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Associations of Grassland Bird Communities with Black-Tailed Prairie Dogs in the North American Great Plains

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Abstract: *Colonial burrowing herbivores can modify vegetation structure, create belowground refugia, and generate landscape heterogeneity, thereby affecting the distribution and abundance of associated species. Black-tailed prairie dogs (*Cynomys ludovicianus*) are such a species, and they may strongly affect the abundance and composition of grassland bird communities. We examined how prairie dog colonies in the North American Great Plains affect bird species and community composition. Areas occupied by prairie dogs, characterized by low percent cover of grass, high percent cover of bare soil, and low vegetation height and density, supported a breeding bird community that differed substantially from surrounding areas that lacked prairie dogs. Bird communities on colony sites had significantly greater densities of large-bodied carnivores (Burrowing Owls [*Athene cunicularia*], Mountain Plovers, [*Charadrius montanus*], and Killdeer [*Charadrius vociferus*]) and omnivores consisting of Horned Larks (*Eremophila alpestris*) and McCown's Longspurs (*Rhynchophanes mccownii*) than bird communities off colony sites. Bird communities off colony sites were dominated by small-bodied insectivorous sparrows (*Ammodramus spp.*) and omnivorous Lark Buntings (*Calamospiza melanocorys*), Vesper Sparrows (*Pooecetes gramineus*), and Lark Sparrows (*Chondestes grammacus*). Densities of 3 species of conservation concern and 1 game species were significantly higher on colony sites than off colony sites, and the strength of prairie dog effects was consistent across the northern Great Plains. Vegetation modification by prairie dogs sustains a diverse suite of bird species in these grasslands. Collectively, our findings and those from previous studies show that areas in the North American Great Plains with prairie dog colonies support higher densities of at least 9 vertebrate species than sites without colonies. Prairie dogs affect habitat for these species through multiple pathways, including creation of belowground refugia, supply of prey for specialized predators, modification of vegetation structure within colonies, and increased landscape heterogeneity.*

Keywords: keystone species, multiple ecosystem services, northern mixed prairie, prairie dog conservation, rangeland biodiversity, semiarid grasslands, spatial heterogeneity

Asociaciones de Comunidades de Aves de Pastizales con Perros de la Pradera en la Gran Llanura de Norte América

Resumen: *Los herbívoros excavadores coloniales pueden modificar la estructura de la vegetación, crear refugios subterráneos y generar heterogeneidad en el paisaje, por lo tanto afectan la distribución y abundancia de especies asociadas. Los perros de la pradera (*Cynomys ludovicianus*) son una de esas especies, y pueden afectar significativamente la abundancia y composición de comunidades de aves de pastizales. Examinamos como afectan las colonias de perros de la pradera a las especies de aves y la composición de la comunidad en la Gran Llanura de Norte América. Las áreas ocupadas por perros de la pradera, caracterizadas por un bajo porcentaje de cobertura de pasto, alto porcentaje de cobertura de suelo desnudo y baja altura y densidad de la vegetación, soportaban una comunidad de aves que difirió sustancialmente en áreas que no tenían perros de la pradera. Las comunidades de aves en sitios con colonias tuvieron significativamente mayores densidades de carnívoros de talla grande (*Athene cunicularia*, Charadrius montanus y Charadrius vociferus*)*

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*y omnívoros (*Eremophila alpestris *y* Rhynchophanes mccownii*) que las comunidades de aves en sitios sin colonias. Las comunidades de aves en sitios sin colonias fueron dominadas por gorriones insectívoros de talla pequeña (*Ammodramus spp.*) y omnívoros (*Calamospiza melanocorys, Pooecetes gramineus *y* Chondestes grammacus*). Las densidades de 3 especies de preocupación para la conservación y una especie cinegética fueron significativamente mayores en los sitios con colonias, y la fuerza de los efectos de los perros de la pradera fue consistente en el norte de Gran Llanura. La modificación de la vegetación por los perros de la pradera sostiene a un conjunto diverso de especies de aves estos pastizales. Colectivamente, nuestros resultados y los de estudios previos muestran que las áreas con colonias de perros de la pradera en la Gran Llanura de Norte América soportan densidades más altas de por lo menos 9 especies de vertebrados que en los sitios sin colonias. Los perros de la pradera afectan el hábitat de esas especies por diferentes vías, incluyendo la creación de refugios subterráneos, proveyendo presas para depredadores especializados, modificando la estructura de vegetación en las colonias e incrementando la heterogeneidad del paisaje.*

