper Sparrow (*Ammodramus savannarum*) occur locally in grasslands in eastern Colorado, southeastern Arizona, northern Chihuahua, and west Texas (Vickery 1996), but only four individuals were detected in our 3-year study. It is possible that this species occurred on Ft. Bliss at the time of European settlement and that its absence signifies an impoverished bird community relative to that of the 1880s. It is also possible that, despite the apparently suitable breeding habitat and area requirements (Herkert 1994; Vickery 1996), there are factors that make Ft. Bliss black grama grasslands unsuitable for Grasshopper Sparrows. The Lark Bunting (*Calamospiza melanocorys*) occurs as a migrant on the study area in the 1990s, and the more extensive tracts of black grama grassland may have contributed to higher Lark Bunting abundance in the 1880s. This species is among the least philopatric species and may be area-sensitive (Dechant et al. 1999). These additional species would still have resulted in at least 20% fewer species in grassland than in shrubland.

Population levels of those species more abundant in desert shrubland have likely increased with changes in landcover. Assuming that avian species had the same habitat needs in pre-settlement times as they do now, grassland birds were likely far more populous in this area in the 1880s, when the extent of grasslands was much greater. The effect of landcover changes on avian populations is variable and depends on the distribution and abundance patterns of a species as a whole. Of the species that occur regularly in our study area in the 1990s, landcover change has probably affected populations of Cassin's Sparrow most severely. In the United States, this species' range includes the semiarid grasslands and short-grass prairie of the Southwest. The relative abundance of Cassin's Sparrow in summer is highest in a band from south-central to northeastern New Mexico (Price et al. 1995). The conversion of grassland to shrubland represents substantial loss of habitat from the center of this species' distribution. These data suggest that populations of Cassin's Sparrow are vulnerable and merit close monitoring.

For other grassland species, including both the Eastern Meadowlark and the Horned Lark, traits specifically adapted to the northern Chihuahuan Desert will not be selected for as the range of suitable habitat is narrowed in this region, resulting in a potential loss of adaptive flexibility for the species as a whole and for the populations of the Southwest in particular. Little is known about the relationship of the Eastern Meadowlark subspecies *S. m. lilianae* that occurs in New Mexico with other subspecies. It appears to be an allopatric population and, as such, merits particular conservation attention (Lanyon 1995).

Our finding that all desert-shrubland types are not equal is critical to understanding the probable change in avian community patterns through time. We demonstrate that many species show distinct patterns of abundance among shrub communities. One or more species reached highest abundance in each of the habitat types. Although several of these species have large geographic ranges (Common Nighthawk, Western Kingbird, House Finch), others are habitat specialists (Pyrrhuloxia, Black-tailed Gnatcatcher) or are experiencing population declines (Loggerhead Shrike, Cassin's Sparrow). The area encompassed by these desert-shrub habitats may play an important and unique role in the health of these avian populations.

The increase of mesquite, a habitat type considered among the most degraded in this ecosystem (Whitford 1997), has received considerable attention. In a comparison of black grama and mesquite-dominated habitat, the diversity (Smith et al. 1996; Whitford 1997) and abundance of several wildlife species (Germano et al. 1983) were higher in areas with a mesquite component. Information about wildlife use of other shrub communities is equally important but practically nonexistent. We found that although species richness was consistently highest in mesquite, species diversity was generally higher in whitethorn.

Little is known of the abundance of sandsage prior to the turn of the century. A comparison of photograph pairs from the late 1890s and the 1940s suggests that it has increased in extent, at least in some localities (Leopold 1951). New Mexico plant ecologists suggest that heavy grazing on sandy soil likely results in an increase in sandsage (W. A. Dick-Peddie, personal communication; R. Spellenberg, personal communication). Although our sandsage plots were grass-covered in the 1880s, they also had localized areas of "dense undergrowth" (i.e., shrubs). We can therefore cautiously speculate that the area of sandsage has increased recently and that, with this increase, population levels of Western Kingbirds, Loggerhead Shrikes, and Crissal Thrashers have increased. Similarly, no information exists on the extent of whitethorn in the 1880s, but the general mechanisms favoring shrubs over grassland again suggest that this habitat type has probably increased in extent at the expense of black grama grassland (L. F. Huenneke, personal communication), and with it the population levels of House Finches and Verdins.

