EFFECTS OF INVASIVE EXOTIC GRASSES ON SOUTH TEXAS RANGELAND BREEDING BIRDS

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Abstract.—Invasive exotic plants are a major threat to many species of wild birds. When these plants become established and widespread, the floristic composition of native plant communities becomes simplified, which can result in long-term and often irreversible habitat degradation for birds and other animals. Until recently, few studies have focused on the effect of invasive exotic grasses on breeding birds in southwestern rangelands. During the 2001 and 2002 breeding seasons (May–June), we compared the abundance and species richness of breeding birds, native flora, and arthropods on South Texas rangeland plots dominated by native grasses and plots dominated by two invasive exotic grasses, Lehmann lovegrass (*Eragrostis lehmanniana*) and buffelgrass (*Cenchrus ciliaris*). Native-grass cover was >400% greater on native-grass sites than on exotic-grass sites. Forb and grass species-richness were higher on native-grass sites. Shrub canopy cover, bare ground, and vegetation height measurements were similar on native-grass and exotic-grass sites. Overall bird abundance was 32% greater on native-grass sites than on exotic-grass sites. Lark Sparrows (*Chondestes grammacus*) were 73% more abundant on native-grass sites. Four other species—Black-throated Sparrow (*Amphispiza bilineata*), Northern Mockingbird (*Mimus polyglottos*), Northern Bobwhite (*Colinus virginianus*), and Cassin's Sparrow (*Aimophilla cassini*)—were 26–70% more abundant on native-grass sites. The guild of birds that foraged on the ground under open brush canopies was almost twice as abundant on native-grass sites. Arthropod abundance was 60% greater on the native-grass site we sampled. Specifically, spiders, beetles, and ants were 42–83% more abundant on a native-grass site than on a buffelgrass site. Compared with rangelands dominated by native vegetation, areas dominated by Lehmann lovegrass and buffelgrass in South Texas appear to provide less suitable habitat for breeding birds, especially for bird species that forage on or near the ground. *Received 16 June 2004, accepted 28 June 2005.*

Key words: breeding birds, exotic grasses, guilds, invertebrates, South Texas.

Efectos de Pastos Invasores Exóticos en las Aves que Nidifican en los Campos de Pastoreo del Sur de Texas

Resumen.—Las plantas invasoras exóticas son una gran amenaza para muchas especies de aves silvestres. Cuando las plantas invasoras exóticas se establecen y se expanden, la composición florística de las comunidades de plantas nativas se

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simplifica, lo que pude resultar en una degradación a largo plazo y generalmente irreversible del hábitat para las aves y otros animales. Hasta tiempos recientes, pocos estudios se enfocaron en el efecto de los pastos invasores exóticos en las aves que nidifican en los campos de pastoreo del sudoeste. Durante las estaciones reproductivas de 2001 y 2002 (mayo–junio), comparamos la abundancia y la riqueza de las especies de aves nidificantes, de la flora nativa y de los artrópodos en parcelas de campos de pastoreo del sur de Texas dominadas por pastos nativos y por dos pastos invasores exóticos, *Eragrostis lehmanniana* y *Cenchrus ciliaris*. La cobertura de los pastos nativos fue un 400% mayor en los sitios de pastos nativos que en los sitios de pastos exóticos. La riqueza de especies de hierbas y pastos fue mayor en los sitios de pastos nativos. Las medidas de cobertura del dosel de los arbustos, de suelo desnudo y de la altura de la vegetación fueron similares en los sitios de pastos nativos y de pastos exóticos. La abundancia general de las aves fue un 32% mayor en los sitios de pastos nativos que en los sitios de pastos exóticos. *Chondestes grammacus* fue un 73% más abundante en los sitios de pastos nativos. Otras cuatro especies de aves (*Amphispiza bilineata*, *Mimus polyglottos*, *Colinus virginianus* y *Aimophilla cassini*) fueron entre 26 y 70% más abundantes en los sitios de pastos nativos. El gremio de aves que forrajeó en el suelo, debajo del dosel abierto de los arbustos, fue casi dos veces más abundante en los sitios de pastos nativos. La abundancia de los artrópodos fue un 60% mayor en el sitio de pastos nativos que muestreamos. Específicamente, las arañas, los escarabajos y las hormigas fueron 42 a 83% más abundantes en los sitios de pastos nativos que en el sitio con *C. ciliaris*. En comparación con los campos de pastoreo dominados por vegetación nativa, las áreas dominadas por *E. lehmanniana* y *C. ciliaris* en el sur de Texas parecen brindar hábitat menos adecuado para las aves nidificantes, especialmente para las especies que forrajean en o cerca del suelo.

