

POPULATION TRENDS AND ECOLOGY OF GRASSLAND BIRDS



Mountain Plover (*Charadrius montanus*) © David J. Krueper

## INFLUENCE OF DESERTIFICATION ON SITE OCCUPANCY BY GRASSLAND AND SHRUBLAND BIRDS DURING THE NON-BREEDING PERIOD IN THE NORTHERN CHIHUAHUAN DESERT

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*Abstract.* Desertification occurs widely in the southwestern US, but its effects on non-breeding avian communities have been poorly studied. Shrub encroachment is considered a major indicator of desertification. We studied the associations of landscape and vegetation characteristics on grassland and shrubland bird communities in 27 Chihuahuan Desert grassland patches between 2003 and 2006. Overall avian abundance, richness and diversity were low within seasons and across years. Shrubland birds were dominant during the period of study while open grassland species were in low numbers or absent from study sites. In general, variables associated with guild abundance varied among years and seasons due to differences in guild composition. Variables associated with abundance within the grassland guild were more consistent because of lower species diversity and less seasonal and annual turnover within the guild. The most consistent variable predicting grassland bird abundance at the guild level and in single-species models was the number of invasive shrubs, negatively associated with abundance. Grass cover, grass height, and degree of isolation were also important. The shrubland guild was strongly and positively associated with the density of invasive shrubs and the interaction between density of invasive shrubs and patch size, however this was not consistently reflected in the single species models. Some single-species models showed a negative association with invasive shrubs or the interaction between invasive shrubs and patch size indicating that some shrubland birds may be sensitive to levels of shrub encroachment. Single-species models for shrubland birds had variable associations with grass cover and height suggesting differences in vegetative growth among years and foraging strategies influenced site selection. This research suggests shrub encroachment into grasslands degrades grassland quality and influences species composition, making grassland patches unsuitable for open grassland species and possibly altering patch quality for some shrubland birds.

*Key Words:* avian guilds, Chihuahuan Desert, degree of isolation, desertification, grassland birds, invasive shrubs, landscape, patch size, shrub encroachment, shrubland birds.

### LA INFLUENCIA DE LA DESERTIFICACIÓN EN LA SELECCIÓN DE SITIO POR PARTE DE AVES ADAPTADAS A PASTIZALES Y AVES ADAPTADAS A ZONAS ARBUSTIVAS DURANTE LA ÉPOCA NO REPRODUCTIVA EN EL EXTREMO NORTE DEL DESIERTO CHIHUAHUENSE

*Resumen.* El proceso de desertificación se ha extendido ampliamente en el suroeste de los Estados Unidos, pero sus efectos sobre las comunidades de aves en época no reproductiva han sido poco estudiados. El incremento de plantas arbustivas es considerado como un importante indicador del proceso de desertificación. La asociación del paisaje y la vegetación local con comunidades de aves adaptadas a pastizales y zonas arbustivas durante la época no reproductiva fueron estudiadas en 27 fragmentos de pastizal en el Desierto Chihuahuense entre el 2003 y el 2006, con el fin de documentar los efectos de la degradación del hábitat y la fragmentación como resultado del proceso de desertificación sobre gremios de aves en el suroeste de Los Estados Unidos. La abundancia, riqueza y diversidad total de aves fueron bajas entre estaciones y a través de los años. Las aves adaptadas a zonas arbustivas dominaron a lo largo del periodo de estudio, mientras las especies especialistas de pastizales tuvieron bajas abundancias o estuvieron ausentes en los sitios de estudio. En general, las variables asociadas con la abundancia de gremios de aves, variaron entre años y estaciones, debido a diferencias en la composición de especies dentro de cada gremio. Las variables asociadas con la abundancia del gremio de aves de pastizal fueron más consistentes debido a una diversidad menor de especies y a un cambio menor en la composición de especies dentro de este gremio, entre estaciones y años. La variable más consistente en predecir la abundancia de aves de pastizal al nivel de gremio y de especies individuales, fue el número de arbustos invasores, ejerciendo una asociación negativa con la abundancia. La cobertura y la altura de pastos, junto con el grado de aislamiento del pastizal, fueron también variables importantes. El gremio de aves adaptadas a zonas con arbustivas estuvo fuertemente asociado de manera positiva con la densidad de arbustos invasores y con la interacción entre densidad de arbustos y área del pastizal, sin embargo esta respuesta a nivel de gremio no fue consistente con lo obtenido a nivel de especies individuales. Algunos de los modelos para especies individuales mostraron una asociación negativa con la densidad de arbustos invasores o con la interacción entre densidad de arbustos y área del pastizal,

indicando la posible sensibilidad de algunas especies propias de zonas arbustivas, a ciertos niveles de invasión de arbustos. Los modelos individuales para el gremio de aves adaptadas a zonas arbustivas mostraron asociaciones variables con la cobertura y altura de pastos, sugiriendo que diferencias en el crecimiento vegetativo entre años y diferentes estrategias de forrajeo influenciaron la selección del sitio. Este estudio sugiere que el grado de invasión de arbustos dentro del área del pastizal, degrada la calidad del mismo e influye en la composición de especies, convirtiendo estos fragmentos en áreas inhóspitas para aves propias de pastizal y posiblemente alterando la calidad del pastizal para algunas aves propias de zonas arbustivas.

In North America, birds associated with grasslands are exhibiting greater population declines than any other avian assemblage (Knopf 1994, Peterjohn and Sauer 1999, Coppedge et al. 2001). Similarly, 30% of shrubland birds are in decline (Sauer et al. 2006). Many bird species in these guilds are short-distance migrants that breed across the western US and southern Canada and winter in the southwestern US and northern Mexico (Howell and Webb 1995, Rising 2005). Declines have been attributed to various causes including habitat loss, degradation, and fragmentation on wintering, breeding, and migratory grounds due to agricultural activities, urban expansion, livestock grazing, habitat alteration, pesticide use, and climate change (Vickery et al 1999, Holmes and Sherry 2001, Jones and Bock 2002). The majority of research on these declining avian guilds has focused on breeding ecology and considerably less is known about non-breeding ecology, habitat use, and effects of habitat fragmentation and degradation during winter and migration (Helzer and Jelinski 1999, Coppedge et al. 2001).

In general, non-breeding birds have been found to use a wider range of habitats than breeding birds. For example, many migrant species in western Mexico broaden their habitat use in the non-breeding period to include agricultural hedgerows (Villaseñor and Hutto 1995). Seasonal changes in habitat use during stopover in Pennsylvania led Yahner (1993) to hypothesize that migrating birds may be less sensitive to fragmentation. During migration, birds do not have the opportunity to search for the most suitable stopover habitat and may be forced to use sub-optimal sites (Moore et al. 1990). Decisions involving the use of a patch, however, are scale dependent, extending from a landscape level to more local perspectives, and migrants have been found to be selective at the micro-habitat scale (Hutto 1985). Settlement at a stopover site must be driven by some ecological cues, and habitat selection during stopover should be related to the intrinsic suitability of the habitat (Moore and Simmons 1992, Kelly et al. 1999), extrinsic landscape factors (Maurer 1985, Dooley and Bowers 1998),

or a combination of the two. Selection of winter grounds should be driven by similar cues, such as resource availability (Pulliam and Dunning 1987, Ginter and Desmond 2005), but also by patch characteristics including patch size, shape, connectivity, and vegetative composition (Graham and Blake 2001, Pearson and Simons 2002).

In the southwestern US, large expanses of native perennial grasslands have been lost to shrub encroachment (Buffington and Herbel 1965, Brown 1982, Saab et al. 1995, Kerley and Whitford 2000). Where patches of intact grassland persist, these grasslands are frequently fragmented and degraded, with many experiencing various levels of isolation and shrub encroachment (Bahre and Shelton 1993, Reynolds et al. 1999). In the northern Chihuahuan Desert, the percentage of grasslands in the Jornada del Muerto Basin (New Mexico) has declined substantially. In 1858, grasslands comprised more than 80% of the area, whereas today grasses comprise only 7% of the landscape (Gibbens et al. 2005). By 1998, 59% of the area was occupied by honey mesquite (*Prosopis glandulosa*) and 25% by creosote bush (*Larrea tridentata*). The encroachment of shrubs into desert grasslands has irreversibly changed the landscape through the formation of coppice dunes where mesquite shrubs trap wind-blown sand (Gibbens et al. 1983, Gibbens and Beck 1988, Herrick et al. 1997). These landscape changes have resulted in increased runoff and soil erosion and increased invasion by non-native species (Herrick et al. 1997, Havstad et al. 2000).