Our findings agree with those of Lloyd et al. (1998) regarding the high abundance of Pyrrhuloxia in mesquite habitat; the expansion of this habitat type over the southern part of New Mexico has likely resulted in a manyfold increase in the population of Pyrrhuloxia. Population levels of Western Kingbirds, Brown-headed Cowbirds, Crissal Thrashers, and Black-tailed Gnatcatchers have probably also increased as mesquite has increased.

Trends in bird abundance in the northern Chihuahuan Desert are poorly understood. Because of the sparse coverage of surveys, the North American breeding bird survey (Sauer et al. 1997) yields inconclusive information about many of the avian species that occur in this area. Abundance patterns, however, may not adequately reflect the importance of habitat type to avian populations (Van Horne 1983). For example, given the consistently high species richness of breeding birds in mesquite, one conclusion might be that mesquite is high-quality habitat for a number of species. Whitford (1997) found, however, that although up to 10 species forage in mesquite habitat, only 3 nest in that habitat type. Also, for some species average reproductive success may be constant or may decline with increasing mesquite density (Pulliam & Danielson 1991).

Avian diversity and species richness on Ft. Bliss have increased as the range of desert shrubland has expanded. Concomitantly, biological integrity, defined as conditions under the influence of natural evolutionary and geographical processes and sheltered from anthropogenic influences (Angermeier & Karr 1994), has declined with the extensive loss of grasslands. This sets up a paradox. On one hand, the richness and abundance of wildlife species has increased as shrubland has encroached into former grassland (Germano et al. 1983; Whitford 1997). It has been suggested that desert habitat with a substantial shrub component, rather than black grama grassland habitat, "will better meet the needs of most wildlife species" (Smith et al. 1996). This calls into question whether the conversion to shrubland is indeed degradation (Whitford et al. 1998). On the other hand, black grama grassland has undergone fragmentation and substantial reduction of its former extent (Dick-Peddie 1993), and the avian grassland community has decreased in abundance and extent and perhaps in membership. Clearly, these are signs of loss of integrity.

The historic degradation in extent and quality of black grama grasslands potentially jeopardizes the avian species that depend on it. The extent of black grama has declined substantially; restoration of black grama grasslands after conversion to shrubland may not be possible (Archer 1989). Hence, the conservation value of black grama is high. Conversely, there is no shortage of desert-shrub habitat and no foreseeable threat to its continued persistence. Therefore, to retain key elements of the native landscape, protection of remaining black grama grassland patches should be a high conservation priority.

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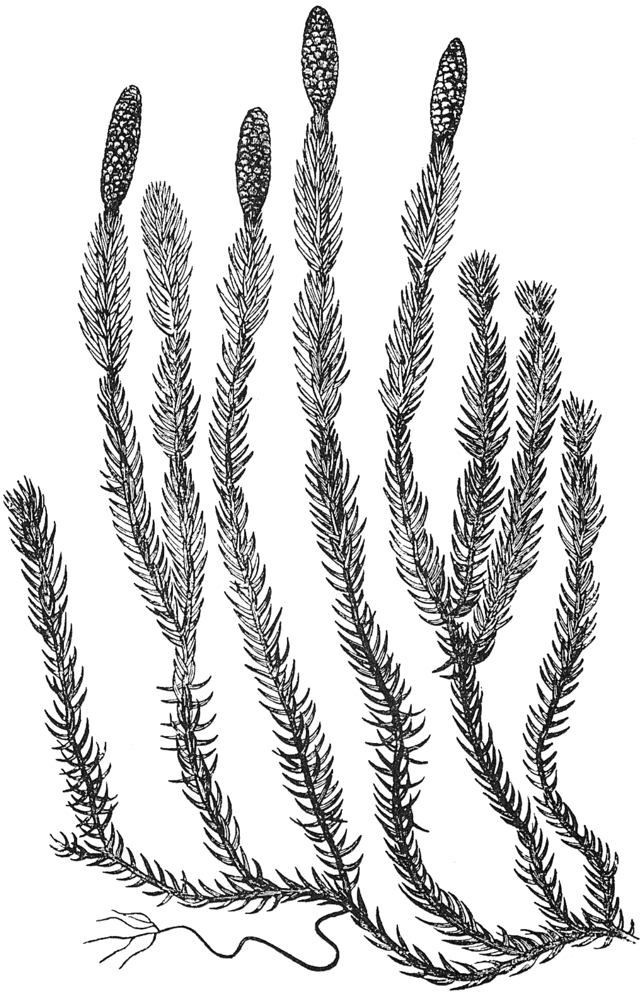

