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Black-tailed prairie dogs and the structure of avian communities on the shortgrass plains

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Abstract We tested the hypothesis that black-tailed prairie dogs (*Cynomys ludovicianus*) influence avian community structure on the shortgrass prairie. We surveyed 36 prairie dog towns and 36 paired sites without prairie dogs during summer and fall of 1997, 1998, and 1999 in the Oklahoma Panhandle. Our surveys totaled 9,040 individual observations for 73 avian species. Significantly distinct avian communities were present on prairie dog towns when compared to sites within four different macrohabitats of the surrounding landscape: open rangeland, scrub/sandsage (*Artemisia filifolia*) habitats, Conservation Reserve Program (CRP) plots, and fallow crop fields. Relative densities of all bird species combined was higher on prairie dog towns versus paired sites in summer and fall. Mean species richness of birds was significantly higher on prairie dog towns than paired sites during summer, but there were no significant differences in fall. Open rangeland had the highest mean species richness in fall. Assemblages of avian communities differed significantly between prairie dog towns and the four macrohabitat types during summer. Burrowing owls (*Athene cunicularia*), killdeer (*Charadrius vociferous*), horned larks (*Eremophila alpestris*), and meadowlarks (*Sturnella* spp.) were positively and significantly associated with prairie dog towns during summer, while horned larks and ferruginous hawks (*Buteo regalis*) were significantly associated with prairie dog towns during fall.

Even in their current remnant state, black-tailed prairie dogs continue to play a significant role in the assembly of ecological communities across the Great Plains. Conservation of prairie dogs goes well beyond a single species, and is an important strategy for the preservation of the prairie ecosystem as a whole.

Keywords Biological diversity · Conservation · Fragmentation · Grassland birds · Keystone species

Introduction

A small percentage of North American birds are endemic to the Great Plains (Udvardy 1958; Mengel 1970). As a group, grassland birds have shown more significant declines over the past 30 years than any other avian guild (Askins 1993; Knopf 1994, 1996a). Seven of 12 endemic avian species of the Great Plains have steadily declined in recent decades (Table 1; Knopf 1996a; Peterjohn and Sauer 1999). Likewise, 14 of 25 more widespread grassland species have also shown declines (Table 1). One reason for such declines is alteration in the vegetative structure of Great Plains grasslands (Knopf 1994).

Historically, the Great Plains were a “shifting mosaic” of habitat patches shaped by fire and grazing by large and small herbivores. Having evolved in variable fire and grazing regimes, avian grassland endemic birds thus display a range of preferences for disturbance frequency; from mountain plovers (*Charadrius montanus*) nesting on intensively grazed bare ground, to long-billed curlews (*Numenius americanus*) and lark buntings (*Calamospiza melanocorys*) choosing moderately grazed patches, to Cassin’s sparrows (*Aimophila cassinii*) breeding in shrubby habitat with little or no grazing (Knopf 1996a, 1996b; Askins 2000). Today, anthropogenic changes to the landscape have homogenized the ecosystem in which these species evolved (Lomolino et al. 2001; see also Lockwood and McKinney 2001). The suppression of fire, conversion of native prairie to agricultural land, and

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Table 1 North American grassland avifauna of the Great Plains (modified from Mengel 1970 and Knopf 1996). Species in bold have shown overall declining trends on Breeding Bird Survey routes from 1966 to 1993 (Knopf 1996) or from 1966 to 1996 (Peterjohn and

Sauer 1999). An asterisk indicates species generally associated with wetlands and sagebrush (*Artemisia* spp.) habitat of the Great Plains and Great Basin

Nonpasserines	Passerines
<p>Primary species (endemics)</p> <p>Ferruginous Hawk (<i>Buteo regalis</i>)</p> <p>Mountain Plover (<i>Charadrius montanus</i>)</p> <p>Long-billed Curlew (<i>Numenius americanus</i>)</p> <p>*Marbled Godwit (<i>Limosa fedoa</i>)</p> <p>*Wilson's Phalarope (<i>Phalaropus tricolor</i>)</p> <p>*Franklin's Gull (<i>Larus pipixcan</i>)</p> <p>Secondary species (more widespread)</p> <p>Mississippi Kite (<i>Ictinia mississippiensis</i>)</p> <p>Northern Harrier (<i>Circus cyaneus</i>)</p> <p>Swainson's Hawk (<i>Buteo swainsoni</i>)</p> <p>Prairie Falcon (<i>Falco mexicanus</i>)</p> <p>Greater Prairie-Chicken (<i>Tympanuchus cupido</i>)</p> <p>Lesser Prairie-Chicken (<i>Tympanuchus pallidicinctus</i>)</p> <p>Sharp-tailed Grouse (<i>Tympanuchus phasianellus</i>)</p> <p>*Sage Grouse (<i>Centrocercus</i> spp.)</p> <p>Upland Sandpiper (<i>Bartramia longicauda</i>)</p> <p>Short-eared Owl (<i>Asio flammeus</i>)</p> <p>Burrowing Owl (<i>Athene cunicularia</i>)</p>	<p>Sprague's Pipit (<i>Anthus spragueii</i>)</p> <p>Cassin's Sparrow (<i>Aimophila cassinii</i>)</p> <p>Baird's Sparrow (<i>Ammodramus bairdii</i>)</p> <p>Lark Bunting (<i>Calamospiza melanocorys</i>)</p> <p>Chestnut-collard Longspur (<i>Calcarius ornatus</i>)</p> <p>McCown's Longspur (<i>Calcarius mccownii</i>)</p> <p>Horned Lark (<i>Eremophila alpestris</i>)</p> <p>*Sage Thrasher (<i>Oreoscoptes montanus</i>)</p> <p>*Green-tailed Towhee (<i>Pipilo chlorurus</i>)</p> <p>Clay-colored Sparrow (<i>Spizella pallida</i>)</p> <p>*Brewer's Sparrow (<i>Spizella breweri</i>)</p> <p>Lark Sparrow (<i>Chondestes grammacus</i>)</p> <p>*Sage Sparrow (<i>Amphispiza belli</i>)</p> <p>Grasshopper Sparrow (<i>Ammodramus savannarum</i>)</p> <p>Henslow's Sparrow (<i>Ammodramus henslowii</i>)</p> <p>Savannah Sparrow (<i>Passerculus sandwichensis</i>)</p> <p>Vesper Sparrow (<i>Pooecetes gramineus</i>)</p> <p>Dickcissel (<i>Spiza americana</i>)</p> <p>Eastern Meadowlark (<i>Sturnella magna</i>)</p> <p>Western Meadowlark (<i>Sturnella neglecta</i>)</p>

reduction of grazing guilds of the prairie have significantly and permanently altered the landscape on which these birds depend. Fire and grazing by large, native herbivores may, in fact, be functionally extinct processes on the plains (Knopf 1994; McPherson 1995), and the current role of the once dominant, small herbivore, prairie dogs, has recently been brought to the forefront of grassland conservation (Wuerthner 1997; Miller and Cully 2001).