The large-scale vegetation change occurring in the Chihuahuan Desert has been linked to desertification (Buffington and Herbel 1965, Schlesinger et al. 1990, Schlesinger 2002). Desertification is considered an essentially irreversible process in arid, semi-arid, and dry sub-humid areas where land degradation results from factors that include climatic variation and human activities (United Nations 1992). The reduction and alteration of vegetation cover and structure in the northern Chihuahua Desert has resulted in the formation of coppice dunes, reduced grass cover, and increased heterogeneity in soil resource

distribution. This shift in resources and the degradation of the landscape has contributed to a reduction in livestock carrying capacity, a decrease in biodiversity, alteration of nutrient cycling, and increased soil erosion (Nielson 1986, Whitford 1997, 2002). The exact cause of this shift is uncertain; however, excessive livestock grazing, climatic change, and fire suppression have been implicated as possible factors (Fredrickson et al. 1998). While a large body of literature has addressed abiotic factors associated with desertification and vegetation response in the Chihuahuan Desert, little research has addressed the response of vertebrates to the desertification process. Kerley and Whitford (2000) reported an increase in rodent abundance in shrub-encroached systems in the Chihuahuan Desert. Similarly, avian species richness and abundances were higher in desertified habitats due to the combination of species with affiliations to both shrubland and grassland habitats occupying these sites (Whitford 1997). While some grassland species may persist in degraded grasslands, species breeding in open grassland did not occupy degraded sites in south-central New Mexico and these sites have likely experienced a substantial turnover in species composition over the past 150 yr (Pidgeon et al. 2001).

In this study we examined the effects of desertification, including grassland fragmentation, shrub encroachment, and the subsequent reduction and alteration of vegetation cover and structure, on abundance of various grassland and shrubland bird species during the non-breeding period in the northern Chihuahuan Desert. We hypothesized that abundance of grassland and shrubland birds would be associated with factors at both within-patch and landscape scales. At the within-patch scale we predicted that: (1) heterogeneous grasslands (grasslands with higher shrub densities) would support more diverse bird communities than homogeneous grasslands due to the presence of species from both grassland and shrubland guilds, (2) grassland birds would respond negatively and shrubland birds would respond positively to shrub density, and (3) avian abundance and community composition would differ among grassland types. At the landscape scale we predicted that: (1) grassland bird abundance would be positively related to patch size and negatively related to degree of isolation and patch shape, and (2) the shrubland avian community would not be related to landscape characteristics because of the matrix of shrub habitats within which the remaining grassland patches are embedded.

## STUDY AREA AND METHODS

### STUDY AREA

Research was conducted on the Jornada Experimental Range (JER) and adjacent Chihuahuan Desert Rangeland Research Center (CDRRC) during the non-breeding period for three consecutive years, between September 2003 and May 2006. Together this area comprises a block of 104,166 ha located at the northern edge of the Chihuahuan Desert, in southcentral New Mexico (32°62'N, 106°74'W). The predominant use of these sites is for research related to rangeland and livestock management and long-term studies examining desertification processes in the Chihuahuan Desert. Livestock stocking densities were low across study sites, ranging from 2.6–16.5 animal unit year/section (AUU/S) (E. Fredrickson, pers. comm.). The predominant vegetation types representative of the Jornada del Muerto Basin are grasslands of black grama (*Bouteloua eriopoda*), tobosa (*Pleuraphis mutica*), and dropseed (*Sporobolus* sp.). Dominant native invasive shrubs include creosote bush, honey mesquite, and tarbush (*Flourensia cernua*). Non-invasive native shrubs or shrub-like plants include yucca (*Yucca* sp.), longleaf jointfir (*Ephedra trifurca*), and cholla (*Opuntia* sp.) (Allred 1988, Dick-Peddie et al. 1993, Schlesinger 1994).

The climate in south-central New Mexico typically consists of hot summers and mild winters. The average maximum temperature in June is 36°C; the average minimum temperature in December is -6.8°C. Precipitation averages 23 cm annually, with 52% occurring between July and September. Summer precipitation comes in the form of intense monsoonal thunderstorms that are highly localized (Sims et al. 1978, Conley and Conley 1984). Winter precipitation is less predictable and is characterized by low-intensity precipitation covering wide areas. The elevation of the study area is approximately 1,186 m (Jornada Basin Long Term Ecological Network 2006).

### PATCH SELECTION

We selected 27 grassland patches with each of nine patches being dominated by black grama, tobosa, and dropseed species, respectively. To select grassland patches as study sites, we used GIS vegetation maps of the JER and the CDRRC derived from photos and ground reconnaissance; variables included distribution, size, dominant vegetation type, and location of different grassland patches. Patch selection was

based on grassland type, topography (Renfrew and Ribic 2002), patch size, patch shape, and degree of isolation (Coleman et al. 1982, With and Crist 1995). Patch size ranged from 6.18 to 684 ha.

When possible, a continuous 1,000 m permanent transect for avian surveys was established centrally within each grassland fragment and marked at 100-m intervals. Due to variation in fragment shape and size, some transects ( $N = 12$ ) were composed of two or three segments, spaced by a minimum of 65 m (Whitmore 1979). Minimum distance between each 1,000 m transect was 384 m.

#### AVIAN SURVEYS

In the non-breeding seasons of 2003–2004, 2004–2005, and 2005–2006, study sites were surveyed three times each during the fall (1 September–15 October) and spring migration periods (15 March–30 April) and four times over the winter period (15 November–28 February), with the exception of fall 2004 when no surveys were conducted. This resulted in 2 yr of fall migration data and 3 yr of winter and spring migration data. Surveys of the same patch within a season were spaced at 3 days apart. Censuses were conducted within 4 hr after sunrise (Kirkpatrick et al. 2002). A single observer walked the transect, counting and identifying all birds within 30 m each side of the transect. Birds flying over or detected outside these 60,000 m<sup>2</sup> plots were not included in the analyses (Carlisle et al. 2004). Observers were careful to note the position and movement of birds to avoid double sampling. Surveys were not conducted during precipitation and winds speed exceeding 20 km/hr (Gutzwiller and Barrow 2002).

#### LANDSCAPE- AND WITHIN-PATCH-LEVEL VARIABLES

For each transect, we recorded a series of within-patch and landscape-level factors. ARC/INFO Software (Environmental Systems Research Institute 1990) was used to determine the area and perimeter of each grassland patch. To account for edge effects, we calculated the patch shape (perimeter-to-area ratio) and the length of disjunct edge types (Bender et al. 1998, Winter et al. 2000), differentiating between two edge types, shrubland edge (edge between the grassland patch and surrounding shrubland) and grassland edge (edge between the grassland patch and a different type of grassland patch), based on ARCVIEW maps. ARCVIEW maps of the study area were also used to calculate the percent of grass cover within 1,500 m

of the perimeter of each grassland patch as a measure of the degree of isolation.

Each winter we sampled 30 vegetation points stratified along each avian transect. Because grazing pressure was low across the study area, with an average of 9.35 (AUY/S) during the study period (E. Fredrickson, pers. comm.), vegetation sampling was conducted once annually following the growing season. We estimated percent canopy cover and percent cover of grass, forbs, and woody vegetation using a Daubenmire frame (Daubenmire 1959). Random and maximum grass heights were also recorded. Random grass height was measured at the closest standing grass and maximum grass height was defined as the tallest standing grass within 1 m of the far left corner of the frame. All shrubs within 1.5 m of each side of the transect were counted and identified, resulting in a measure of shrub density (number of shrubs per 3,000 m<sup>2</sup> within each patch). More specifically, we quantified the density and total number of native invasive shrubs, defined as shrub species (honey mesquite, creosote bush, and tarbush) that have increased substantially in abundance throughout the northern Chihuahuan Desert over the past 50 yr (Rango et al. 2005). The total number of invasive shrubs within a grassland patch was calculated from density of invasive shrubs per unit area multiplied by the area of the grassland patch. The invasive shrubs were the dominant shrub type (>60%) on each patch; on 21 out of the 27 plots greater than 85% of shrubs present were invasive.

#### STATISTICAL ANALYSIS

All landscape- and within-patch-level predictor variables were tested for normality and homogeneity of variance prior to the analysis, and nonparametric tests were used since assumptions could not be met. Differences in structural characteristics of the vegetation among the three grassland types were examined using the Kruskal-Wallis test. Bird abundance, species richness and Shannon-Weaver diversity indices (Zar 1999) were calculated at the within-patch level for each avian guild. The SPECRICH program (Hines 1996) was used to estimate species richness using the bootstrapping approach, to avoid bias by species detected only on a few occasions (Burnham and Overton 1979). Avian abundance, richness, diversity, and the abundance of grassland and shrubland birds were compared among the three grassland types using the Kruskal-Wallis test (denoted by  $H_1$ ), by season and year. We also compared vegetation variables among years and grassland types using the Kruskal-Wallis test.