Lehmann lovegrass (*Eragrostis lehmanniana*) and buffelgrass (*Cenchrus ciliaris*) are warm-season perennial bunchgrasses native to South Africa (Freeman 1979, Holt 1985). These grasses were originally introduced to the New World during the 1940s to restore overgrazed rangelands and mitigate soil erosion. Today, these two exotic grass species dominate millions of hectares of rangelands in the southwestern United States (Cable 1971, Holt 1985, Hussey 1985, Clavero and Holt 1987, Ibarra-F. et al. 1995). Lehmann lovegrass and buffelgrass displace native herbaceous species and thereby reduce species diversity of native vegetation communities, resulting in simplification of ecosystems (Cable 1971, Bock et al. 1986, Cox et al. 1988, Medina 1988, Anable et al. 1992). Additionally, exotic grass invasions have a cascading effect on ecosystems, because simplification of the plant community results in simplification of invertebrate and vertebrate communities as well (Bock et al. 1986).

Grassland bird populations have exhibited greater declines than any other avian guild in North America during the past 25 years (Askins 1993, Knopf 1994, Peterjohn and Sauer 1999), and these trends are evident in grassland birds in South Texas (U.S. Geological Survey 2001). Habitat loss is often cited as an important factor contributing to this decline (Askins 1993, Knopf 1994). Because exotic plant invasions are synonymous with habitat loss, the magnitude of their threat to native bird communities may be larger than previously believed.

The objective here was to compare plant, arthropod, and avian communities in native-grass- and exotic-grass-dominated rangelands in the western Rio Grande Plains of South Texas. Our overall goal was to assess whether patterns of abundance of birds, plants, and arthropods differed between the native-grass and exotic-grass study sites.

Methods

Study Area and Comparisons

We conducted our study on the 6,151-ha Chaparral Wildlife Management Area (CWMA) and on a 5,261-ha portion of the 41,279-ha

Piloncillo Ranch (PILO) in LaSalle and Dimmit counties, Texas. The climate in the region is classified as subtropical (Office of the State Climatologist and Texas A & M University 1987). Average annual rainfall recorded at the CWMA from 1989 to 1999 was 54 cm, with 60% falling between April and September. Average annual temperatures range from 5°C in January to 37°C in July (Chaparral Wildlife Management Area unpubl. data). Soils were similar among sites and consisted of Duval fine-sandy loam, Duval loamy-fine sand, and Dilley fine-sandy loam (Stevens and Arriaga 1985, Gabriel et al. 1994). The Duval series are fine-loamy, mixed hyperthermic Aridic Haplustalfs and the Dilley series are loamy, mixed, hyperthermic shallow Ustalfic Haplargids. Topography was gently sloping with elevations from 90 to 196 m (Stevens and Arriaga 1985).

Vegetation communities were representative of the western Rio Grande Plains mixed-brush shrublands (McLendon 1991). Woody vegetation was dominated by honey mesquite (*Prosopis glandulosa*), Texas hogplum (*Colubrina texensis*), brasil (*Condalia hookeri*), guajillo (*Acacia berlandieri*), whitebrush (*Aloysia gratissima*), and cactus (*Opuntia* spp.) (Ruthven et al. 2000). Common herbaceous plants included plains dozedaisy (*Aphanostephus ramosissimus*), partridge pea (*Chamaescrista nictitans*), plantain (*Plantago* spp.), bristlegrass (*Setaria* spp.), grama grasses (*Bouteloua* spp.), and hooded windmill grass (*Chloris cucullata*). With the exception of a few isolated locations, exotic grasses had not been planted on the PILO or CWMA; therefore, the exotic grass stands present appear to have resulted from invasions from surrounding areas or accidental introductions via livestock, which have been present on the study areas since the 18th century (Lehmann 1969). Stocker cattle— young steers raised for market—were grazed on a rotational basis on CWMA study areas before and during the study period. The PILO had a high-intensity, low-frequency grazing system.

During reconnaissance sampling conducted in March and April 2001, study sites were selected on the basis of similar soil, vegetation, topography, and land-use history. Areas with >50% exotic-grass relative dominance were assigned to exotic-grass-dominated replicates, and areas with >50% native-grass relative dominance were assigned to native-grass-dominated replicates. On the basis of reconnaissance

sampling, three native- and three exotic-grass-dominated study sites were selected. Native and exotic study sites were paired in a randomized complete block design consisting of three blocks. Each study site encompassed ~200 ha (182–202 ha), and sites were separated by ≥800 m within each block.