The black-tailed prairie dog (*Cynomys ludovicianus*) is one of five members of the genus *Cynomys* (Order Rodentia, Family Scuridae) found only in North America (Hoogland 1996). Black-tailed prairie dogs have the widest distribution of any prairie dog species and are the only prairie dog species occurring in Oklahoma (Hoogland 1995). (Use of the term prairie dog for the remainder of this paper will refer to black-tailed prairie dogs). Prairie dogs are ecosystem engineers (Lawton and Jones 1995) and appear to be keystone species, strongly influencing community structure and creating a dynamic landscape across short and mixed-grass prairies (Kotliar et al. 1999; Kotliar 2000; Miller et al. 2000; Lomolino and Smith 2004). Prairie dogs create and maintain a unique habitat by keeping vegetation clipped low to the ground and by construction of extensive, underground tunnel systems. Other species use dog towns as foraging sites, use burrows as dens or refugia from predators or severe weather, or use prairie dogs themselves as prey. A number of grassland species may be closely associated with prairie dog towns

(Reading et al. 1989; Hoogland 1996) which, until the previous century, constituted some of the most expansive and predictable resources and refugia for Great Plains species (see Goodwin 1995). Many vertebrates generally considered to be town associates are species of special concern, including several members of the grassland bird assemblage: burrowing owl (*Athene cunicularia*), mountain plover, golden eagle (*Aquila chrysaetos*), ferruginous hawk (*Buteo regalis*), Swainson's hawk (*B. swainsoni*), prairie falcon (*Falco mexicanus*), lesser prairie-chicken (*Tympanuchus pallidicinctus*), and long-billed curlew (Butts 1976; Knowles et al. 1982; Allison et al. 1995; Desmond et al. 1995; Barko et al. 1999). In addition, numerous non-volant terrestrial vertebrates of conservation concern are positively associated with prairie dog towns, including tiger salamander (*Ambystoma tigrinum*), prairie rattlesnake (*Crotalus viridis*), ornate box turtle (*Terrapene ornata*), black-footed ferret (*Mustela nigripes*) and swift fox (*Vulpes velox*) (Tyler 1968; Agnew et al. 1986; Shackford and Tyler 1991; Sidle et al. 2001).

Black-tailed prairie dogs are now sparsely distributed across their historic range, and their numbers have been drastically reduced as a result of habitat loss, poisoning campaigns, and outbreaks of sylvatic plague (*Yersinia pestis*) (Miller and Cully 2001). Prairie dog towns are believed to have covered from 40 to 100 million hectares around the turn of the century, but cover less than 5% of this area today (Miller et al. 1994). Our recent surveys of

towns in Oklahoma have also documented declines within the past 10–15 years (Lomolino and Smith 2001). In the Panhandle alone, areal coverage of prairie dog towns during this period has been reduced by almost 45%. The remaining towns are becoming increasingly smaller, fragmented, and more isolated.

Here we test the hypothesis that prairie dogs, even with their presently fragmented distribution, continue to influence local community structure on the shortgrass prairie. In particular, we hypothesize that the species composition, richness, and abundance of bird species differs between prairie dog towns and their adjacent habitat patches. We also discuss the relevance of observed patterns in avian community structure for conserving the character of Great Plains ecosystems.

Materials and methods

Study site

All field work was in the Oklahoma Panhandle, which is a transition zone from mixed grass prairies in the east to shortgrass prairies in the west. The Panhandle is a three county area covering 14,737 km² surrounded by the body of the state of Oklahoma, Kansas, Colorado, New Mexico, and Texas. Mean annual precipitation falls from approximately 60 cm in the east to 40 cm in the far west. Elevation rises from approximately 730 m in the east to 1,516 m in the west.

Historically, much of the Panhandle was shortgrass plains dominated by buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) (Blair and Hubbell 1938; Sims and Risser 2000) along with dense concentrations of sand sage (*Artemisia* spp.) in the east. Over the past two centuries, agricultural development and cattle ranching have expanded westward (see Ramankutty and Foley 1999) across the region leaving some remnants of native prairie, fragmented prairie dog towns, and riparian corridors sparsely distributed amongst large parcels of cropland. Rocky mesas are a prominent feature of the extreme western portion of the panhandle. Today, approximately 20–40% of potential natural vegetation remains in this region (Sieg et al. 1999).

Survey methods

Paired community studies were conducted in summer and fall of 1997, 1998, and 1999. Summer surveys were done between mid-May and early August, while fall surveys were conducted from mid-November to mid-December. Prairie dog towns were located from previous roadside surveys conducted across the panhandle region of Oklahoma (Lomolino and Smith 2001) as well as from information from land owners and Game Wardens. Permission was obtained for every site used. Once a prairie dog town was located, we searched for a paired habitat site (without prairie dogs) within the surrounding habitat matrix, between 0.6 and 8.0 km of the town, and obtained permission to use the site. Paired sites were located using roadside surveys extending out from the focal prairie dog town and were classified using habitat measurements (see below) and visual observations as open rangeland (shortgrass prairie in the absence of prairie dogs), scrub/sandsage, CRP grasses (Conservation Reserve Program, primarily *Bothriochloa ischaemum*), or fallow crop field. Including prairie dog towns we identified five macrohabitat types. During each summer we conducted avian surveys at 12 prairie dog towns and 12 paired sites resulting in 36 total dog towns and 36 total paired sites (19 open rangeland, 8 scrub/sandsage, 6 fallow crop field, and 3 CRP) over 3 years combined. During each fall, we repeated surveys at half of these sites for a total of 6 prairie dog towns and 6 paired sites per fall, and 18 towns and

18 paired sites (10 open rangeland, 6 scrub/sandsage, and 2 CRP) total during all fall surveys. Therefore, we conducted 108 survey sessions (72 summer, 36 fall) combining all sites, years, and seasons. Prairie dog towns ranged in size from 9.0 to 211.0 ha and paired sites were habitat patches at least as large as the dog town it was paired with.