Predictive analyses by individual species were difficult due to low sample sizes and a bimodal distribution of species numbers. Therefore we grouped species into shrubland and grassland assemblages and also attempted to model the dominant species for each guild for data analyses (Appendix 1). Guild composition was determined based on available information on non-breeding habitat associations (Raitt and Pimm 1976, Grzybowski 1982, Igl and Ballard 1999, Niemela 2002, Desmond 2004, Desmond et al. 2005), personal observations of scientists (M. Desmond, D. Griffin, C. Mendez, R. Meyer, and D. Krueper) familiar with non-breeding grassland and shrubland birds in the Southwest, and on information on breeding habitat associations (American Ornithologists' Union 1998, Sauer et al. 2006).

We selected a subset of landscape- and within-patch-level variables from the set of all measured explanatory variables predicted to have the greatest influence on assemblage abundances. These variables were selected based on important breeding habitat described in the literature, since literature addressing the importance of these predictor variables during the non-breeding season is limited, and relevance to ecological change in the southwest. The landscape-level variables considered for inclusion in the models were: (1) patch size, (2) patch shape, (3) degree of isolation, and (4) grassland type. The within-patch level variables were: (1) density of invasive shrubs, (2) mean percent grass cover, (3) mean random grass height, and (4) interaction between density of invasive shrubs and patch size. Patch shape was correlated with patch size (Pearson  $r^2 =$

0.83,  $P < 0.001$ ) and therefore only patch size was retained in models. Of all shrubs counted on plots, >60% were invasive shrubs. Dominant non-invasive shrubs were species not known to influence avian abundance (longleaf jointfir, prickly pear, and yucca), therefore, we felt invasive shrubs would have the greatest impact on avian occupancy of a plot and we chose to include this variable in models as a measure of desertification. Grassland type was not included in the models because no difference in bird guild abundance, species richness or diversity, were detected among grassland types (Kruskal-Wallis,  $P > 0.05$ ).

We performed Poisson multiple regression analyses to examine factors affecting shrubland and grassland avian abundances (count data) separately, by evaluating a set of 15 a priori balanced models, where each one of the chosen variables was represented an equal number of times (Table 1). These models represented hypotheses based on previous knowledge of habitat selection by wintering grassland and shrubland birds and the specific hypotheses of this study (Anderson and Burnham 2002). The number of parameters allowed in each model was limited by the sample size of  $N = 27$  and did not exceed six. Only two-way interaction terms were included.

We evaluated possible over-dispersion of Poisson models using the ratio of deviance/degrees of freedom (Littell et al. 2002) and models with severe over-dispersion (greater than one) were not considered further. Subsequently, we used Akaike's information criterion corrected for small sample sizes and over-dispersed data (QAIC<sub>c</sub>) for model ranking of the

TABLE 1. A PRIORI MODELS TESTED IN THE POISSON MULTIPLE REGRESSION ANALYSIS TO TEST RELATIONSHIPS BETWEEN AVIAN ABUNDANCES BY GUILD AND SELECTED PREDICTOR VARIABLES. MODEL PARAMETERS INCLUDE DENSITY OF INVASIVE SHRUBS, MEAN PERCENT GRASS COVER, PATCH SIZE, ISOLATION (DEFINED BY PERCENT GRASS COVER WITHIN 1,500 M OF THE GRASSLAND PERIMETER), MEAN RANDOM GRASS HEIGHT, AND THE INTERACTION OF DENSITY OF INVASIVE SHRUBS AND PATCH SIZE.

Model
Invasive shrubs, mean percent grass cover, mean random grass height, patch size, isolation, invasive shrubs x patch size.
Invasive shrubs.
Invasive shrubs, mean percent grass cover, mean random grass height.
Mean percent grass cover, mean random grass height.
Invasive shrubs x patch size.
Isolation, invasive shrubs x patch size.
Mean percent grass cover, mean random grass height, invasive shrubs x patch size.
Mean random grass height, patch size, invasive shrubs x patch size.
Isolation, invasive shrubs, invasive shrubs x patch size.
Isolation, mean percent grass cover, invasive shrubs x patch size.
Patch size, invasive shrubs.
Patch size, isolation.
Invasive shrubs, patch size, isolation.
Invasive shrubs, patch size, mean percent grass cover, mean random grass height.
Patch size, mean percent grass cover, mean random grass height, isolation.

a priori models (Burnham and Anderson 1998). A model containing main effects and relevant interactions was used as the global model for each season, by avian guild and common species (Anderson et al. 1994). Candidate models were evaluated using model weight ( $w_i$ ) and  $\Delta\text{QAIC}_c$ . We determined the five most parsimonious models for each guild and dominant species by season and year and calculated the deviance,  $\text{QAIC}_c$ ,  $\Delta\text{QAIC}_c$  and Akaike weights. However, in the interest of space, we only report the top three models in our tables. The relative importance of the predictor variables across the top five models ( $w + (j)$ ) was estimated by summing Akaike weights across the models in which each variable ( $j$ ) was present. In our discussion we focus on variables with cumulative model weight of 0.5 and higher. The GENMOD procedure in SAS (SAS Institute 1999) was used to fit the Poisson regression.

## RESULTS

Long-term mean precipitation for the study area (1992–2002) was 24.18 cm (Jornada Basin Long Term Ecological Network 2006). Mean precipitation in 2003 was low compared to the long-term average and relative to precipitation recorded in 2004 and 2005. Precipitation for 2004 was the highest; total annual values of 12.06 cm, 35.53 cm, and 21.81 cm were recorded for 2003, 2004, and 2005, respectively. Average winter temperatures during the study period were 7.9°C, 8.5°C, and 8.9°C for 2003–2004, 2004–2005, and 2005–2006, respectively.

Structural characteristics of the vegetation differed among the three winters, including mean percent canopy cover ( $H_1 = 24.61$ ,  $P = 0.0001$ ), mean percent grass cover ( $H_1 = 6.90$ ,  $P = 0.031$ ), mean percent forb cover ( $H_1 = 18.57$ ,  $P < 0.0001$ ) and mean maximum grass height ( $H_1 = 11.93$ ,  $P = 0.0025$ ), with all variables lowest in 2003–2004. For all years, differences were found among the three grassland types in mean percent canopy cover ( $H_1 = 9.46$ ,  $P = 0.009$ ;  $H_1 = 7.70$ ,  $P = 0.02$ ;  $H_1 = 8.13$ ,  $P = 0.01$ , for 2004, 2005, and 2006, respectively) and mean percent grass cover ( $H_1 = 7.62$ ,  $P = 0.02$ ;  $H_1 = 7.19$ ,  $P = 0.02$ ;  $H_1 = 10.40$ ,  $P = 0.005$ , for 2004, 2005, and 2006 respectively). Dropseed grasslands accounted for the lowest averages in mean percent canopy and grass cover. No differences were found in the number and density of invasive shrubs among years or grassland types.

## AVIAN SURVEYS

In the entire 2003–2004 non-breeding period, 60 bird species were recorded on plots compared

to 75 species for 2005–2006. Fifty bird species were recorded during winter and spring 2004–2005. Species richness was significantly different among seasons in all years ( $H_1 = 21.05$ ,  $P < 0.0001$  for 2003–2004;  $H_1 = 5.73$ ,  $P = 0.01$  for 2004–2005;  $H_1 = 6.15$ ,  $P = 0.04$  for 2005–2006), with two to three times more species observed during migration than winter (Table 2). Total avian abundance in spring was significantly different among years ( $H_1 = 26.39$ ,  $P < 0.0001$ ), with higher abundance during spring of 2006 compared to the springs of 2004 and 2005 (Table 2). Avian abundance in winter was significantly different among years ( $H_1 = 20.13$ ,  $P < 0.0001$ ), with the winter of 2005–2006 supporting significantly more birds than any other winter (Table 2). Fall abundance was significantly different between years ( $H_1 = 26.39$ ,  $P = 0.001$ ), with twice the number of birds observed in fall of 2005 than in 2003 (Table 2). Avian diversity was low across all seasons (Table 2).