Avian Point Counts

We used the point-count method from 10 May to 26 June 2001 and 13 May to 18 June 2002 to estimate breeding bird density (Ralph et al. 1995). Surveys began at sunrise and continued for 4 h to minimize hourly variation in detection rates. Surveys were not conducted during periods of rain or when winds exceeded 24 km h^{-1}. Wind speed, percentage of cloud cover, temperature, and precipitation were recorded during point counts to ensure similar conditions during surveys. Surveys were repeated three times each during the 2001 and 2002 native-bird breeding seasons.

Fifteen point-count stations were located on each study site. Point-count stations were placed in areas dominated by either native or exotic grasses within replicates; therefore, stations were not considered independent samples. Station placement was stratified among soil types in equal proportion to the amount of each soil type on each study site. Study sites averaged 60% Duval soil, 36% Dilley soil, and 4% drainage soil types. Point-count stations were also equally distributed among areas of high (≥60%) or low (≤40%) shrub canopy cover on both native and exotic study sites. The distance that point-count stations were placed from roads, windmills, and drainages was similar between paired exotic and native study sites.

To minimize repeated observations from adjacent point-count sites, stations were separated by >150 m (Hutto et al. 1986, Gutzwiller 1991, Hamel et al. 1996). To further reduce the probability of repeated observations, locations and movements of individual birds were monitored during each point count. A 25-m fixed detection radius was established for point-count surveys (Hutto et al. 1986, Ralph et al. 1995, Hamel et al. 1996). Detections were also recorded within a 50-m radius and for an unlimited distance to estimate the effective detection distance (Reynolds et al. 1980, Hutto et al. 1986, Guttzwiller 1991). Because of the

broad distance intervals used, bird-density estimates may have been under- or overestimated, but methods were consistent among study sites. Birds heard and seen were recorded for 7 min at each point-count station (Hamel et al. 1996). We began recording data upon arrival within 50 m of point-count stations (Hutto et al. 1986, Guttzwiller 1991), thus recording individuals that flushed upon approach. Common and scientific nomenclature of birds follows the American Ornithologists' Union (1983).

Vegetation Sampling

We conducted vegetation sampling from mid-May through early July 2001 and 2002. All vegetation was measured within a 25-m radius (0.19 ha) from the center of each avian point-count station. The line-intercept method was used to quantify percentage of shrub canopy cover and woody species composition during the 2002 field season (Bonham 1989). To avoid oversampling the center of each station, we used a 25-m and two 17.5-m lines to measure shrub canopy cover and open interspace distances. The direction of the 25-m line-intercept direction was randomly chosen for the first sampling point. The 17.5-m intercepts were spaced 16.6 m on each side of the 25-m intercept, parallel to the 25-m intercept. The origin of the 17.5-m intercepts overlapped with the 25-m intercept by 2.25 m and extended in opposite directions from the direction of the 25-m intercept. Woody-plant species diversity, cover, and frequency were estimated along each sampling intercept.

Percentage of cover of grass, forbs, litter, and bare ground was estimated within twelve 20 × 50 cm (0.10 m²) Daubenmire frames (Daubenmire 1959) in each 25-m radius (0.19 ha) point-count station (180 frames per study area). Three transects were spaced 14.6 m apart within the point-count station. The middle transect crossed the center of the point-count station. Four frames were spaced 11 m apart on each transect (12 frames per station). Transect direction was randomly chosen for the first sampling station and this direction was kept constant for the remaining stations. In the northeast corner of each frame, vegetation height was measured in centimeters with a ruler. Vegetation was identified to at least the family level, and to the species level when possible. Cover (i.e. relative dominance) was defined as the proportion of cover composed by a species or group of species. Common names and scientific nomenclature of Texas plants follows Hatch et al. (1990).

A vegetation profile board (Bookhout 1996) was used to measure the vertical structure of shrubs and herbaceous cover during the 2001 field season. The profile board was 2.5 m tall, 15 cm wide, and divided into 0.5-m intervals. Percentage of obstruction was recorded as 1, 2, 3, 4, or 5 for percentage-of-obstruction classes (0–20, 21–40, 41–60, 61–80, 81–100%) at each interval. The profile board was placed at a random bearing and distance from the center of the point-count station and viewed at a distance of 15 m in each of the cardinal directions (Bookhout 1996). Shrubs were not sampled.

Arthropod Sampling

To determine the effects of exotic-grass invasions on invertebrate populations, arthropod samples were obtained during the 2002 field season from five random points selected in the native-grass study site in block 3 and five random points selected in the exotic study site in block 3, which was predominantly buffelgrass (92%). A sweep net (0.6 m in diameter) was used to sample ~0.42 m³ volume of space consisting of herbaceous vegetation and the air immediately above it (Bookhout 1996). One hundred sweep samples were obtained along a randomly selected transect at each sampling point. Consequently, 500 arthropod samples were collected in both the native site and the exotic site. Arthropods were identified to order and, if possible, family.