Appendix

Mean abundance[a] (SD) of 22 avian species in black grama grassland, desert shrubland overall, and four shrubland habitat types separated.[b]

Bird species and habitat type	*1996*	*1997*	*1998*
Scaled Quail (*Callipepla squamata*)			
Black grama grassland	0.3(0.4) b	2.6(3.7)	3.1(3.9)
Desert shrubland	1.4(1.5) a	4.9(3.1)	5.3(2.5)
p[c]	0.021	0.072	0.114
Sandsage	1.8(1.6)	4.8(1.4) a	6.0(3.5)
Mesquite	1.1(1.3)	2.8(3.7) b	5.4(2.5)
Creosote	1.3(2.1)	4.9(1.6) a	4.6(1.9)
Whitethorn	1.3(1.0)	7.5(2.9) a	5.3(2.4)
p	0.821	0.015 a	0.913
Gambel's Quail (*Callipepla gambelii*)			
Black grama grassland	0.1(0.2)	0.5(1.0)	0.1(0.2)
Desert shrubland	0.8(1.4)	0.8(1.0)	1.6(2.5)
p[c]	0.153	0.351	0.061
Sandsage	0.5(0.9)	0.9(1.0)	0.5(.7) b
Mesquite	1.4(2.2)	0.9(1.2)	4.7(2.9) a
Creosote	0.7(0.9)	0.9(1.1)	0.3(.4) b
Whitethorn	0.4(0.8)	0.6(1.0)	0.3(.5) b
p	0.781	0.903	<0.001
Mourning Dove (*Zenaida macroura*)			
Black grama grassland	4.8(3.1)	10.6(7.4)	4.3(2.4)
Desert shrubland	5.5(3.5)	9.5(8.4)	9.9(7.9)
p[c]	0.611	0.387	0.086
Sandsage	5.1(3.6)	8.5(6.3)	12.2(6.6)
Mesquite	6.8(4.2)	3.8(2.7)	9.6(8.5)
Creosote	3.4(3.0)	12.6(12.0)	9.7(12.5)
Whitethorn	6.5(2.8)	14.0(7.7)	8.8(2.9)
p	0.204	0.067	0.553
Greater Roadrunner (*Geococcyx californianus*)			
Black grama grassland	0.0(0.0)	0.0(0.0)	0.1(0.2) b
Desert shrubland	0.3(0.5)	0.4(0.6)	1.9(1.8) a
p[c]	0.109	0.062	0.004
Sandsage	0.3(0.5)	0.3(0.5) ab	1.5(2.0)
Mesquite	0.6(0.7)	0.0(0.0) b	1.8(2.5)
Creosote	0.1(0.2)	0.7(0.9) a	2.9(1.3)
Whitethorn	0.1(0.2)	0.8(0.5) a	1.5(1.2)
p[c]	0.246	0.031	0.231
Lesser Nighthawk (*Chordeiles acutipennis*)			
Black grama grassland	0.3(0.6)	0.0(0.0) b	0.0(0.0) b
Desert shrubland	0.8(1.2)	1.0(1.8) a	1.00(1.1) a
p[c]	0.222	0.045	0.022
Sandsage	0.3(0.5)	0.3(0.7)	0.5(0.7)
Mesquite	1.1(1.4)	0.8(1.2)	0.9(0.9)
Creosote	1.0(1.5)	2.4(2.9)	1.6(1.4)
Whitethorn	0.6(1.2)	0.4(0.5)	1.0(1.2)
p	0.648	0.341	0.707
Common Nighthawk (*Chordeiles minor*)			
Black grama grassland	5.9(3.2) a	5.3(2.4)	3.5(1.5)
Desert shrubland	2.3(2.7) b	3.2(3.7)	2.2(2.9)
p[c]	0.009	0.139	0.540
Sandsage	0.1(0.2) c	0.1(0.2) b	0.3(0.3) c
Mesquite	0.6(0.4) b	0.6(0.7) b	0.4(0.6) c
Creosote	3.3(2.0) a	5.1(3.3) a	1.8(1.3) b
Whitethorn	5.3(2.8) a	7.1(3.4) a	6.3(2.9) a
p	<0.001	<0.001	<0.001

continued

Appendix (continued)