Mean abundance of grassland and shrubland birds varied among the three non-breeding periods—fall migration, winter, and spring migration. Abundance of shrubland birds was significantly higher than grassland species across all seasons and years except for the fall 2003 when the difference was not significant ( $H_1 = 0.40$ ,  $P = 0.57$ ;  $H_1 = 6.69$ ,  $P = 0.001$  for falls 2003 and 2005, respectively;  $H_1 = 6.60$ ,  $P = 0.01$ ;  $H_1 = 10.29$ ,  $P = 0.001$ ;  $H_1 = 14.43$ ,  $P = 0.0001$  for winters 2003–2004, 2004–2005, and 2005–2006, respectively;  $H_1 = 6.01$ ,  $P = 0.01$ ;  $H_1 = 11.96$ ,  $P = 0.0005$ ;  $H_1 = 27.59$ ,  $P < 0.0001$  for springs 2004, 2005, and 2006, respectively). The fall of 2005 supported greater grassland and shrubland bird abundance and species richness compared to any other season (Table 2). The majority of dominant species (present in >40% of transects) in all years and seasons were shrubland birds. The dominant species during the fall migration period were Horned Lark (*Eremophila alpestris*) and Vesper Sparrow (*Pooecetes gramineus*) in both 2003 and 2005, as well as Loggerhead Shrike (*Lanius ludovicianus*), Brewer's Sparrow (*Spizella breweri*), Black-throated Sparrow (*Amphispiza bilineata*), Sage Sparrow (*Amphispiza belli*), and White-crowned Sparrow (*Zonotrichia leucophrys*) in 2005. The dominant species in all winters was Sage Sparrow, occurring on 46%, 68%, and 70% of transects for the winters of 2003–2004, 2004–2005, and 2005–2006, respectively. In the winter of 2004–2005, Horned Lark, Brewer's Sparrow and meadowlark species (*Sturnella* sp.) were also dominant (Appendix 1). During spring migration, Black-throated Sparrow was the dominant species each year (on 68%, 46%, and 74% of transects for 2004, 2005, and 2006, respectively). In addition,

TABLE 2. WITHIN-PATCH MEAN RELATIVE AVIAN ABUNDANCE  $\pm$  SD, DIVERSITY AND RICHNESS BY YEAR AND SEASON FOR EACH OF THE 60,000 M<sup>2</sup> PLOTS.

	Fall		Winter			Spring		
	2003	2005	2003-2004	2004-2005	2005-2006	2004	2005	2006
Grassland birds	3.36 $\pm$ 4.86	4.98 $\pm$ 1.92	0.30 $\pm$ 0.66	0.72 $\pm$ 0.96	1.38 $\pm$ 0.36	0.96 $\pm$ 1.20	0.84 $\pm$ 1.32	1.32 $\pm$ 0.48
Shrubland birds	4.32 $\pm$ 3.96	9.78 $\pm$ 2.52	1.62 $\pm$ 2.16	3.42 $\pm$ 3.00	6.12 $\pm$ 1.62	2.28 $\pm$ 1.92	3.60 $\pm$ 4.80	8.46 $\pm$ 2.04
Abundance	7.74 $\pm$ 5.88	14.76 $\pm$ 3.66	1.92 $\pm$ 2.22	3.90 $\pm$ 3.00	7.50 $\pm$ 1.80	3.30 $\pm$ 2.04	4.44 $\pm$ 3.00	9.78 $\pm$ 1.98
Diversity	0.06	0.08	0.02	0.03	0.04	0.04	0.04	0.05
Richness	6.02 $\pm$ 1.50	4.94 $\pm$ 1.49	1.30 $\pm$ 0.75	0.74 $\pm$ 0.36	2.26 $\pm$ 0.76	3.34 $\pm$ 1.19	2.82 $\pm$ 1.16	4.24 $\pm$ 1.03

in 2006 Mourning Dove (*Zenaida macroura*), Western Kingbird (*Tyrannus verticalis*), Horned Lark, Brewer's Sparrow, and White-crowned Sparrow were also dominant.

#### LANDSCAPE- AND WITHIN-PATCH-LEVEL ASSOCIATIONS

Avian abundances (total and by guilds), richness and diversity did not differ among the three grassland types (Kruskal-Wallis,  $P > 0.05$ ) within each season and year. Poisson regression models included within-patch and landscape scale variables for grassland and shrubland bird guilds and the most abundant or dominant species per guild (Tables 3-6).

#### Grassland bird-guild models

Density of invasive shrubs, degree of isolation, mean percent grass cover, and mean random grass height were the most consistent variables associated with the abundance of grassland birds across sampling periods (Table 3). These variables consistently had the highest cumulative model weights (Table 7). Density of invasive shrubs, the most consistent variable present in models, was negatively associated with grassland bird abundance across years and seasons, except in winter 2005-2006. In winter 2003-2004, spring 2004, and spring 2005 this variable was present in three-five of the top models for each season with cumulative model weights ranging from 0.59-1.00. Degree of isolation was negatively associated with the abundance of grassland birds across years and seasons (lower bird abundance on grassland patches surrounded by less grassland), except spring 2006. This variable was most important during fall 2003 and spring 2004 with cumulative model weights of 1.00 and 0.76, respectively.

Mean percent grass cover was an important variable associated with grassland bird abundance in several models across seasons and years. In the fall 2005, winter of 2003-2004, and spring 2006, this variable was present in all five models with cumulative model weights of 1.00. Across seasons this variable had a positive association with grassland bird abundance, except for the winter 2003-2004 (Table 3). Mean random grass height was strongly associated with abundance of grassland birds in the same models as the mean percent grass cover; negatively associated with abundance in the fall 2005 and winter of 2003-2004, and positively associated with abundance in the spring of 2006 (Table 3), with cumulative model weights of 1.00 for these seasons (Table 7).

TABLE 3. TOP THREE A PRIORI MODELS FOR THE GRASSLAND BIRD GUILD BY SEASON AND YEAR. EXPLANATORY VARIABLES ARE: DENSITY OF INVASIVE SHRUBS (IS), MEAN PERCENT GRASS COVER (GC), PATCH SIZE (PS), ISOLATION (I), MEAN RANDOM GRASS HEIGHT (GH), AND INTERACTION OF DENSITY OF INVASIVE SHRUBS AND PATCH SIZE (IS X PS). SAMPLE SIZE  $N = 27$ . TOP FIVE A PRIORI MODELS WERE USED FOR ANALYSES BUT ONLY THE TOP THREE ARE PRESENTED.

Season/year/models	Dev/df	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	$w_i$
Fall 2003				
-I -IS x PS	11.50	-82.41	0.00	0.30
-PS -I	11.50	-82.40	0.02	0.30
-IS -PS -I	11.11	-81.58	0.83	0.20
Fall 2005				
+GC -GH +IS x PS	8.20	-212.83	0.00	0.39
+GC -GH	8.69	-212.76	0.07	0.37
-IS +GC -GH	8.88	-210.78	2.05	0.14
Winter 2003–2004				
-IS -GC -GH	2.75	10.31	0.00	0.45
-GC -GH -IS x PS	2.94	11.80	1.49	0.21
-GC -GH	3.14	11.96	1.65	0.20
Winter 2004–2005				
-IS x PS	4.84	-5.95	0.00	0.37
-IS	4.97	-5.32	0.63	0.27
+GC -GH	4.85	-4.48	1.47	0.18
Winter 2005–2006				
+IS	6.50	-24.59	0.00	0.36
+IS x PS	6.59	-24.28	0.31	0.31
-PS +IS	6.72	-22.39	2.19	0.12
Spring 2004				
-I -IS -IS x PS	3.63	-18.34	0.00	0.38
-IS -PS -I	3.65	-18.22	0.13	0.35
-IS +GC -GH	3.84	-16.98	1.36	0.19
Spring 2005				
-IS	3.22	3.42	0.00	0.54
-PS -IS	3.34	5.72	2.30	0.17
-IS +GC -GH	3.13	6.37	2.95	0.12
Spring 2006				
+GC +GH	3.62	-43.38	0.00	0.46
+PS +GC +GH +I	3.45	-41.51	1.87	0.18
-IS +GC +GH	3.71	-41.27	2.11	0.16

#### *Grassland bird-species models*

Horned Lark was consistently the most abundant and dominant grassland species on plots across seasons and years (Appendix 1). Similar to the guild models, Horned Lark abundance was most strongly associated with invasive shrubs (negatively except in winter 2005–2006), degree of isolation, mean percent grass cover (positive), and mean random grass height (mix of positive and negative associations; Table 4). Degree of isolation was strongly and negatively associated with abundance in fall 2003, spring 2004, and spring 2005.

#### *Shrubland bird-guild models*

Density of invasive shrubs and the interaction between density of invasive shrubs and patch size were the most consistent variables associated with shrubland bird abundance across seasons and years (Table 5). The density of invasive shrubs was positively associated

with shrubland bird abundance in all seasons and years with the exception of spring 2004 and winter 2004–2005. This variable had a particularly strong association with shrubland birds in the fall 2003 and spring 2006, with cumulative model weights of 0.50 and 0.88, respectively (Table 7). The interaction between density of invasive shrubs and patch size was also strongly associated with shrubland bird abundance with cumulative model weights for fall 2005, winter 2005–2006, spring 2004 and spring 2005 ranging between 0.51 and 0.82 (Table 7). This variable was positively associated with shrubland bird abundance in all seasons and years except spring 2004 when the relationship was negative.