Avian surveys were conducted as variable distance line transects, using modifications of Emlen's (1971; 1977) methods (Bibby et al. 1992). A transect 300–700 m long was established on each prairie dog town based on the size of that town. Birds were recorded within band widths of 10 m, 25 m, 50 m, 100 m, 150 m, and 150+ m from the center line. Survey protocol and transect dimensions were exactly duplicated on paired sites. Each transect was walked twice in the morning within 2–3 h of sunrise and twice in the evening within 2–3 h of sunset (432 total bird counts were performed in >220 h of surveys). Counts were conducted on a prairie dog town and its paired site on two consecutive mornings and evenings. Count order was reversed so that if a prairie dog town was counted first one morning, the paired site would be counted first the second morning. Count order in the evening was also reversed. All counts were conducted by a single observer (G.A.S.) using 10×25 binoculars, a 15×60x spotting scope, data sheets, and a field guide. Transects were walked slowly with occasional stops such that each count lasted 30–45 min. Individual birds were recorded by sight and call to species within a specific band width from the center line. The observer was allowed to move away from the center line, but the position of the individual bird was always recorded as distance from the center line and not distance from the observer. Avian densities were calculated using the program DISTANCE with the half-normal cosine detection function and all data truncated to include only observations within 150 m of the center line (Thomas et al. 1998). For these analyses, all observations from the four counts were combined and transect length was multiplied by four. This was done in order to reduce problems of duplicating counts of individuals but renders our results as relative densities of individuals.

Habitat measurements were taken as point counts along each transect. Regardless of transect length, 20 stops were established along the transect. Counting the initial starting point, each transect had 21 stops. At each stop, a 10-m rope with a knot at 1-m intervals was laid perpendicular to the transect to the left and to the right. Therefore, habitat measurements were taken across a 20-m line perpendicular to the center line of the transect. The center point was only counted once so at each stop there were 21 measurement points giving 441 points (21 stops x 21 points at each stop) per transect. At each point, vegetation height was recorded as <10 cm, 11–25 cm, 26–50 cm, 51–75 cm, 76–100 cm, and >100 cm. Vegetation type was also recorded at each point as grass, forb, soil, litter, cacti, yucca, cow patty, shrub/woody, rock, and other. For each site, vegetation was recorded as the percentage of 441 total points within each category listed above.

Statistical analyses

Paired *t*-tests were used to compare mean species richness of avian species on prairie dog towns versus paired sites. Analyses were also run on a subset of species which are of conservation priority (threatened or endangered, rare, or species of special concern). Repeated measures ANOVA tested for differences between years and between seasons for those species that occurred across years and seasons. To compare relative densities of each species on prairie dog towns versus paired sites, a resampling program was written using Resampling Stats, version 4.1b4 (Resampling Stats 1997). This program tested the hypothesis that relative densities of individual bird species differ significantly between prairie dog towns and paired sites. The program first calculates the observed differences and sum of differences in population densities between each pairing of the actual data and then calculates the observed number of times the relative density of that species was higher on the prairie dog town versus its paired site. The data are then pooled and shuffled. Half of the observations are selected (regardless of identity as a

prairie dog town or a paired site) and paired with the remaining half. Differences and sums of differences are calculated for this random data set, and the program calculates the number of times values in the first set of shuffled observations ("prairie dog towns") exceed those of the second set ("paired sites"). These values are compared to those for the observed data where treatment effects (prairie dog town vs non-town site) were preserved. The program repeats these routines 10,000 times and calculates the number of iterations in which the sum of differences were higher, the same, or lower than the observed sum of differences. *P*-values were calculated as the proportion of randomized iterations greater than or equal to the observed (unshuffled) data.

To test the hypothesis that prairie dog towns harbor distinct assemblages of birds, we used discriminant function analysis. In order to eliminate problems associated with zero data (i.e., very rare species), we used only species that were recorded on at least five pairings of the summer or fall sites. We counted an occurrence as presence on either the dog town or paired site of a particular pairing. The species did not have to occur on both sites of a pair. The analysis was run twice using relative density measures and presence/absence data. First, we treated all paired sites as one macrohabitat and compared prairie dog towns versus paired sites. Second, paired sites were split into separate macrohabitat categories (see above) and all macrohabitats were compared against prairie dog towns as well as against each other. Finally, we used correspondence analysis to investigate differences in environmental characteristics and species composition among macrohabitats. SYSTAT, version 10 (SPSS 2000), was used for all statistical analyses except resampling routines.

Results

Local habitat variables differed significantly between prairie dog towns and paired sites during summer (discriminant function analysis, between groups $F_{14,57}=14.678$, $P<0.001$) and fall ($F_{13,22}=7.863$; $P<0.001$). Likewise, for each season there were significant differences in habitat between the five macrohabitats: CRP, fallow crop fields, prairie dog towns, rangeland, and scrub (summer, $F_{13,55}=17.415$, $P<0.001$; fall, $F_{8,25}=7.348$, $P<0.001$; Fig. 1). Thus, the macrohabitats can be considered distinct landscape level treatments in subsequent analyses. Based on the jackknifed classification matrix of the DFA, fallow crop fields, prairie dog towns, and scrub habitats were the most distinct (% classification success = 100, 97, and 88, respectively). During fall, prairie dog towns and scrub habitats remained distinct (100% and 83%, respectively).

Seventy-three species of birds were detected during our surveys. Across all seasons, there were 9,040 individual observations. After removing observations >150 m, 7,928 observations remained in the analyses: 5,044 during summer and 2,884 during fall. Prairie dog towns accounted for 2,817 observations (55.8%) during summer, and 2,175 observations (75.4%) during fall. Typical of these grassland communities, horned larks (*Eremophila alpestris*) and meadowlarks (eastern and western combined, *Sturnella* spp.) accounted for 54.5% of all summer detections (66.2% on prairie dog towns), while horned larks alone accounted for 55.8% of fall detections (68.0% on prairie dog towns) (Kantrud and Kologiski 1982; Knopf 1996a). Although not as abundant as horned larks, grasshopper sparrows (*Ammodramus savannarum*) and