Bird species and habitat type	*1996*	*1997*	*1998*
Ash-throated Flycatcher (*Myiarchus cinerascens*)			
Black grama grassland	3.3(3.0)	2.9(2.4) b	2.1(2.2)
Desert shrubland	5.8(3.8)	6.8(3.3) a	4.2(3.4)
p^c	0.156	0.013	0.064
Sandsage	2.8(1.1) b	7.1(4.0)	1.9(0.4)
Mesquite	5.0(2.6) b	5.7(2.3)	6.6(5.2)
Creosote	5.3(2.9) ab	6.8(4.4)	2.8(1.1)
Whitethorn	9.6(4.8) ab	8.0(3.1)	4.8(1.2)
p	0.014	0.721	0.166
Western Kingbird (*Tyrannus verticalis*)			
Black grama grassland	3.8(3.2)	4.6(5.7)	3.9(4.8)
Desert shrubland	6.8(5.1)	8.0(6.1)	7.1(4.3)
p^c	0.199	0.081	0.056
Sandsage	8.2(5.2) ab	10.5(6.1) ab	9.7(3.0) a
Mesquite	10.4(4.6) ab	12.2(6.6) a	9.9(4.5) a
Creosote	3.3(1.3) b	4.9(4.4) bc	6.2(3.1) ab
Whitethorn	4.8(5.3) b	4.0(2.4) c	2.8(1.5) b
p	0.035	0.025	0.004
Loggerhead Shrike (*Lanius ludovicianus*)			
Black grama grassland	1.8(0.9)	1.5(1.3)	1.8(1.3)
Desert shrubland	1.5(1.4)	1.5(2.1)	1.0(1.8)
p^c	0.314	0.484	0.064
Sandsage	2.8(1.8) a	4.3(3.0) a	3.6(2.7) a
Mesquite	0.4(0.6) b	0.4(0.9) b	0.1(1.9) b
Creosote	1.8(1.3) a	1.1(1.1) b	0.3(0.4) b
Whitethorn	1.3(0.8) ab	0.7(0.5) b	0.7(0.8) b
p	0.012	0.008	0.009
Horned Lark (*Eremophila alpestris*)			
Black grama grassland	15.6(14.8) a	18.4(10.8) a	11.5(8.1) a
Desert shrubland	0.0(0.1) b	0.1(0.3) b	0.0(0.0) b
p^c	<0.001	<0.001	<0.001
Verdin (*Auriparus flaviceps*)			
Black grama grassland	0.0(0.0) b	0.0(0.0) b	0.0(0.0) b
Desert shrubland	3.4(3.7) a	4.8(4.1) a	2.8(2.4) a
p^c	0.004	0.001	0.004
Sandsage	0.5(0.7) b	1.3(1.9) c	0.3(0.7) b
Mesquite	3.1(2.7) ab	5.7(3.6) ab	3.2(2.2) ab
Creosote	2.8(4.0) b	3.4(5.3) bc	2.0(2.6) b
Whitethorn	6.8(3.6) a	8.0(1.4) a	5.2(0.68) a
p	0.022	0.024	0.036
Cactus Wren (*Campylorhynchus brunneicapillus*)			
Black grama grassland	2.7(2.0)	2.9(3.4) b	0.8(0.9) b
Desert shrubland	4.5(2.5)	7.5(4.1) a	4.0(2.7) a
p^c	0.107	0.026	0.003
Sandsage	4.1(2.2)	8.2(4.3)	3.8(0.8)
Mesquite	4.9(2.9)	8.0(4.9)	4.9(3.9)
Creosote	4.5(2.2)	9.0(3.1)	3.8(2.2)
Whitethorn	4.6(3.1)	5.0(3.6)	3.2(2.8)
p	0.971	0.369	0.752
Black-tailed Gnatcatcher (*Polioptila melanura*)			
Black grama grassland	0.1(0.2)	0.0(0.0)	0.0(0.0)
Desert shrubland	1.4(1.5)	2.4(2.6)	2.8(2.5)
p^c	0.007	0.006	0.002
Sandsage	0.2(0.3) c	0.7(1.3) b	0.2(0.4) b
Mesquite	2.9(1.4) ab	5.4(2.3) a	4.9(2.2) a
Creosote	0.7(0.8) bc	0.4(1.0) b	1.2(1.5) b
Whitethorn	1.5(1.3) ab	2.3(1.7) a	4.0(2.0) a
p	0.002	<0.001	<0.001

continued

Appendix (continued)