#### *Shrubland bird-species models*

Abundance and dominance of shrubland bird species was less consistent across seasons and years than grassland species. Sage Sparrow was consistently the most abundant species in

TABLE 4. TOP THREE A PRIORI MODELS FOR HORNED LARK. EXPLANATORY VARIABLES ARE: DENSITY OF INVASIVE SHRUBS (IS), MEAN PERCENT GRASS COVER (GC), PATCH SIZE (PS), ISOLATION (I), MEAN RANDOM GRASS HEIGHT (GH), AND INTERACTION OF DENSITY OF INVASIVE SHRUBS AND PATCH SIZE (IS X PS). SAMPLE SIZE  $N = 27$ . TOP FIVE A PRIORI MODELS WERE USED FOR ANALYSES BUT ONLY THE TOP THREE ARE PRESENTED.

Season/year/models	Dev/df	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	$w_i$
Fall 2003				
-IS +PS -I	4.96	-12.92	0.00	0.37
-I -IS +IS x PS	4.98	-12.85	0.07	0.36
-IS x PS	6.07	-11.02	1.90	0.15
Fall 2005				
+GC -GH	11.00	-56.82	0.00	0.42
-IS +GC -GH	11.00	-55.21	1.61	0.19
-I +GC -IS x PS	11.07	-55.08	1.75	0.18
Winter 2004–2005				
-IS	5.64	7.06	0.00	0.44
-PS -IS	5.44	7.66	0.60	0.27
+GC -GH	5.67	8.60	1.53	0.16
Winter 2005–2006				
+IS	4.11	2.64	0.00	0.32
+IS x PS	8.29	2.87	0.23	0.29
-PS -I	8.23	4.06	1.42	0.16
Spring 2004				
-I -IS -IS x PS	3.46	-9.08	0.00	0.48
-IS -PS -I	3.63	-7.56	1.53	0.23
-IS +GC -GH -PS -I +IS x PS	3.04	-7.24	1.84	0.19
Spring 2005				
-IS +GC -GH	1.13	9.04	0.00	0.55
-IS +GC -GH -PS -I +IS x PS	0.90	9.41	0.38	0.45
-IS	1.67	21.61	12.57	0.001
Spring 2006				
-IS +GC +GH	2.89	-5.87	0.00	0.35
+GC +GH	3.07	-5.64	0.24	0.31
-IS -PS +GC +GH	2.85	-4.60	1.27	0.18

all three winters (Appendix 1). Mean percent grass cover negatively, and mean random grass height positively, were associated with Sage Sparrow abundance across winters (Table 6), with cumulative model weights ranging from 0.48–1.00 (Table 7). Black-throated Sparrow was dominant and abundant over fall and spring migration. Vegetation structure was most strongly associated with abundance in fall. Mean random grass height negatively impacted abundance in both years (cumulative model weights ranging from 0.62–1.00); mean percent grass cover negatively impacted abundance in fall 2003 and positively impacted abundance in fall 2005 (Table 6). The interaction between invasive shrub density and patch size (total number of shrubs) was most influential in spring, showing a negative association with Black-throated Sparrow abundance (cumulative model weights ranging from 0.40–0.59).

## DISCUSSION

As predicted, heterogeneous grasslands did support a greater diversity of birds. This was mainly due to the greater diversity of shrubland

species occupying shrub-encroached grasslands. In addition, some grassland species, such as meadowlark species and Horned Lark have been found to exhibit flexibility, occupying both open grasslands and shrub-invaded grasslands (Whitford 1997). However, our observations that Horned Lark was, in general, negatively associated with invasive shrubs (except winter 2005–2006) conflicts with Whitford (1997) and may emphasize differences in habitat associations for breeding compared to non-breeding Horned Lark.

We predicted that landscape-scale variables such as patch size, shape, and degree of isolation would impact migratory and wintering grassland birds in a way similar to observed effects on breeding grounds (Graham and Blake 2001, Pearson and Simons 2002). However, we did not observe important grassland bird associations with patch size or shape. This could be related to differences in landscape fragmentation on breeding and non-breeding grounds or to differences in the response of breeding and non-breeding grassland birds to fragmentation. In the Chihuahuan Desert, desertification processes contribute to the fragmentation of

TABLE 5. TOP THREE A PRIORI MODELS FOR THE SHRUBLAND BIRD GUILD BY SEASON AND YEAR. EXPLANATORY VARIABLES ARE: DENSITY OF INVASIVE SHRUBS (IS), MEAN PERCENT GRASS COVER (GC), PATCH SIZE (PS), ISOLATION (I), MEAN RANDOM GRASS HEIGHT (GH), AND INTERACTION OF DENSITY OF INVASIVE SHRUBS AND PATCH SIZE (IS X PS). SAMPLE SIZE N = 27. TOP FIVE A PRIORI MODELS WERE USED FOR ANALYSES BUT ONLY THE TOP THREE ARE PRESENTED.

Season/year/models	Dev/df	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>
Fall 2003				
+IS	7.53	-62.88	0.00	0.38
+IS x PS	7.76	-62.26	0.62	0.28
+PS +IS	7.82	-60.61	2.27	0.12
Fall 2005				
+IS x PS	16.25	-187.05	0.00	0.40
+IS	16.59	-186.60	0.46	0.32
+GC -GH	16.47	-185.30	1.75	0.17
Winter 2003–2004				
+IS x PS	8.12	-13.52	0.00	0.35
+IS	8.28	-13.11	0.41	0.29
+PS +I	8.36	-11.44	2.08	0.13
Winter 2004–2005				
-IS	12.53	-73.08	0.00	0.36
+IS x PS	12.79	-72.58	0.50	0.28
+GC +GH	12.34	-72.05	1.03	0.21
Winter 2005–2006				
+IS x PS	22.95	-110.66	0.00	0.44
-GC -GH	22.25	-109.85	0.80	0.29
-GC -GH +IS x PS	22.75	-107.72	2.94	0.10
Spring 2004				
-IS x PS	4.07	-53.49	0.00	0.37
-IS	4.25	-52.53	0.96	0.23
+I -IS x PS	4.10	-51.80	1.69	0.16
Spring 2005				
+IS x PS	7.85	-57.36	0.00	0.49
-I +IS x PS	7.78	-56.07	1.29	0.25
+PS -I	8.02	-55.43	1.93	0.18
Spring 2006				
+IS	11.34	-210.63	0.00	0.54
-PS +IS	11.66	-208.58	2.05	0.19
-GH -PS +IS x PS	11.34	-207.55	3.09	0.12

grasslands by a gradual interspersation of invasive shrubs into remnant grasslands, degrading grassland quality, and making it difficult to identify patch boundaries from surrounding shrublands (Mason et al. 2005). This is substantially different from traditional views of fragmentation where patch edges have distinct boundaries created by agricultural fields and forests that are easily identifiable and have been found to influence avian abundance and species composition (Winter et al. 2000, Davis 2004). The gradual fragmentation and degradation of grasslands in the Chihuahuan Desert appears to have rendered these patches unsuitable for most grassland species, and may explain why landscape-scale factors such as patch size and shape were not more important in this study.

Although not important during winter for grassland species, the degree of patch isolation was important for grassland species during two migratory periods. The lower densities for the grassland bird guild in the most isolated grassland patches (patches surrounded by less

grassland) in fall 2003 were heavily influenced by the responses of Horned Lark, which was strongly negatively associated with degree of isolation in fall 2003 and spring 2004 and 2005. Although Horned Lark is a resident species in our study area, our abundance data suggest a large influx of migrants passed through the area in fall 2003, fall 2005 and spring 2004. These data suggest that isolated grassland patches across a highly fragmented landscape may be important stopover sites for Horned Lark, a generalist grassland species. However, the absence of open grassland species suggests these fragments are not suitable stopover sites for grassland specialist species. Consistent with our predictions, we did not observe shrubland bird densities to be associated with any landscape level characteristics.

For guilds and species models, we predicted several responses to within-patch-scale variables. Dominant variables associated with abundance within guilds varied among years and seasons, suggesting that variation in

TABLE 6. TOP THREE A PRIORI MODELS FOR SAGE AND BLACK-THROATED SPARROWS BY SEASON AND YEAR. EXPLANATORY VARIABLES ARE: DENSITY OF INVASIVE SHRUBS (IS), MEAN PERCENT GRASS COVER (GC), PATCH SIZE (PS), ISOLATION (I), MEAN RANDOM GRASS HEIGHT (GH), AND INTERACTION OF DENSITY OF INVASIVE SHRUBS AND PATCH SIZE (IS X PS). SAMPLE SIZE N = 27. TOP FIVE A PRIORI MODELS WERE USED FOR ANALYSES BUT ONLY THE TOP THREE ARE PRESENTED.