Statistical Analysis

The analysis of variance (ANOVA) model included block (three areas), year, type (exotic or native site), and interaction terms. The ANOVA model we used was

$$y_{ijk} = \mu + T_i + b_j + Y_k + (Tb)_{ij} + (TY)_{ik} + e_{ijk},$$

where T_i is the fixed effect of the ith treatment, b_j is the random effect of the jth block, Y_k is the fixed effect of the kth year, and e_{ijk} is the experimental error term. We used this model to compare mean bird abundance between native and exotic sites. We also used this model to compare

vegetation variables between native and exotic sites. Only herbaceous plant and bird species with ≥25% detection rates in each block of a study type (exotic or native) were statistically analyzed and are reported here; therefore, species with a low frequency of detection were not compared among native and exotic sites.

We measured species richness of birds (number of species per 2.85 ha) and of herbaceous plants (number of species per 1.5 m^2). Mean insect abundance on native and exotic sites was compared using a five-independent-sample, one-tailed *t*-test. Bird species that did not breed in the area and species with wide-ranging movements were omitted from data analyses and listed in Flanders (2003). All statistical analyses were accomplished using SAS software (SAS Institute, Cary, North Carolina; Cody and Smith 1991). Statistical significance was accepted at $P \leq 0.05$.

Microhabitat affinities.—Bird species were classified according to primary foraging and microhabitat affinities during the breeding season to evaluate potential effects of exotic grasses on specific foraging guilds. The primary foraging-microhabitat was the substrate used for the highest percentage of time for foraging activities by bird species during the breeding season, as determined from a literature review including the *Birds of North America* species accounts, various studies (Nolan and Wooldridge 1962, Taylor 1971, Foreman 1978, Fischer 1980, Fitzpatrick 1980, Flood 1990, George et al. 1994), and field observations (Flanders 2003). Foraging-microhabitat classifications were as follows: ground foraging under open canopy; ground foraging under dense canopy; facultative shrub and ground foraging; opportunistic foraging; shrub foraging; and air, shrub, and herbaceous hawking.

Effective detection distances.—An effective detection distance for individual bird species was determined (Reynolds et al. 1980) to increase accuracy of density estimates and to limit undetected individuals. The density for each species was determined within the 25-m and 50-m radii. These densities were then expanded to a constant of 500 ha. If an individual species' density estimate within the 50-m radius was <50% of the species density estimate within the 25-m radius, then the observations from the 25-m radius were used for analysis. The 25-m radius was used as the effective detection

distance for all species except White-winged Dove (*Zenaida asiatica*), Yellow-billed Cuckoo (*Coccyzus americanus*), Audubon's Oriole (*Icterus graduacauda*), Greater Roadrunner (*Geococcyx californianus*), Curve-billed Thrasher (*Toxostoma curvirostre*), Long-billed Thrasher (*T. longirostre*), Olive Sparrow (*Arremonops rufivirgatus*), and White-eyed Vireo (*Vireo griseus*), which were analyzed at the 50-m radius. Cassin's Sparrow (*Aimophila cassinii*) was examined at the 50-m radius because of lack of detections during the 2002 breeding season; analysis for Cassin's Sparrow data was therefore not replicated temporally. All bird densities were reported as the number of individuals per hectare.

Results

Shrub Cover

Twenty-six species of shrubs and three species of cacti were documented on the study sites. Total percentage of shrub canopy cover was similar on native ($\overline{x}$ = 23.45 ± 1.06 [SE]) and exotic sites ($\overline{x}$ = 24.32 ± 2.54). Exotic study sites ($\overline{x}$ = 22.67 ± 0.67) had higher (F = 28.00, df = 2, P = 0.034) shrub species richness than native sites ($\overline{x}$ = 18.00 ± 1.53).

Vertical Vegetation Structure

Percentage of obstruction of woody and herbaceous cover was similar on native ($\overline{x}$ = 2.17 ± 0.04) and exotic sites ($\overline{x}$ = 2.09 ± 0.10). Percentage of obstruction of vegetative cover was also similar between native and exotic sites from ground level to 0.5 m (native: $\overline{x}$ = 2.70 ± 0.28; exotic: $\overline{x}$ = 2.55 ± 0.27); from 0.5 to 1.0 m (native: $\overline{x}$ = 2.32 ± 0.05; exotic: $\overline{x}$ = 2.37 ± 0.21); from 1.0 to 1.5 m (native: $\overline{x}$ = 2.02 ± 0.03; exotic: $\overline{x}$ = 1.97 ± 0.18); from 1.5 to 2.0 m (native: $\overline{x}$ = 2.08 ± 0.08; exotic: $\overline{x}$ = 1.81 ± 0.09); and from 2.0 to 2.5 m (native: $\overline{x}$ = 1.88 ± 0.15; exotic: $\overline{x}$ = 1.62 ± 0.03).