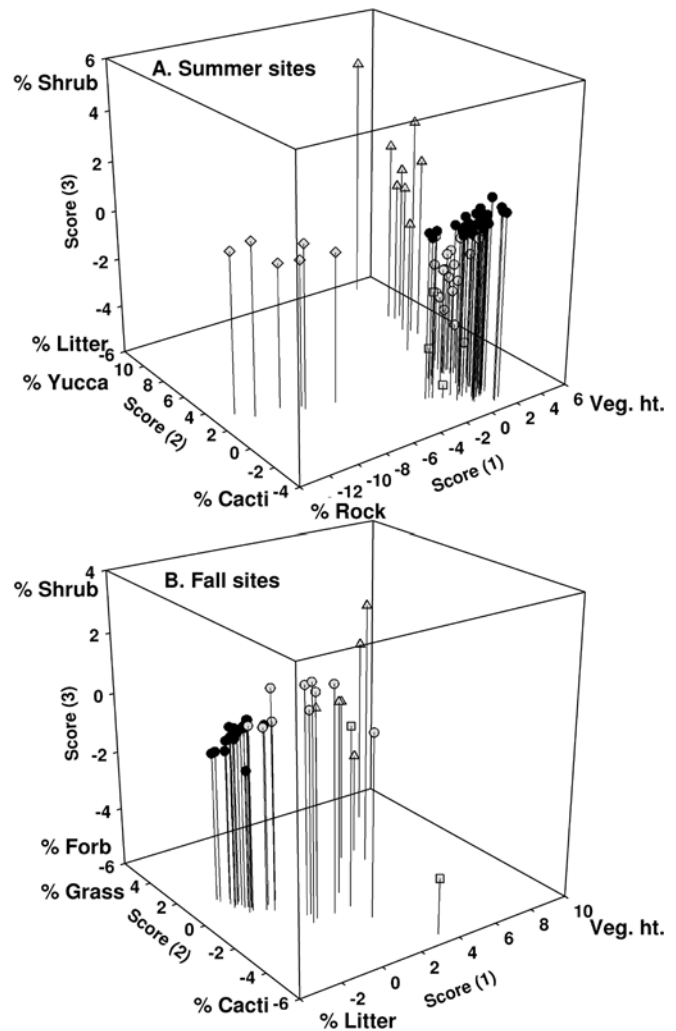


Fig. 1 Plot of discriminant function factor scores for habitat variables at **A** 72 summer sites and **B** 36 fall sites for black-tailed prairie dogs (*Cynomys ludovicianus*) in the Oklahoma Panhandle during 1997, 1998, and 1999. Habitat differed significantly between five macrohabitat types (prairie dog towns, open range, scrub/sandsage, CRP grasses, and fallow crop field) in summer ($F_{13,55}=17.415$, $P<0.001$) and between four macrohabitat types (prairie dog towns, open range, scrub/sandsage, and CRP grasses) in fall ($F_{8,25}=7.348$, $P<0.001$). Explanation of symbols: black dot prairie dog towns; grey dot open rangeland; triangle scrub/sandsage; square CRP grasses; diamond fallow crop fields

meadowlarks accounted for 48.3% of observations on paired sites during summer, while meadowlarks and longspurs (*Calcarius* spp.) dominated paired sites during fall (62.5%).

None of the species used in our analyses exhibited significant differences in relative density across years (repeated measures ANOVA model), thus we combined data within a season across years. Relative densities of all birds, combined, was highest on prairie dog towns, in comparison to all other habitats, during summer and fall (Fig. 2). The high relative density of species in fall was due to very large flocks (mostly horned larks) that gathered at this time of year. Such large flocks, often hundreds of birds, were not observed in summer. When

comparing birds across macrohabitats, fallow crop fields and prairie dog towns had the highest relative density of birds in summer, while prairie dog towns and CRP had high abundance levels during fall (Fig. 2). Again, horned larks and meadowlarks were dominant species on prairie dog towns during summer, while grasshopper sparrows were relatively common at paired sites. Horned larks and longspurs were the most abundant fall species.

Avian species richness in summer was significantly higher on prairie dog towns than at paired sites (data from all summers combined: mean=9.5 for prairie dog towns and 8.2 for paired sites; $t=2.714$, $P=0.010$; Fig. 3). There were no significant differences in species richness for fall surveys (mean=5.7 for prairie dog towns and 5.6 for paired sites; $t=0.251$, $P=0.805$; Fig. 3). Overall, prairie dog towns and fallow crop fields were the most species-rich summer macrohabitats while rangeland and prairie dog towns had the highest mean richness in fall (Fig. 3).

Similar results were obtained when analyses were limited to species of conservation concern; significant differences in species richness were evident between prairie dog towns and paired sites in summer and fall

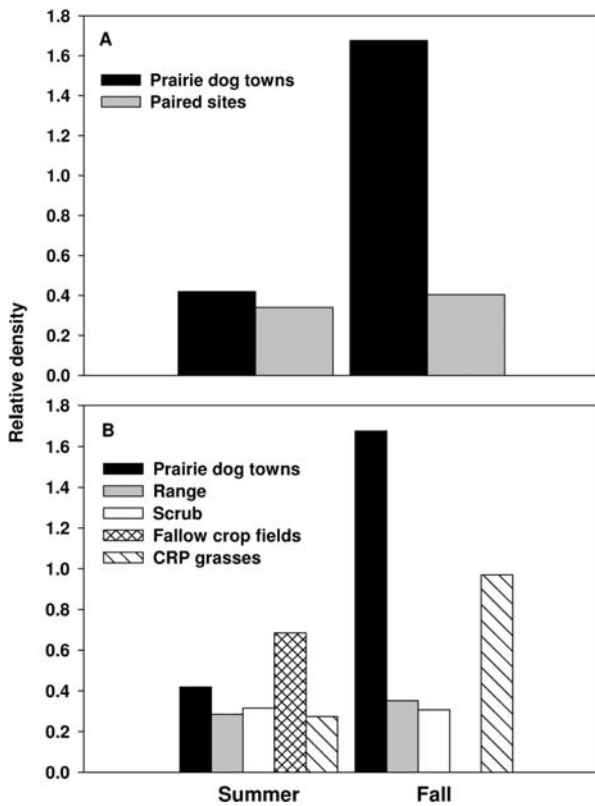


Fig. 2 Relative density of all observations combined, calculated with DISTANCE from variable distance line transect counts (see Materials and methods), of grassland bird species during summer and fall (1997, 1998, and 1999 combined) on **A** prairie dog towns and paired sites ($n=36$ sites for each treatment in summer, 18 sites for each treatment in fall) and **B** five macrohabitats of the Oklahoma Panhandle (prairie dog towns: $n=36$ summer sites, 18 fall sites; open rangeland: $n=19$ summer sites, 10 fall sites; scrub/sandsage: $n=8$ summer sites, 6 fall sites; fallow crop fields: $n=6$ summer sites, 0 fall sites; CRP grasses: $n=3$ summer sites, 2 fall sites)