Season/year	Model	Dev/df	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>
Black-throated Sparrow					
Fall 2003	-GC -GH	1.53	19.56	0.00	0.57
	-GC -GH +IS x PS	1.59	22.04	2.48	0.17
Fall 2005	+IS -GC -GH	1.59	22.07	2.51	0.16
	-IS	4.88	-45.43	0.00	0.38
	+GC -GH	4.69	-45.09	0.34	0.32
	+GC -GH +IS x PS	4.69	-43.58	1.85	0.16
Sage Sparrow					
Winter 2003-2004	-GC +GH	6.06	1.64	0.00	0.38
	-GC +GH +IS x PS	5.86	2.52	0.88	0.24
	-I -GC +IS x PS	5.91	2.68	1.03	0.22
Winter 2004-2005	-IS -GC +GH	7.92	-21.33	0.00	0.41
	-I -IS +IS x PS	8.56	-19.66	1.67	0.18
	-IS +PS -I	8.61	-19.53	1.80	0.17
Winter 2005-2006	-IS x PS	8.30	-29.46	0.00	0.45
	-GC +GH	8.13	-28.50	0.96	0.28
	-GC +GH -IS x PS	8.23	-26.62	2.84	0.11
Black-throated Sparrow					
Spring 2004	+I -IS x PS	2.49	12.79	0.00	0.35
	-PS +I	2.51	13.09	0.30	0.30
	-PS +GC -GH +I	2.30	14.21	1.42	0.17
Spring 2005	-IS x PS	2.24	23.54	0.16	0.31
	+IS	2.24	23.62	0.24	0.30
	-PS +IS	2.23	24.99	1.61	0.15
Spring 2006	-IS x PS	4.18	-10.61	0.00	0.38
	-IS	4.27	-9.97	0.64	0.28
	+I -IS x PS	4.21	-8.82	1.79	0.16

community composition at the guild level had a large influence on avian abundance and how the guild responded to within-patch explanatory variables.

Variables associated with abundance within the grassland guild were more consistent than the shrubland guild because of lower species diversity and less seasonal and annual turnover within this guild. The negative association of this guild with shrub encroachment is consistent with our predictions and with the literature for many grassland species (Whitmore 1981, Herkert 1994, Coppedge et al. 2001, Desmond 2004); it is most strongly reflected in the single species models for Horned Lark. This suggests that some patches were sufficiently degraded by shrub encroachment that even a grassland generalist species, such as the Horned Lark, avoided them. The mainly positive association of this guild with grass cover and negative association with grass height is reflected in the single species models for Horned Lark, consistent with Desmond et al. (2005), who reported similar results for wintering Horned Lark in Chihuahua, Mexico, and may well be driven by this species due to the lack of diversity in the grassland guild. Other studies, however, have

reported Horned Lark to be associated with heterogeneous grass cover and overgrazing during winter (Beason 1995, Kelly et al. 2006)

The shrubland bird guild was most strongly associated with density of invasive shrubs and the interaction between density of invasive shrubs and patch size, with both variables being positively associated with abundance (except spring 2004 and winter 2004-2005). However this was not consistently reflected in the single species models for Sage Sparrow and Black-throated Sparrow which did not exhibit a consistent association (positive, negative, strong, or weak) with invasive shrub density. These results are not consistent with studies on breeding Sage and Black-throated Sparrows that have found both species to be positively associated with shrub cover (Misenhelter and Rotenberry 2000, Pidgeon et al. 2006). Although the Sage Sparrow was consistently a dominant winter species in our study, the presence of other common species in winters 2003-2004 (Brewer's Sparrow) and 2005-2006 (Chipping Sparrow [*Spizella passerina*] and Lark Bunting [*Calamospiza melanocorys*]) likely influenced habitat associations at the guild level. Similar fluctuations were observed during migration

TABLE 7. RELATIVE IMPORTANCE OF PREDICTOR VARIABLES USED IN A PRIORI MODELS BY CUMULATIVE MODEL WEIGHT. VALUES ARE ORDERED BY AVIAN GUILD AND SEASON. VARIABLES ARE: DENSITY OF INVASIVE SHRUBS (IS), MEAN PERCENT GRASS COVER (GC), PATCH SIZE (PS), ISOLATION (I), MEAN RANDOM GRASS HEIGHT (GH), AND INTERACTION OF DENSITY OF INVASIVE SHRUBS AND PATCH SIZE (IS X PS).

Variable	Fall			Winter			Spring		
	2003	2005	2005	2003-2004	2004-2005	2005-2006	2004	2005	2006
<b>Guild level</b>									
<b>Grassland birds</b>									
PS	0.51	0.10	0.14	0.00	0.23	0.43	0.22	0.22	0.22
IS	0.40	0.18	0.59	0.27	0.48	1.00	0.88	0.88	0.20
I	1.00	0.10	1.00	0.18	0.22	0.76	0.00	0.00	0.22
GC	0.01	1.00	1.00	0.23	0.00	0.27	0.29	0.29	1.00
GH	0.01	1.00	1.00	0.18	0.00	0.27	0.29	0.29	1.00
IS x PS	0.50	0.43	0.22	0.55	0.42	0.41	0.00	0.00	0.20
<b>Individual species level</b>									
<b>Horned Lark</b>									
PS	0.38	0.06	- <sup>a</sup>	0.40	0.26	0.44	0.447	0.447	0.34
IS	0.74	0.24	-	0.71	0.32	0.92	1.00	1.00	0.60
I	0.85	0.18	-	0.12	0.29	0.98	0.448	0.448	0.16
GC	0.12	1.00	-	0.28	0.00	0.29	0.997	0.997	1.00
GH	0.01	0.82	-	0.29	0.10	0.21	0.997	0.997	1.00
IS x PS	0.63	0.33	-	0.25	0.52	0.75	0.447	0.447	0.07
<b>Guild level</b>									
<b>Shrubland birds</b>									
PS	0.23	0.06	0.24	0.00	0.00	0.24	0.18	0.18	0.35
IS	0.50	0.32	0.40	0.45	0.09	0.33	0.08	0.08	0.88
I	0.22	0.00	0.25	0.00	0.08	0.30	0.51	0.51	0.00
GC	0.00	0.22	0.00	0.36	0.56	0.00	0.00	0.00	0.15
GH	0.00	0.28	0.00	0.36	0.48	0.00	0.00	0.00	0.27
IS x PS	0.39	0.51	0.47	0.34	0.62	0.53	0.82	0.82	0.12
<b>Individual species level</b>									
<b>Black-throated Sparrow</b>									
PS	0.10	0.01	-	-	-	0.49	0.39	0.39	0.13
IS	0.21	0.52	-	-	-	0.02	0.45	0.45	0.28
I	0.05	0.01	-	-	-	1.00	1.00	1.00	0.34
GC	1.00	0.62	-	-	-	0.35	0.00	0.00	0.05
GH	1.00	0.62	-	-	-	0.19	0.09	0.09	0.00
IS x PS	0.17	0.17	-	-	-	0.53	0.40	0.40	0.59
<b>Sage Sparrow</b>									
PS	-	-	0.16	0.41	0.00	-	-	-	-
IS	-	-	0.08	0.87	0.09	-	-	-	-
I	-	-	0.30	0.35	0.07	-	-	-	-
GC	-	-	1.00	0.52	0.55	-	-	-	-
GH	-	-	0.78	0.65	0.48	-	-	-	-
IS x PS	-	-	0.46	0.31	0.63	-	-	-	-

<sup>a</sup> not available.

resulting in inconsistent effects of invasive shrubs on guild abundance across years and seasons. This variability suggests that some shrubland species may have a stronger affinity to shrub density than others, but data encompassing the entire range of shrub densities would be necessary to test this. Finally, our measurements focused on the density of invasive shrubs and not the density of total shrubs and it is possible that birds may have been responding more to total shrub density. However, we do not think this is likely because the shrubs not included as invasive shrubs that most strongly influenced total shrub density (longleaf jointfir, prickly pear, and yucca) are not the types of shrubs typically associated with shrubland birds.

Our other measure of invasive shrubs, the interaction between invasive shrub density and patch size, presents an interesting comparison to the associations showed by invasive shrub density. This variable represents the total number of shrubs in a grassland patch. In general, the effect of this variable was consistent with that of invasive shrub density at the guild level, positively associated with the number of shrubland birds, suggesting that the abundance of shrubland birds was higher in grassland patches with a greater number and density of invasive shrubs (except spring 2004). However, results were not consistent for single species models. The observed positive association of Sage Sparrow with the total number of invasive shrubs in winter 2004–2005 but negative association with invasive shrub density indicates a possible sensitivity to shrub density, while the negative association with total number of invasive shrubs in the following winter but no association with density indicates possible avoidance of shrubs. The Black-throated Sparrow had no strong association with the total number of invasive shrubs during fall but was consistently negatively associated with this variable in spring suggesting possible seasonal shrub affiliations. A threshold level of shrub encroachment, beyond which select shrubland species will not occupy a patch, independent of its size may exist, however additional research, that includes shrub dominated plots, would be necessary to address this.