Groundcover

Eighty-seven herbaceous plant species were recorded during the 2001 and 2002 study periods. Native and exotic grasses dominated their respective blocks of the study design, though percentages of native- and exotic-grass cover varied by block. Exotic-grass cover ranged from 11% to 20% on exotic-grass-dominated blocks and from

1% to 3% on native-grass-dominated blocks. Native-grass cover ranged from 10% to 20% on native blocks and from 2% to 4% on exotic blocks. Percentage of forb cover ranged from 12% to 16% on exotic blocks and from 15% to 23% on native blocks. Percentage of litter cover ranged from 11% to 32% on native blocks and from 16% to 24% on exotic blocks. Bare ground was the most prevalent groundcover parameter measured, varying from 32% on an exotic site to 61% on a native site. Herbaceous vegetation height ranged from 14.7 to 25.1 cm on the study areas.

Statistical interactions between year and study sites were not evident for the herbaceous groundcover parameters measured, except for percentage of canopy cover of exotic grasses and percentage of canopy cover of native grasses. These interactions were not considered biologically significant; therefore, data were pooled between years (Table 1).

We did not calculate ANOVAs for percentage of cover of Lehmann lovegrass and buffelgrass between native and exotic sites, because of failure to meet the assumption of equal variances. Nevertheless, Lehmann lovegrass cover on exotic sites ($\overline{x} = 4.39 \pm 2.00$) was >200% higher than on native sites ($\overline{x} = 1.78 \pm 0.44$), and buffelgrass cover was >10× higher on exotic sites ($\overline{x} = 10.16 \pm 4.52$) than on native sites ($\overline{x} = 0.23 \pm 0.12$) (Table 1).

Native forb and grass species were also more abundant on native sites than on exotic sites, which provides additional evidence that exotic-grass invasions suppress native plant species. Percentage of cover of 9 native grass species and 11 forb species were at least twice as high on native sites as on exotic sites. Specifically, one grass species and two forb species were significantly more abundant on native sites, and mean differences in abundance approached significance for eight of the remaining grass species and nine of the remaining forb species (Flanders 2003).

BIRD COMMUNITY

Fifty-one species of birds were observed in surveys conducted during the 2001 and 2002

TABLE 1. Percentage of canopy cover (mean ± SE) of exotic grass, buffelgrass, Lehmann lovegrass, native grass, forbs, litter, and bare ground; forb and grass species diversity; forb and grass species richness; forb species richness; grass species richness; and vegetation height for three blocks, averaged across years, and year * study site interaction tests for vegetation-community parameters sampled on native-grass and exotic-grass study sites in Dimmit and LaSalle counties, Texas, 2001–2002.

Parameter measurement [a]	ANOVA interaction terms (year * type)			Habitat type			
	MSE [b]	F [c]	P [d]	Native $\overline{x} \pm SE$	Exotic $\overline{x} \pm SE$	F [e]	P [f]
Percentage of canopy cover:							
Exotic grass	64.70	45.37	0.003	3.03 ± 0.36	14.56 ± 2.54	35.42	0.027
Buffelgrass	– [g]	–	–	0.23 ± 0.12	10.16 ± 4.52	–	–
Lehmann lovegrass	–	–	–	1.78 ± 0.44	4.39 ± 2.00	–	–
Native grass	51.58	32.11	0.004	13.60 ± 2.36	3.03 ± 0.36	18.75	0.025
Forbs	1.76	0.09	0.783	18.10 ± 2.40	14.30 ± 1.12	3.88	0.900
Litter	0.69	0.03	0.870	20.09 ± 4.37	19.29 ± 1.68	0.04	0.857
Bare ground	0.04	0.00	0.986	47.64 ± 8.92	50.67 ± 7.40	0.51	0.550
Forb and grass species richness	16.30	0.83	0.413	46.67 ± 1.89	40.67 ± 1.69	144.00	0.003
Forb species richness	30.08	3.14	0.151	32.50 ± 1.32	28.50 ± 1.26	27.77	0.017
Grass species richness	0.33	0.14	0.722	15.00 ± 1.04	12.17 ± 0.60	27.98	0.017
Vegetation height	16.30	0.96	0.383	19.68 ± 4.92	20.73 ± 3.41	0.14	0.744

[a] n = 3 blocks with 2 habitat types per block and 15 sampling points per habitat type.