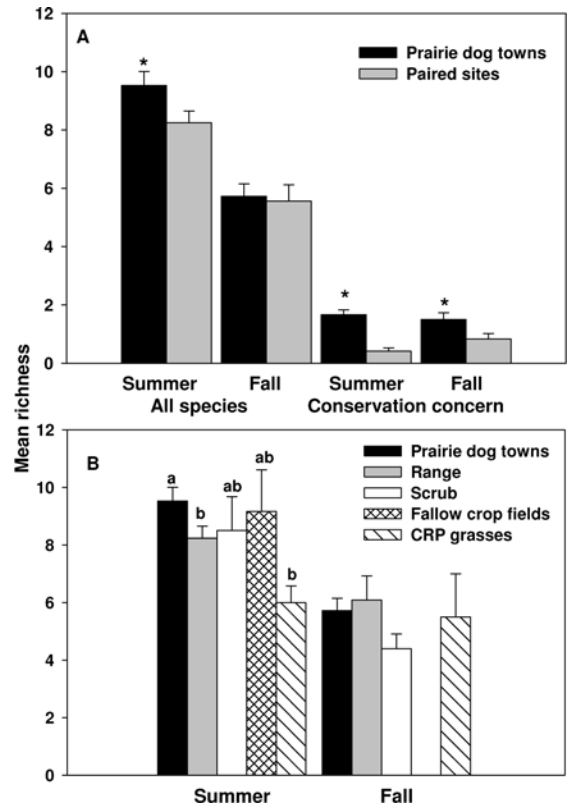


Fig. 3 Mean richness of avian species during summer and fall (1997, 1998, and 1999 combined) on **A** prairie dog towns and paired sites (for all species and only those of conservation concern; $n=36$ sites for each treatment in summer, 18 sites for each treatment in fall) and **B** five macrohabitats of the Oklahoma Panhandle (prairie dog towns: $n=36$ summer sites, 18 fall sites; open rangeland: $n=19$ summer sites, 10 fall sites; scrub/sandsage: $n=8$ summer sites, 6 fall sites; fallow crop fields: $n=6$ summer sites, 0 fall sites; CRP grasses: $n=3$ summer sites, 2 fall sites). Bars represent mean+1 SE (* $P<0.05$, based on paired t -tests; bars with different letters are significantly different at the 0.05 level based on two-sample t -tests)

(summer: mean=1.7 for prairie dog towns and 0.4 for paired sites, $t=6.489$, $P<0.001$; fall mean=1.5 for prairie dog towns and 0.8 for paired sites, $t=2.608$, $P=0.018$; Fig. 3). With burrowing owls removed from the summer analyses, marginally significant differences between prairie dog towns and paired sites relative to richness of species of conservation priority were still observed (mean=0.7 for prairie dog towns and 0.4 for paired sites, $t=1.919$, $P=0.063$).

Individual species often appeared to prefer or avoid prairie dog towns. Thirteen species detected during summer surveys met the requirements for analysis with the resampling routine. Of these species, burrowing owls ($P<0.001$), killdeer ($P=0.042$), horned lark ($P=0.003$), and meadowlarks ($P=0.014$) exhibited significant, positive associations with prairie dog towns, while northern bobwhites (*Colinus virginianus*) ($P=0.027$), Cassin's sparrows ($P<0.001$), and grasshopper sparrows ($P<0.001$) were significantly associated with paired sites (all summer data combined). Although not significant, scissor-tailed flycatcher (*Tyrannus forficatus*), brown-headed cowbird (*Molothrus ater*), and lark sparrow

(*Chondestes grammacus*) were more common on prairie dog towns than at paired sites while Mourning doves (*Zenaida macroura*) were more common on paired sites.

At the community level, discriminant function analysis showed a highly significant difference in species composition of avian assemblages between summer prairie dog towns and paired sites (all paired sites combined as one treatment: using relative density measures, between groups F -value_{13,58}=6.328, P <0.001; using presence/absence data, F _{30,41}=11.965, P <0.001). During fall, avian assemblages were also significantly different based on relative density measures (F _{6,29}=2.739, P =0.031), but were only marginally significant using presence/absence data (F _{12,23}=1.885, P =0.092). When paired sites were split into their respective macrohabitats, we detected highly significant differences in summer avian assemblages across the five macrohabitats: prairie dog towns, open rangeland, scrub/sandsage, CRP, and fallow crop fields (overall differences for summer data using relative density data, F _{13,55}=3.127, P <0.001; Fig. 4; using presence/absence data, F _{30,38}=3.718, P <0.001; Table 2). All five macrohabitats were identifiable by distinct assemblages of summer species, with jackknifed classification successes for avian communities of 94% for prairie dog towns, 84% rangeland, 75% scrub, 67% CRP, and 50% fallow crop fields. Differences among avian communities across macrohabitats during fall were much less distinct than those for summer surveys (using relative density data, F _{6,27}=1.047, P =0.421; using presence/absence data, F _{12,21}=1.361, P =0.142). However, species assemblages at prairie dog towns were significantly different from those inhabiting scrub/sandsage habitat (based on presence/absence data, F _{12,21}=3.335, $0.01 > P > 0.005$; Table 3). In addition, prairie dog towns had the highest jackknifed

classification success (50%) based on species incidence data during fall. Classification success for avian communities at scrub followed that for prairie dog towns at 33%,