Vegetation variables (grass cover and height) were of little importance for shrubland birds at the guild level but were important in several single species models. The use of guilds may have masked important individual species associations with vegetation variables. Vegetation characteristics were important for Black-throated Sparrow during fall migration only. This species was strongly negatively associated

with mean random grass height in both falls, suggesting Black-throated Sparrow forages in a shrubland with a low stature understory. Sage Sparrow was positively associated with mean random grass height and negatively associated with mean percent grass cover in all three winters suggesting they consistently occupied shrub-dominated grasslands with an understory of tall but heterogeneous grass cover.

Contrary to our predictions, we did not detect differences in avian abundance, richness or diversity among grassland types. Although black grama, tobosa, and dropseed grasslands vary substantially in horizontal and vertical structure we only detected a consistent (not significant) lower species richness in *Sporobolus* sp. grasslands throughout the period of study. This lack of differences among grassland types may, in part, be related to the low avian abundance and richness across seasons and years. In addition, dropseed grasslands may have been dominated by fewer species that were better adapted to foraging on the small seed size produced in this grassland type. Niemela (2002) found a positive correlation between Horned Lark abundance and the production of *Sporobolus* sp. seeds in semidesert grasslands suggesting some species may exploit specific seed types.

Pulliam and Mills (1977) were able to predict the number of dominant species and bill sizes based on seed types in southwest Arizona. In this study, the Horned Lark was the third most abundant species in dropseed grasslands in 2004–2005, and together with Sage and Brewer's Sparrow, comprised >90% of all individuals detected in this grassland type. The distribution and abundance of forbs (not measured in this study) may also have an important role in the distribution and abundance of granivorous sparrows, as forb seeds have been found to be important in the diets of many sparrows (Pulliam 1980, 1986; Desmond et al., *this volume*)

Bird species abundance and dominance, and guild abundance and composition underwent substantial seasonal and among-year fluctuations throughout the period of this study, perhaps partially due to variation in food abundance, a factor not addressed in this study. The majority of species studied are granivorous during the non-breeding season (Raitt and Pimm 1976, Bock and Bock 1999) and are dependent on seed production which can vary by orders of magnitude among years, linked to the amount and pattern of monsoonal summer precipitation (Pulliam and Parker 1979, Dunning and Brown 1982, Niemela 2002). Pulliam and Mills (1977) found the winter sparrow community was more diverse in years when higher precipitation

resulted in higher seed production. Similarly, we observed only one dominant resident (Sage Sparrow) when seed availability was likely low due to below normal precipitation, but three-five species when conditions for seed production improved. Pulliam and Dunning (1987) suggested that winter sparrows are facultative migrants only traveling as far south as necessary to find a seed supply capable of supporting them throughout the winter period. Therefore, avian abundance and diversity in the northern portion of wintering grounds (including southern New Mexico) should fluctuate with precipitation patterns as observed in this study. Although we experienced years of high rainfall and associated higher abundance and diversity of birds, we observed an absence of open grassland species (i.e., Grasshopper [*Ammodramus savannarum*], Baird's [*Ammodramus bairdii*], and Savannah [*Passerculus sandwichensis*] Sparrows, Chestnut-collared Longspur [*Calcarius ornatus*], and Sprague's Pipit [*Anthus spragueii*]), despite historical records of their presence in our study area (Jornada Basin Long Term Ecological Network 2006). These species were all common winter migrants occupying grasslands in the vicinity of our study area. The paucity of grassland species despite favorable conditions for seed production, suggests that other conditions rendered these patches unsuitable for occupation by most grassland species.

Migrants have been found to be less selective of habitat characteristics during the non-breeding season (Yahner 1993, Villaseñor and Hutto 1995) and patch quality may not be driving site selection for many species as they head toward wintering or breeding grounds (Moore et al. 1990). This may be particularly pertinent in the spring as through migrants move quickly northward to breeding grounds to acquire territories, but may be confounded by partial migrants that arrive early on breeding territories in our study area (i.e., Black-throated Sparrow and Horned Lark). This, along with differences in precipitation and vegetative growth among years and the foraging strategies of various species, particularly shrubland birds, likely contributed to the variable associations with within-patch characteristics in this study.

Some caution should be exercised when interpreting these results among seasons and years. First, any grouping of avian guilds masks unique life history characteristics associated with individual species (Mannan et al. 1984). For example, both *Ammodramus* sparrows and longspurs are open grassland species. However *Ammodramus* sparrows tend to be solitary and associated with medium to dense grass cover while longspurs are flocking and associated with

vegetation of much shorter stature (Desmond et al. 2005). By pooling species into a guild, some of these associations with within-patch characteristics are lost. Second, this analysis considered only semi-desert grassland fragments in the northern Chihuahuan Desert. Many of these species are widely distributed during the non-breeding period and our study area is in the northern part of the wintering grounds for many grassland and shrubland species. Population patterns observed in this study may be related to conditions in other parts of the non-breeding range of these short distance migrants. For example, Pulliam and Parker (1979) found winter Chipping Sparrow abundance was higher in the Sierra Madre Occidental of Mexico when seed production was poor in southeast Arizona. Finally, abundance alone is a poor indicator of habitat quality. Pidgeon et al. (2006) found Black-throated Sparrow abundance in Chihuahuan Desert grasslands was highest and negatively correlated with fecundity and nest success in mesquite dominated areas; these mesquite encroached habitats acted as ecological traps, suggesting factors other than avian abundance, such as measures of individual condition, should be used to assess suitability of habitat during the non-breeding season.

#### MANAGEMENT IMPLICATIONS

Desertification is a major conservation issue in the northern Chihuahuan Desert. Grassland patches embedded in a matrix of shrub-dominated landscapes as defined in this study no longer appear to be suitable for many migrant and wintering grassland species requiring open grassland habitat. Shrubland birds may also be sensitive to the density and distribution of invasive shrubs. Thresholds levels may exist beyond which select shrubland species will no longer occupy a patch. Research on shrubland species should address habitat associations and measures of avian condition across a gradient of shrub density and patchiness. Management efforts across the Chihuahuan Desert should identify and protect remaining expanses of desert grasslands that have not been impacted by invasive shrub encroachment. Avian community composition varies substantially among seasons and years apparently due to variation in seed production, and it is essential that suitable habitat exists throughout the non-breeding range of these short-distance migrants. Many grassland and shrubland species winter across the area that extends from southeastern Arizona, through southern New Mexico, and southern Texas, south into the Mexican Plateau to the states of

Zacatecas and San Luis Potosí; a region that has been, and continues to be, strongly impacted by desertification processes.

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APPENDIX 1. BIRDS INCLUDED IN THE GRASSLAND AND SHRUBLAND GUILDS. MEAN RELATIVE ABUNDANCE FOR EACH OF THE 60,000 M<sup>2</sup> PLOTS ARE GIVEN FOR EACH SPECIES AND SEASON.