[b] Mean squared error.

[c] F-value testing for a type * year interaction; df = 1 and 4.

[d] P-value for interaction test.

[e] F-value testing for type main effect; df = 1 and 2.

[f] P-value for type main effect test.

[g] ANOVAs not calculated because of failure to meet assumptions of equal variance.

field seasons. No statistical interaction was detected between years for bird parameter measurements and type of study site (native and exotic) (Table 2); therefore, data were pooled for the 2001 and 2002 breeding seasons. Bird species richness (number of species per 2.85 ha) did not differ ($F = 0.31$, df = 2, $P = 0.635$) on native ($\bar{x} = 23.00 \pm 0.52$) and exotic ($\bar{x} = 22.67 \pm 0.80$) study sites.

Exotic sites supported fewer birds: total bird density (number of individuals ha^{-1}) was significantly higher on native sites than on exotic sites (Table 2). Resident breeding species and Neotropical migrants responded differently to exotic grass invasions (Table 2). Resident bird density was significantly higher on native sites than on exotic sites, whereas Neotropical migrant density was similar on native and exotic sites. On an individual species basis, only Lark Sparrow (*Chondestes grammacus*) density was significantly higher ($F = 27.10$, df = 2, $P = 0.017$) on native sites ($\bar{x} = 2.21 \pm 0.35$)

than on exotic sites ($\bar{x} = 0.56 \pm 0.06$). However, Black-throated Sparrows (*Amphispiza bilineata*), Northern Mockingbirds (*Mimus polyglottos*), Northern Bobwhites (*Colinus virginianus*), and Cassin's Sparrows were approximately twice as abundant on native sites compared with exotic sites, and differences in mean abundance between native and exotic sites approached significance for Black-throated Sparrow and Northern Mockingbird (Table 3).

Grouping bird species into specific foraging guilds revealed that the presence of exotic grasses appeared to affect members of certain guilds more than members of other guilds. Significantly higher densities of "ground foraging under open-canopy" species ($F = 48.62$, df = 2, $P = 0.010$) and "air, shrub, and herbaceous hawking" ($F = 6.36$, df = 2, $P = 0.064$) occurred on native sites ($\bar{x} = 15.51 \pm 0.49$ and $\bar{x} = 5.10 \pm 0.30$, respectively) as compared with exotic sites ($\bar{x} = 8.27 \pm 0.57$ and $\bar{x} = 3.34 \pm 0.41$, respectively) (Table 2). Members of the "ground and shrub

TABLE 2. Density (birds ha^{-1}; mean ± SE) of breeding birds, Neotropical migrants, and residents; bird species richness (number of birds per 2.85 ha; mean ± SE); and number of bird guilds (1) ground-foraging under open canopy; (2) ground- and shrub-foraging; (3) shrub-foraging; (4) ground-foraging under dense shrub canopy cover; and (5) air, shrub, and herbaceous hawking on three blocks, averaged across years; and year * study site interaction tests for density estimates of avian parameters sampled on native-grass and exotic-grass study sites in Dimmit and LaSalle counties, Texas, 2001–2002.

| | ANOVA interaction terms (year * type) | | | Habitat type | | | |
| | | | | Native | Exotic | | |
Parameter measurement[a]	MSE[b]	F[c]	P[d]	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	F[e]	P[f]
Bird density							
Neotropical migrants	0.01	9.00	0.096	2.77 ± 0.20	2.83 ± 0.23	1.00	0.423
Resident density	5.17	1.04	0.415	8.40 ± 0.07	5.44 ± 0.72	15.29	0.030
Community composition							
Species richness	8.33	5.26	0.084	23.00 ± 0.52	22.67 ± 0.80	0.31	0.635
Ground foraging under open canopy	0.96	0.15	0.717	15.51 ± 0.49	8.27 ± 0.57	48.62	0.010
Ground and shrub foraging	5.09	4.27	0.108	4.59 ± 0.05	4.76 ± 0.74	0.11	0.771
Shrub foraging	1.88	1.06	0.362	2.32 ± 0.11	2.21 ± 0.35	0.21	0.691
Ground foraging under dense shrub canopy	0.09	0.12	0.745	0.45 ± 0.20	0.51 ± 0.26	0.25	0.333
Air, shrub, and herbaceous hawking	0.24	0.58	0.488	5.10 ± 0.30	3.34 ± 0.41	6.36	0.064

[a] $n = 3$ blocks with 2 habitat types per block and 15 sampling points per habitat type.
[b] Mean squared error.
[c] F-value testing for a type * year interaction; df = 1 and 4.
[d] P-value for interaction test.
[e] F-value testing for type main effect; df = 1 and 2.
[f] P-value for type main effect test.