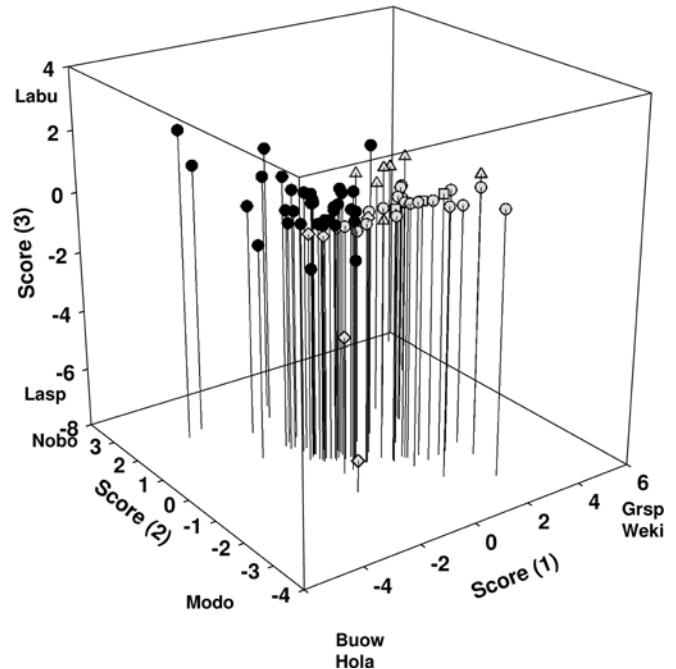


Fig. 4 Plot of discriminant function factor scores for avian communities at 72 sites in the Oklahoma Panhandle during summers of 1997, 1998, and 1999. Sites are subdivided into five macrohabitat types (prairie dog towns, open range, scrub/sandsage, CRP, and fallow crop field) and scores reflect relative density of avian species at each site (between groups F -value_{13,58}=6.328, P <0.001; see Table 2). Explanation of symbols: *black dot* prairie dog towns; *grey dot* open rangeland; *triangle* scrub/sandsage; *square* CRP grasses; *diamond* fallow crop fields. Species codes: *Buow* Burrowing Owl; *Grsp* Grasshopper Sparrow; *Hola* Horned Lark; *Labu* Lark Bunting; *Lasp* Lark Sparrow; *Modo* Mourning Dove; *Nobo* Northern Bobwhite; *Weki* Western Kingbird

Table 2 Between-groups F -matrix based on discriminant function analysis for five macrohabitats in the Oklahoma Panhandle. Data are for avian communities during summers 1997–1999, and were either relative abundance measures or presence/absence data. Values in bold are significant to at least the 0.05 level. *P-dog* prairie dog towns

Relative abundance Data (df=13,55)					
	CRP	Fallow crop	P-dog	Range	Scrub
CRP	–				
Fallow crop	1.611	–			
P-dog	1.646	1.844	–		
Range	0.322	3.016	5.961	–	
Scrub	1.765	5.486	8.849	3.354	–
Relative abundance Data (df=30,38)					
	CRP	Fallow crop	P-dog	Range	Scrub
CRP	–				
Fallow crop	1.654	–			
P-dog	4.700	2.961	–		
Range	1.452	2.244	14.013	–	
Scrub	2.500	2.269	6.183	4.199	–

Table 3 Between-groups F -matrix based on discriminant function analysis for five macrohabitats in the Oklahoma Panhandle. Data are for avian communities during falls 1997–1999, and were either relative abundance measures or presence/absence data. Values in bold are significant to at least the 0.05 level. *P-dog* prairie dog towns

Relative abundance data (df=6,27)				
	CRP	P-dog	Range	Scrub
CRP	–			
P-dog	1.418	–		
Range	0.550	1.334	–	
Scrub	0.380	1.936	0.343	–
Relative abundance data (df=12,21)				
	CRP	P-dog	Range	Scrub
CRP	–			
P-dog	1.228	–		
Range	0.815	0.841	–	
Scrub	1.027	3.335	1.609	–

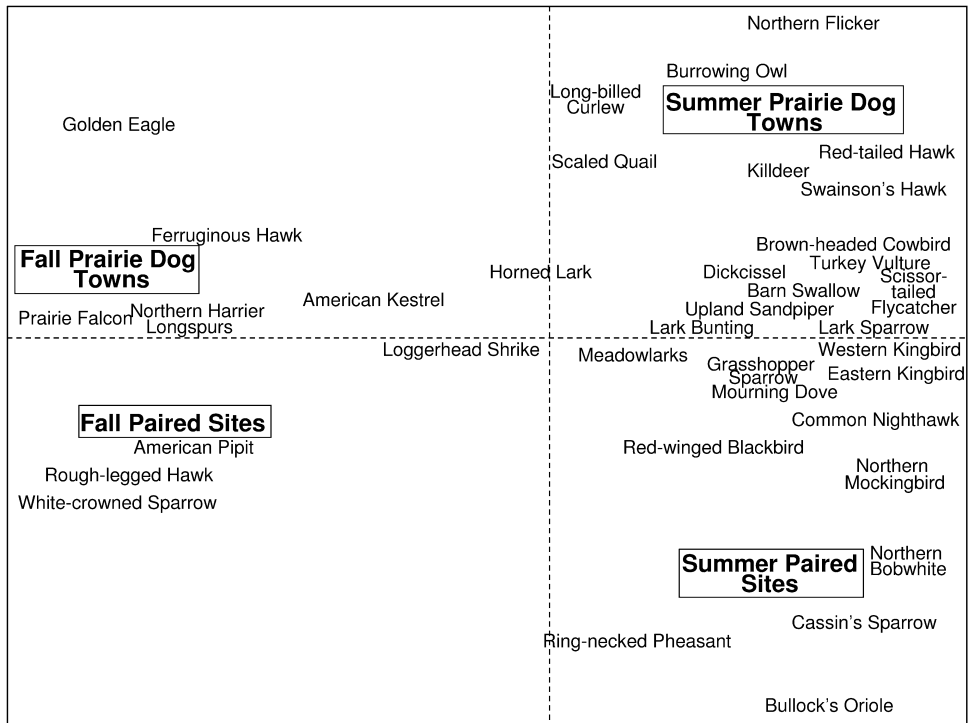
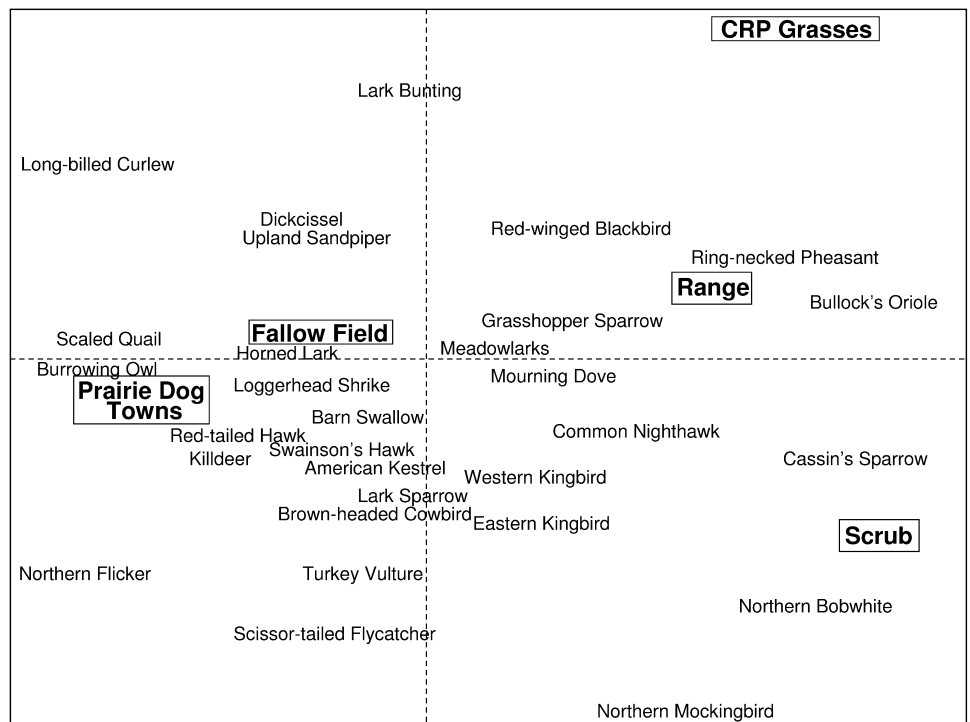