	Fall						Winter						Spring					
	2003		2005		2003–2004		2004–2005		2005–2006		2004		2005		2006			
<b>Grassland birds</b>																		
Scaled Quail ( <i>Callipepla squamata</i> )	0.30	0.30	- <sup>a</sup>	-	-	-	-	-	-	-	0.01	0.02	0.12	0.12	-	-		
Northern Harrier ( <i>Circus cyaneus</i> )	0.01	0.04	-	0.02	0.03	-	-	-	-	-	-	-	-	-	0.06	-		
Swainson's Hawk ( <i>Buteo swainsoni</i> )	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Ferruginous Hawk ( <i>Buteo regalis</i> )	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
American Kestrel ( <i>Falco sparverius</i> )	-	0.04	0.01	-	-	-	-	-	-	-	-	0.02	0.01	0.01	-	-		
Prairie Falcon ( <i>Falco mexicanus</i> )	-	0.01	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-		
Burrowing Owl ( <i>Athene cunicularia</i> )	0.06	0.02	-	<0.01	<0.01	-	-	-	-	-	0.02	-	-	-	0.01	-		
Say's Phoebe ( <i>Sayornis saya</i> )	0.02	0.06	0.02	-	0.02	0.02	0.02	0.02	0.02	0.04	0.04	0.01	0.01	0.06	0.06	0.66 <sup>b</sup>		
Horned Lark ( <i>Eremophila alpestris</i> )	1.26 <sup>b</sup>	9.00 <sup>b</sup>	0.18	0.54 <sup>b</sup>	0.66	0.66	0.66	0.66	0.66	0.72	0.72	0.30	0.30	0.30	0.66 <sup>b</sup>	0.66 <sup>b</sup>		
Vesper Sparrow ( <i>Poocetes gramineus</i> )	0.66 <sup>b</sup>	1.20 <sup>b</sup>	-	0.05	0.18	-	-	-	-	0.18	0.18	0.12	0.12	0.06	0.06	0.06		
Savannah Sparrow ( <i>Passerculus sandwichensis</i> )	0.03	0.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Grasshopper Sparrow ( <i>Ammodramus sacannarum</i> )	0.06	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Baird's Sparrow ( <i>Ammodramus bairdii</i> )	0.01	-	-	-	-	-	-	-	-	-	0.01	0.03	0.01	0.01	-	-		
Chestnut-collared Longspur ( <i>Calcarius ornatus</i> )	0.96	-	-	0.12	-	-	-	-	-	-	-	-	-	-	-	-		
Meadowlark species ( <i>Sturnella</i> spp.)	0.60	0.54	0.12	0.12 <sup>b</sup>	0.36	-	-	-	-	-	0.12	0.12	0.12	0.12	0.24	0.24		
<b>Shrubland birds</b>																		
Gambel's Quail ( <i>Callipepla gambelii</i> )	0.01	0.01	-	-	-	-	-	-	-	-	-	-	-	-	0.24	0.24		
Cooper's Hawk ( <i>Accipiter cooperii</i> )	-	0.01	<0.01	-	<0.01	-	-	-	-	-	-	-	-	-	-	-		
Red-tailed Hawk ( <i>Buteo jamaicensis</i> )	-	0.03	-	<0.01	<0.01	-	-	-	-	-	0.01	0.02	0.02	0.02	0.02	0.02		
Merlin ( <i>Falco columbarius</i> )	-	0.01	-	-	<0.01	-	-	-	-	-	-	-	-	-	-	-		
White-winged Dove ( <i>Zenaidura asiatica</i> )	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Mourning Dove ( <i>Zenaidura macroura</i> )	0.18	0.30	0.04	0.06	0.24	-	-	-	-	0.24	0.24	0.36	0.54 <sup>b</sup>	0.54 <sup>b</sup>	-	-		
Inca Dove ( <i>Columbina inca</i> )	-	0.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Greater Roadrunner ( <i>Geococcyx californianus</i> )	0.01	-	-	-	0.01	-	-	-	-	-	-	-	-	-	0.03	0.03		
Great Horned Owl ( <i>Bubo virginianus</i> )	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.01		
Lesser Nighthawk ( <i>Chordeiles acutipennis</i> )	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Common Nighthawk ( <i>Chordeiles minor</i> )	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Black-chinned Hummingbird ( <i>Archilochus alexandri</i> )	0.04	0.03	-	-	-	-	-	-	-	-	0.01	0.01	0.02	0.02	0.02	0.02		
Broad-tailed Hummingbird ( <i>Selasphorus platycercus</i> )	-	-	-	-	-	-	-	-	-	-	0.01	0.01	0.01	0.01	0.01	0.01		
Ladder-backed Woodpecker ( <i>Picoides scalaris</i> )	0.02	0.06	<0.01	-	0.01	-	-	-	-	-	0.01	0.01	0.02	0.02	0.02	0.02		
Northern Flicker ( <i>Colaptes auratus</i> )	0.02	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Gray Flycatcher ( <i>Empidonax virens</i> )	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Ash-throated Flycatcher ( <i>Myiarchus cinerascens</i> )	-	-	-	-	-	-	-	-	-	-	0.03	0.12	0.12	0.12	0.12	0.12		
Cassin's Kingbird ( <i>Tyrannus vociferans</i> )	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	0.3 <sup>b</sup>	0.3 <sup>b</sup>		
Western Kingbird ( <i>Tyrannus verticalis</i> )	-	0.01	-	-	-	-	-	-	-	-	0.03	0.06	0.07	0.24	0.24	0.24		
Loggerhead Shrike ( <i>Lanius ludovicianus</i> )	0.24	0.24 <sup>b</sup>	0.05	0.04	0.06	-	-	-	-	-	0.06	0.07	0.24	0.24	0.24	0.24		
Verdin ( <i>Auriparus flaviceps</i> )	0.04	0.02	0.03	-	<0.01	-	-	-	-	-	0.04	-	-	-	0.01	0.01		
Cactus Wren ( <i>Campylorhynchus brunneicapillus</i> )	0.12	0.18	0.04	0.02	0.04	0.02	0.02	0.04	0.04	0.02	0.02	0.02	0.02	0.02	0.24	0.24		

## APPENDIX 1. CONTINUED.

	Fall			Winter			Spring		
	2003	2005	2003-2004	2004-2005	2005-2006	2004	2005	2006	
Rock Wren ( <i>Salpinctes obsoletus</i> )	0.01	0.04	-	-	-	-	-	0.06	
Bewick's Wren ( <i>Thryomanes bewickii</i> )	0.02	0.04	-	-	-	-	-	0.01	
House Wren ( <i>Troglodytes aedon</i> )	0.01	0.01	-	-	-	-	0.01	-	
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	0.01	0.01	-	-	-	-	-	-	
Blue-gray Gnatcatcher ( <i>Poliophtila caerulea</i> )	0.06	0.06	-	-	-	-	-	-	
Black-tailed Gnatcatcher ( <i>Poliophtila melanura</i> )	0.02	0.03	-	-	0.04	0.01	-	0.06	
Northern Mockingbird ( <i>Mimus polyglottos</i> )	0.01	-	-	-	-	0.01	0.03	0.18	
Sage Thrasher ( <i>Oreoscoptes montanus</i> )	0.01	0.02	-	-	-	-	-	-	
Curve-billed Thrasher ( <i>Toxostoma curvirostre</i> )	0.01	0.04	-	-	<0.01	0.01	0.01	0.01	
Crissal Thrasher ( <i>Toxostoma crissale</i> )	0.06	0.02	0.06	<0.01	<0.01	0.02	-	0.04	
Orange-crowned Warbler ( <i>Vermivora celata</i> )	-	0.02	-	-	-	-	-	-	
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	0.12	0.12	-	-	0.01	-	-	-	
MacGillivray's Warbler ( <i>Oporornis tolmiei</i> )	-	0.01	-	-	-	-	-	-	
Green-tailed Towhee ( <i>Pipilo chlorurus</i> )	0.03	0.03	-	-	-	-	-	-	
Spotted Towhee ( <i>Pipilo maculatus</i> )	0.04	-	-	-	-	-	-	-	
Canyon Towhee ( <i>Pipilo fuscus</i> )	-	0.01	-	-	-	-	0.02	0.02	
Rufous-crowned Sparrow ( <i>Aimophila ruficeps</i> )	-	0.12	-	-	-	-	-	-	
Chipping Sparrow ( <i>Spizella passerina</i> )	0.36	1.02	-	0.12	1.02	0.36	0.06	0.48	
Clay-colored Sparrow ( <i>Spizella pallida</i> )	0.01	-	-	-	-	-	-	-	
Brewer's Sparrow ( <i>Spizella breweri</i> )	0.24	0.96 <sup>b</sup>	-	1.32 <sup>b</sup>	0.66	0.12	0.60	0.84 <sup>b</sup>	
Black-chinned Sparrow ( <i>Spizella atrogularis</i> )	-	0.03	-	0.03	0.02	-	0.01	-	
Lark Sparrow ( <i>Chondestes grammacus</i> )	-	0.03	-	-	<0.01	-	0.02	0.06	
Black-throated Sparrow ( <i>Amphispiza bilineata</i> )	0.30	1.86 <sup>b</sup>	0.01	0.18	0.30	0.66 <sup>b</sup>	0.36 <sup>b</sup>	1.2 <sup>b</sup>	
Sage Sparrow ( <i>Amphispiza belli</i> )	0.12	1.62 <sup>b</sup>	0.6 <sup>b</sup>	0.66 <sup>b</sup>	1.56 <sup>b</sup>	-	-	0.18	
Lark Bunting ( <i>Calamospiza melanocorys</i> )	0.12	0.84	-	0.18	0.90	0.03	0.60	0.60	
White-crowned Sparrow ( <i>Zonotrichia leucophrys</i> )	0.12	0.48 <sup>b</sup>	-	0.05	0.54	0.03	0.06	0.78	
Pyrrhuloxia ( <i>Cardinalis sinuatus</i> )	-	-	-	-	-	0.01	0.02	0.01	
Bronzed Cowbird ( <i>Molothrus aeneus</i> )	0.01	-	-	-	-	-	-	-	
Brown-headed Cowbird ( <i>Molothrus ater</i> )	-	0.01	-	-	-	0.01	-	0.04	
Bullock's Oriole ( <i>Icterus bullockii</i> )	-	-	-	-	-	-	0.02	-	
Scott's Oriole ( <i>Icterus parisorum</i> )	-	-	-	-	-	0.01	0.03	0.12	
House Finch ( <i>Carduelis mexicanus</i> )	-	-	-	-	-	0.12	0.18	0.90	
Lesser Goldfinch ( <i>Carduelis psaltria</i> )	0.48	0.60	0.30	0.03	0.66	-	-	-	
House Sparrow ( <i>Passer domesticus</i> )	-	0.03	-	-	0.02	0.04	-	-	
	-	-	-	-	0.02	-	-	-	

<sup>a</sup> Not present.<sup>b</sup> Species present in ≥40% of transects.