Bird species and habitat type	*1996*	*1997*	*1998*
Northern Mockingbird (*Mimus polyglottos*)			
Black grama grassland	8.9(3.9)	13.8(9.5)	7.3(3.5)
Desert shrubland	5.0(3.9)	8.2(10.4)	8.1(4.5)
p^c	0.031	0.108	0.704
Sandsage	3.6(3.9)	2.4(3.6) c	8.7(3.6) a
Mesquite	4.1(2.9)	2.3(3.6) bc	3.6(3.4) b
Creosote	4.0(3.2)	3.4(2.1) b	7.4(2.1) a
Whitethorn	8.1(4.5)	24.8(5.7) a	12.6(4.4) a
p	0.149	0.001[a]	0.003
Curve-billed Thrasher (*Toxostoma curvirostre*)			
Black grama grassland	0.0(0.0)	0.6(0.7)	0.2(0.3)
Desert shrubland	0.3(0.6)	0.7(1.0)	0.5(1.1)
p^c	0.109	1.000	1.000
Crissal Thrasher (*Toxostoma crissale*)			
Black grama grassland	0.1(0.2) b	0.1(0.2) b	0.1(0.2) b
Desert shrubland	1.7(1.6) a	2.8(2.3) a	2.2(2.3) a
p^c	0.001	<0.001	0.001
Sandsage	2.3(1.6) a	4.7(2.5) a	2.4(1.3) a
Mesquite	3.0(1.8) a	3.9(2.3) a	3.9(3.1) a
Creosote	0.3(0.3) b	1.3(1.1) b	0.4(0.5) b
Whitethorn	1.1(0.6) a	1.3(0.9) b	1.9(1.9) a
p	0.001	0.004	0.005
Cassin's Sparrow (*Aimophila cassinii*)			
Black grama grassland	3.0(3.9) a	15.3(6.3) a	2.8(2.2) a
Desert shrubland	0.4(1.0) b	4.8(10.1) b	0.6(1.9) b
p^c	0.005	0.001	<0.001
Sandsage	0.3(0.7) ab	0.3(0.5) bc	0.1(0.2)
Mesquite	0.0(0.0) b	0.0(0.0) c	0.0(0.0)
Creosote	1.3(1.8) a	17.6(14.0) a	2.3(3.6)
Whitethorn	0.1(0.2) b	1.5(2.8) b	0.2(0.4)
p	0.037[a]	<0.001	0.094
Lark Sparrow (*Chondestes grammacus*)			
Black grama grassland	1.8(1.7) a	2.6(3.0) a	2.2(2.5) a
Desert shrubland	0.1(0.3) b	0.1(0.5) b	0.1(0.2) b
p^c	<0.001	<0.001	<0.001
Black-throated Sparrow (*Amphispiza bilineata*)			
Black grama grassland	15.5(7.6) b	16.9(10.6) b	17.2(11.6) b
Desert shrubland	31.9(6.7) a	38.7(8.8) a	28.6(8.7) a
p^c	<0.001	<0.001	0.029
Sandsage	35.8(5.4) a	39.8(11.2)	23.0(9.8)
Mesquite	35.6(5.2) a	41.9(10.4)	30.6(8.1)
Creosote	28.4(5.4) b	34.8(3.6)	33.5(9.4)
Whitethorn	27.8(7.2) b	38.2(8.8)	26.2(5.5)
p	0.041	0.941	0.183
Pyrrhuloxia (*Cardinalis sinatus*)			
Black grama grassland	0.1(0.2) b	0.0(0.0) b	0.0(0.0) b
Desert shrubland	3.0(3.2) a	6.0(6.3) a	4.8(6.7) a
p^c	0.003	0.001	<0.001
Sandsage	2.3(2.4) bc	6.6(4.4) b	2.4(2.9) b
Mesquite	6.9(2.1) a	13.3(5.1) a	13.5(6.1) a
Creosote	1.9(1.4) bc	2.7(2.4) c	1.3(1.4) bc
Whitethorn	0.1 (0.2) c	0.3(0.8) d	0.2(0.3) c
p^c	<0.001	<0.001	<0.001

continued

Appendix (continued)