Fig. 5 Differences in assemblages of avian communities on 36 prairie dog towns and 36 paired sites in the Oklahoma Panhandle during summer and fall of 1997, 1998, and 1999, combined. Ordinations were based on correspondence analysis using presence/absence data and including only those species occurring on at least five sites. Summer paired sites are a combination of four paired habitat types (open rangeland, scrub/sandsage, fallow crop field, and CRP grasses). Fall paired sites do not include fallow crop fields.

Species plot closest to macrohabitats in which they occurred most often. Macrohabitats plot closest to other macrohabitats with similar avian communities. Seasonal turnover in the regional species pool is reflected by the positioning of summer and fall sites on opposite sides of the plot. The location of each species or macrohabitat in ordination space corresponds to the center of each species or macrohabitat name

Fig. 6 Differences in assemblages of avian communities on 5 macrohabitats in the Oklahoma Panhandle during summers of 1997, 1998, and 1999, combined. Ordinations were based on correspondence analysis using presence/absence data and including only those species occurring on at least five sites. Species plot closest to macrohabitats in which they occurred most often. Macrohabitats plot closest to other macrohabitats with similar avian communities. Prairie dog towns were most similar to fallow crop fields relative to their avian communities while open rangeland, scrub/sandsage, and CRP grasses were more similar to each other than any were to prairie dog towns or fallow crop fields. The location of each species or macrohabitat in ordination space corresponds to the center of each species or macrohabitat name



and values for range and CRP were 10% and 0%, respectively.

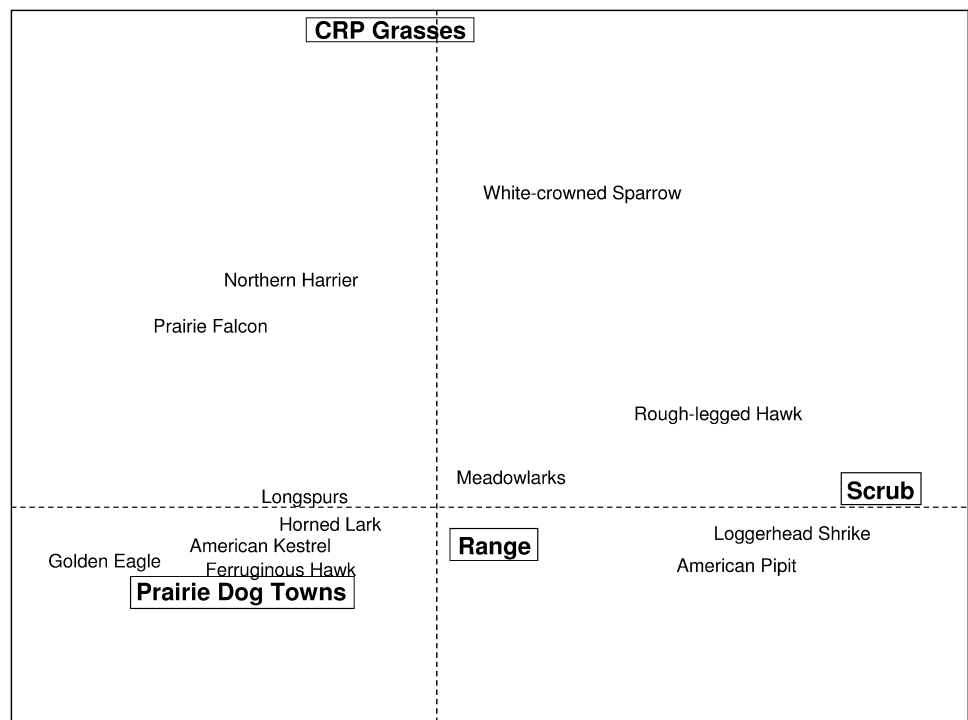
Ordinations of summer avian communities based on correspondence analysis indicated that burrowing owl, scaled quail (*Callipepla squamata*), killdeer, red-tailed hawk (*Buteo jamaicensis*), and to lesser degrees horned lark, long-billed curlew, and loggerhead shrike (*Lanius ludovicianus*) were positively associated with prairie dog towns (Figs. 5, 6). Seasonal turnover in the regional species pool is evident, as summer sites (whether prairie dog town or paired site) ordinate together while fall sites plot together (Fig. 5). When summer sites are split into their respective macrohabitats, the association between prairie dog towns and fallow crop fields is clear (Fig. 6). Avian assemblages in fallow crop fields plot near prairie dog towns while range sites, scrub/sandsage, and CRP plot farther away and closer to each other than any are to prairie dog towns or fallow crop fields (Fig. 6). Thus, summer avian assemblages in fallow crop fields appear to most closely resemble prairie dog towns in vegetation structure and the avian species attracted to this habitat type. During fall, ferruginous hawk, golden eagle, American kestrel (*Falco sparverius*), horned lark, and longspurs were strongly associated with prairie dog towns (Figs. 5, 7). The raptor complex, with the exception of rough-legged hawk (*Buteo lagopus*) and to a lesser degree northern harrier (*Circus cyaneus*), plotted near prairie dog towns (Fig. 7), a possible indication of the importance of this habitat type as a winter resource for these species.