TABLE 3. Density (birds ha^{-1}; mean ± SE) of breeding bird species on three blocks, averaged across years, and year * study site interaction tests for density estimates of avian parameters sampled on native-grass and exotic-grass study sites in Dimmit and LaSalle counties, Texas, 2001–2002.

| Bird species[a] | ANOVA interaction terms (year * type) | | | Habitat type | | | |
	MSE[b]	F[c]	P[d]	Native $\overline{x}$ ± SE	Exotic $\overline{x}$ ± SE	F[e]	P[f]
Lark Sparrow	0.24	0.25	0.643	2.21 ± 0.35	0.56 ± 0.06	27.10	0.017
Black-throated Sparrow	0.03	0.04	0.859	5.15 ± 0.72	3.79 ± 0.25	3.92	0.093
Cassin's Sparrow	0.73	0.81	0.507	1.02 ± 0.67	0.28 ± 0.14	2.20	0.137
Northern Mockingbird	0.62	2.46	0.192	1.98 ± 0.40	0.85 ± 0.27	3.90	0.094
Northern Bobwhite	0.78	0.83	0.415	2.72 ± 0.89	1.42 ± 0.46)	2.70	0.121

[a] n = 3 blocks with 2 habitat types per block and 15 sampling points per habitat type.
[b] Mean squared error.
[c] F-value testing for a type by year interaction; df = 1 and 4.
[d] P-value for interaction test.
[e] F-value testing for type main effect; df = 1 and 2.
[f] P-value for type main effect test.

foraging," "shrub foraging," and "ground foraging under dense shrub canopy" guilds appeared to be indifferent to exotic grass invasions, because densities for each of these foraging guilds were similar on native and exotic sites (Table 2).

ARTHROPODS

Arthropod abundance (mean per 42.0 m^3) was significantly higher (t = 2.29, df = 8, P = 0.039) on native sites ($\overline{x}$ = 7.73 ± 1.94) than on buffelgrass sites ($\overline{x}$ = 3.14 ± 0.50) (Table 4). Specifically, beetles (Coleoptera) and ants (Formicoidea) were significantly more abundant (beetles: t = 1.96, df = 8, P = 0.043; ants: t = 2.08, df = 8, P = 0.36) on native (beetles: $\overline{x}$ = 2.80 ± 0.80; ants: $\overline{x}$ = 33.20 ± 12.61) than on exotic sites (beetles: $\overline{x}$ = 1.00 ± 0.45; ants: $\overline{x}$ = 5.80 ± 3.81) (Table 4). Spider (Araneae) abundance followed a similar trend. Although mean spider densities were not significantly different between native and exotic sites, mean densities were higher on native ($\overline{x}$ = 3.80 ± 0.58) than on exotic sites ($\overline{x}$ = 2.20 ± 0.86), and the difference approached significance (t = 1.54, df = 8, P = 0.081) (Table 4).

DISCUSSION

Exotic-grass dominance appeared to negatively affect the bird community we studied. Overall bird abundance was significantly lower on exotic-grass-dominated study sites than on native-grass-dominated sites. Density of the ground-foraging bird guild was lower on exotic sites, presumably because the seeds and insect resources located on the ground were less abundant on exotic sites, whereas resources used by foraging guilds that are associated with shrubs may not have been limited on exotic sites.

Overall habitat structure did not appear to affect differences in bird abundance among native and exotic sites. Results from other studies have suggested that exotic plant invasions alter habitat structure (Bock et al. 1986, Wilson and Belcher 1989, Scheiman et al. 2003), which reduces habitat suitability for various bird species. However, seasonal grazing and cattle grazing behavior may have affected herbaceous-vegetation structure comparisons among native and exotic study sites in the present study. For example, cattle on the PILO appeared to prefer buffelgrass to other grass species because they grazed it more than other available species and frequented areas with high buffelgrass canopy cover. This grazing behavior may have resulted in underestimation of buffelgrass canopy cover and height, because grazing reduces aboveground biomass. Also, seasonal grazing reduces herbaceous canopy cover available for sampling, especially in a high-intensity, low-frequency grazing regime.