Bird species and habitat type	*1996*	*1997*	*1998*
Blue Grosbeak (*Guiraca caerulea*)			
Black grama grassland	0.0(0.0) b	0.0(0.0) b	0.1(0.2)
Desert shrubland	1.0(1.7) a	1.3(1.5) a	1.1(1.7)
p^c	0.032	0.004	0.102
Sandsage	0.4(0.7)	0.7(0.8)	0.0(0.0) c
Mesquite	0.7(1.1)	0.9(1.2)	1.1(2.8) cb
Creosote	1.8(2.8)	2.5(2.3)	1.6(1.1) a
Whitethorn	1.1(1.5)	0.9(0.6)	1.4(1.1) ab
p	0.826	0.831	0.013[a]
Eastern Meadowlark (*Sturnella magna*)			
Black grama grassland	26.2(9.1) a	40.9(12.9) a	22.5(13.7) a
Desert shrubland	1.1(1.8) b	1.8(2.6) b	0.6(1.1) b
p^c	<0.001	<0.001	<0.001
Sandsage	1.1(1.2) a	0.7(0.9) bc	0.6(0.6) a
Mesquite	0.0(0.0) b	0.1(0.2) c	0.0(0.0) b
Creosote	1.9(2.9) a	4.8(3.5) a	1.2(1.9) a
Whitethorn	1.5(1.8) a	1.6(1.6) b	0.8(0.7) a
p^c	0.039	<0.001	0.017
Brown-headed Cowbird (*Molothrus ater*)			
Black grama grassland	0.2(0.4) b	0.8(1.0) b	0.8(0.8) b
Desert shrubland	2.6(2.4) a	3.9(2.8) a	3.5(3.6) a
p^c	0.007	0.005	0.017
Sandsage	0.3(0.7) b	1.0(0.9) c	1.3(1.8) c
Mesquite	3.7(2.3) a	5.8(2.7) a	5.8(5.5) a
Creosote	2.1(2.7) ab	2.3(1.5) b	2.0(1.8) bc
Whitethorn	3.6(2.1) a	5.8(1.5) a	4.0(1.0) ab
p	0.005	<0.001	0.012
Scott's Oriole (*Icterus parisorum*)			
Black grama grassland	4.7(3.6)	2.2(2.4)	4.3(3.9)
Desert shrubland	7.8(3.3)	8.8(3.5)	6.6(3.1)
p^c	0.120	<0.001	0.283
Sandsage	7.0(0.8) ab	11.5(3.8)	8.3(3.6)
Mesquite	6.9(2.2) b	7.4(3.0)	5.4(3.0)
Creosote	6.2(1.9) b	7.8(3.7)	5.6(3.3)
Whitethorn	11.3(4.4) a	9.2(2.8)	7.6(2.2)
p	0.034	0.199	0.244
House Finch (*Carpodacus mexicanus*)			
Black grama grassland	0.8(1.2) b	0.8(1.0) b	0.6(0.7) b
Desert shrubland	4.1(4.2) a	4.4(4.7) a	3.3(4.7) a
p^c	0.020	0.019	0.199
Sandsage	3.4(3.7)	1.3(0.6) b	0.8(0.9) b
Mesquite	2.2(3.4)	2.1(2.3) b	0.6(1.3) b
Creosote	4.7(5.4)	3.8(2.2) b	1.8(2.6) b
Whitethorn	6.3(3.9)	10.3(5.6) a	10.1(4.1) a
p	0.180	0.002	<0.001

[a] *Mean number per plot, from point counts.*
[b] *For each species, means with different letters within columns are significantly different.*
[c] *Kruskal-Wallis test used; all other results are from analysis of variance; protected least-squares differences method employed in both tests.*