Discussion

Birds are particularly sensitive to landscape patchiness (McIntyre 1995). The historic factors shaping the structure of the Great Plains produced a grassland ecosystem characterized by local homogeneity and regional heterogeneity (Collins 1992). Biological diversity of the Great Plains was derived from this heterogeneity, and black-tailed prairie dogs were a major factor shaping the landscape (Miller et al. 1994). Prairie dogs produce a homogeneous “lawn” of grasses and forbs within an individual town surrounded by significantly different habitats (Whicker and Detling 1988; Weltzin et al. 1997). A number of species depend on these homogeneous patches (Sharps and Uresk 1990) and this has led many ecologists to refer to them, we feel justifiably so, as ecosystem engineers and keystone species (Miller et al. 1994; Kotliar et al. 1999; Kotliar 2000; Miller et al. 2000). Our studies indicate that even after being reduced to less than 5% of their historic range, prairie dog towns in western Oklahoma continue to be inhabited by distinct assemblages of avian species.

Patterns reported here are consistent with those obtained during similar studies of vertebrate species and prairie dog towns (Agnew et al. 1986; Barko et al. 1999; Manzano-Fischer et al. 1999; Winter et al. 1999a; Kretzer and Cully 2001). Our results for avian communities are also consistent with our concurrent studies of mammal, reptile, and amphibian communities at these sites (Lomolino and Smith 2004). That is, prairie dog towns were inhabited by a highly distinct assemblage of these vertebrate species (including species of conservation priority). Non-volant, terrestrial vertebrates strongly associated with prairie dog towns included American badgers (*Taxidea taxus*), thir-

Fig. 7 Differences in assemblages of avian species on 4 macrohabitats in the Oklahoma Panhandle during falls of 1997, 1998, and 1999. Ordinations were based on correspondence analysis using presence/absence data and including only those species occurring on at least 5 sites. Species plot closest to macrohabitats in which they occurred most often. Macrohabitats plot closest to other macrohabitats with similar avian communities. Note the raptor complex clustered around prairie dog towns. The location of each species or macrohabitat in ordination space corresponds to the center of each species or macrohabitat name.



teen-lined ground squirrels (*Spermophilus tridecemlineatus*), domestic cattle (*Bos taurus*), cottontail rabbits (*Sylvilagus* spp.), coyotes (*Canis latrans*), northern grasshopper mice (*Onychomys leucogaster*), swift fox, pronghorn (*Antilocapra americana*), and prairie rattlesnakes (Lomolino and Smith 2004). We found these differences despite not just the decimation of prairie dog towns, but also the homogenization of species pools across the Great Plains. Before the turn of the century, this list of town associates likely would have included black-footed ferrets, and perhaps bison (*Bison bison*), elk (*Cervus elaphus*), wolves (*Canis lupus*), and grizzly bears (*Ursus arctos*) (Benedict et al. 1996). Further, the particular species of vertebrates associated with prairie dog towns and their relative use of dog towns versus paired sites, appear to be variable across regions and their species pools, and also across seasons and multi-annual variation in climate. Previous studies have suggested that the influence of prairie dog towns on habitat choice of grassland birds may be related to precipitation (Barko et al. 1999; Winter et al. 1999a, 1999b). Particularly in mixed-grass prairie, during dry years, vegetation characteristics within paired habitats may not differ much from prairie dog towns. However, during wet years when grasses are taller, prairie dog towns and their associated communities become more distinctive.

We found that seasonal differences in bird communities were more apparent than yearly differences. Prairie dog towns were distinct from all other macrohabitat types during summer (Table 2). This strong distinction was driven not only by species that were positively associated with prairie dog towns (e.g., burrowing owls, horned larks, killdeer, and long-billed curlews), but also by species associated with paired habitats (e.g., Cassin's sparrows, grasshopper sparrows, lark buntings, northern bobwhites, and western kingbirds *Tyrannus verticalis*). Avian communities at prairie dog towns were less distinct from paired sites during fall, however. Meadowlarks, for example, were associated with prairie dogs during summer, but not fall. Loggerhead shrikes showed a similar pattern. We also observed a significant reduction of the regional species pool from summer to fall. That is, species lost due to migration out of the region are not replaced at an equal rate by species moving into the region from farther north. Mean richness during summer was 9.5 and 8.3 for prairie dog towns and paired sites, respectively (Fig. 3). During fall, mean richness dropped to 5.7 for prairie dog towns and 5.6 for paired sites (Fig. 3).

Despite the lack of overall patterns in richness for fall species, species of conservation priority continued to show higher diversity on prairie dog towns than paired sites. Therefore, the role of prairie dogs in winter communities should not be underestimated. For species that depend on prairie dog burrows for winter roosting (e.g., burrowing owls; Butts 1976) or depend on prairie dogs as a prey item (e.g., ferruginous hawks; Allison et al. 1995; Bak et al. 2001), prairie dog towns may be an important overwintering resource. As such, these species were highly associated with prairie dog towns across seasons (Fig. 5). These species continue to depend on prairie

dogs and, therefore, our conservation focus should not be limited to breeding communities. Unlike neotropical migrants that winter into South America, grassland birds winter mostly within the Great Plains (Knopf and Samson 1995). Winter ecology of these species has not been well studied (Knopf 1994). Seasonal changes in species pools, population dynamics, and ecological interactions among species dependent on prairie dog towns or paired sites are important topics for future research. Abundance, richness, and species composition of grassland birds likely varies across the vast, Great Plains region. Therefore, a comparative study using standardized ecological surveys across the historic range of black-tailed prairie dogs will likely provide some key insights into the ecological role, both past and present, of this native community.

Historically, patchiness on the Great Plains was not static, but shifted dynamically in response to unpredictable droughts, irregular fire events, non-random grazing by nomadic large herbivores (Wallace et al. 1995), and correspondingly intense grazing by small herbivores (Vinton and Collins 1997). Fire is now controlled and limited in its extent, and native large grazing guilds have been replaced by domestic cattle. The Great Plains are becoming a more simplified ecological system (Ostlie et al. 1997), one perhaps less capable of renewing itself and adapting to environmental change (Tilman et al. 1996). We believe it is clear that even in their current remnant state, black-tailed prairie dogs play a significant role in the assembly of ecological communities across the Great Plains. Prairie dogs increase diversity on the plains and as a result, increase the complexity of interactions between plant and animal species found there. Prairie dog towns themselves may function as biodiversity islands for certain species groups and as seasonal refugia for other groups. As such, conservation of prairie dogs goes well beyond a single species, but is an important strategy for the preservation of the prairie ecosystem as a whole.

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