Additionally, differences in floristics between exotic and native sites may have contributed to the differences in bird abundance observed. Several studies have indicated that birds select

TABLE 4. Mean abundance of arthropods (mean ± SE per 42.0 m^3) on native-grass (*n* = 5) and exotic-grass (buffelgrass; *n* = 5) study sites in Dimmit County, Texas, 2002 (*t* = Student's *t*-test, df = 8).

Order	Native $\overline{x}$ ± SE	Exotic $\overline{x}$ ± SE	*t* (*P*)
Araneae (spiders)	3.80 ± 0.58	2.20 ± 0.86	1.54 ± 0.081
Coleoptera (beetles)	2.80 ± 0.80	1.00 ± 0.45	1.96 ± 0.043
Hymenoptera (ants)	33.20 ± 12.61	5.80 ± 3.81	2.08 ± 0.036
Hemiptera (true bugs)	2.40 ± 0.93	1.40 ± 0.51	0.95 ± 0.186
Homoptera (white-green flies)	2.00 ± 0.77	1.40 ± 0.40	0.69 ± 0.256
Diptera (flies)	0.40 ± 0.24	0.20 ± 0.20	0.63 ± 0.272
Hymenoptera (bees, wasps)	2.80 ± 1.02	2.20 ± 1.07	0.41 ± 0.348
Orthoptera (grasshoppers)	4.00 ± 1.52	5.40 ± 0.68	0.84 ± 0.788
All orders	7.73 ± 1.94	3.14 ± 0.50	2.29 ± 0.039

habitats on the basis of the species composition of vegetation communities, as well as the presence of certain plant species that are of particular importance to specific bird species (Rotenberry and Wiens 1980, 1998; Wiens and Rotenberry 1981; Meents et al. 1982). Indeed, Block and Brennan (1993) stated that both vegetation structure and floristics are important factors in habitat selection by birds. Therefore, breeding birds in our study may have selected native-grass-dominated sites because native floral species richness and abundance were higher on these areas than on the exotic-grass-dominated sites. Exotic grasses seemed to provide similar habitat structure compared with native grasses, but apparently there was some aspect of floristics that influenced bird abundance, perhaps as a function of arthropod availability and differences in nesting or cover opportunities on exotic sites.

Our results are consistent with research from Arizona indicating that African-lovegrass (*Eragrostis* spp.) infestations of grassland landscapes reduced the abundance of birds (Bock et al. 1986, Bock and Bock 1992). Like the Arizona studies, we also found that breeding birds were less abundant in exotic-grass-dominated habitats. However, Bock et al. (1986) reported that three breeding bird species were significantly more abundant in native-grass-dominated areas, whereas in our study, only Lark Sparrows were significantly more abundant in native areas. Although the abundance of Northern Bobwhites, Black-throated Sparrows, Cassin's Sparrows, and Northern Mockingbirds was not statistically greater in native areas than in exotic areas, all these species followed a trend of higher abundance on native sites. Also, all these species use similar foraging substrates during the breeding season, so it would appear that this foraging guild is affected more dramatically by exotic-grass invasions than the other foraging guilds we evaluated.

Exotic grasses may have negative effects on the functional relationships between birds, their prey, and prey habitat. During the breeding season, bird species rely on an abundance of arthropods to meet dietary requirements for molting, reproduction, and nestling development. For example, coleopterans (beetles), hymenopterans (bees and wasps), and araneids (spiders) have been reported to be primary food items of Northern Bobwhite chicks in South Texas (Lehmann 1984). Also, orthopterans (grasshoppers) were found to be the primary food item of Black-throated Sparrows in New Mexico (Zimmer 1983). Furthermore, orthopterans, lepidoteran larvae (butterflies and moths), coleopterans, hymenopterans (ants), and seeds were the most important food items of common bird species in grassland bird communities (Wiens 1973). Exotic grasses may provide less food for breeding bird communities because native plant species richness is evidently suppressed by exotic grass infestations, thereby reducing the number of niches available for arthropods. For instance, some invertebrates are monophagous or stenotopic, feeding on specific host plants or using specific host plants as a predation substrate (Price 1975). Bock et al. (1986) determined that grasshoppers were significantly less abundant in exotic lovegrass areas than in native-grass areas in Arizona. Sampling during 2002 indicated that insects were significantly less abundant on a buffelgrass-dominated site than

on a native-grass-dominated site (Table 4). Specifically, species of the orders Coleoptera, Araneae, and Formicoidea appeared to be less abundant in bufflegrass stands than in native grass. Therefore, along with the reduced species diversity and abundance of native forbs and grasses that characterized our exotic sites, the reduced abundance of invertebrates that was also evident may have been an important contributing factor responsible for the reduced breeding bird abundance we observed on those sites.

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