Palabras Clave: Biodiversidad de llanuras, conservación del perro de la pradera, especies clave, heterogeneidad espacial, llanura boreal mixta, pastizales semiáridos, servicios ecosistémicos múltiples

Introduction

Managing for spatial and temporal heterogeneity in vegetation structure and composition has emerged as a central component of conservation in grassland and shrubland ecosystems worldwide (Fuhlendorf & Engle 2001; Du Toit et al. 2003; Tews et al. 2004). For example, managing fire and herbivores to enhance landscape heterogeneity can sustain native bird communities in grasslands of Africa and North America (Fuhlendorf et al. 2006; Gregory et al. 2010). Colonial burrowing herbivores are increasingly recognized as species that sustain heterogeneity in grasslands and shrublands by creating belowground refugia and modifying vegetation structure and composition (Noble et al. 2007; Delibes-Mateos et al. 2011; Baker et al. 2012). Colonial burrowing herbivores can also be an essential prey item for specialized predators, such as black-footed ferrets (*Mustela nigripes*) (Roelle et al. 2006) and Iberian lynx (*Lynx pardinus*) (Moreno et al. 2004). These types of herbivores are frequently viewed as pests, but suppression or eradication of their populations may affect the conservation of associated species (Noble et al. 2007; Delibes-Mateos et al. 2011). Although the effects of such herbivores on vegetation structure and heterogeneity are presumed to affect the composition of associated faunal communities, empirical assessments of these effects have been rare.

The black-tailed prairie dog (*Cynomys ludovicianus*) is a colonial burrowing herbivore and the most widely distributed species of prairie dog in North America. It historically inhabited the semiarid portions of the North American Great Plains and is regarded as a keystone species and an ecosystem engineer (Kotliar et al. 1999; Van Nimwegen et al. 2008; Cully et al. 2010). Black-tailed prairie dogs are also often regarded as a pest species (Lamb et al. 2006) because at the extent of an individual ranch or pasture, prairie dogs can compete with livestock for forage and reduce livestock weight gains or stocking rates (Derner et al. 2006; Detling 2006). The distribution and abundance of black-tailed prairie dogs has decreased by 90–98% relative to levels before European settlement (Knowles et al. 2002; Proctor et al. 2006). Because competition with livestock is scale dependent, competition across the geographic range of the black-tailed prairie dog is considerably less than in a given pasture with a prairie dog colony (Detling 2006; Miller et al. 2007). Prairie dogs are a key prey source for black-footed ferrets (Roelle et al. 2006) and Ferruginous Hawks (*Buteo regalis*) (Plumpton & Anderson 1997; Bak et al. 2001), and their burrows provide shelter for Burrowing Owls (*Athene cunicularia*) and reptiles and amphibians (Kretzer & Cully 2001; Sidle et al. 2001; Lantz & Conway 2009). Effects of prairie dogs on communities of small mammals vary across the Great Plains and arise primarily from the creation of belowground refugia (Van Nimwegen et al. 2008; Cully et al. 2010). Modification of vegetation structure by prairie dogs can greatly increase landscape heterogeneity (Baker et al. 2012), but the effects on associated species are less clear.

Grassland bird assemblages are often strongly influenced by changes in the structure and spatial heterogeneity of vegetation (Knopf 1996; Fuhlendorf et al. 2006). Birds that breed in the Great Plains are also one of the most consistently and rapidly declining guilds of bird species on the continent (Knopf 1996; Brennan & Kuvleskey 2005). In the western Great Plains, substantial areas persist as native grassland, and conversion to cropland or other uses has been minimal over the past 40 years (Samson et al. 2004). Here, most remaining grasslands are grazed by livestock. A key question is whether management focused on livestock production, such as the suppression of fire and prairie dogs, may be affecting bird habitat (Knopf 1996; Brennan and Kuvleskey 2005). Although the role of prairie dogs in the conservation of grassland species has been the subject of considerable debate (Vermeire et al. 2004; Miller et al. 2007), there have been few quantitative, spatially extensive studies of the relations between prairie dogs and breeding-bird communities (Smith & Lomolino 2004).

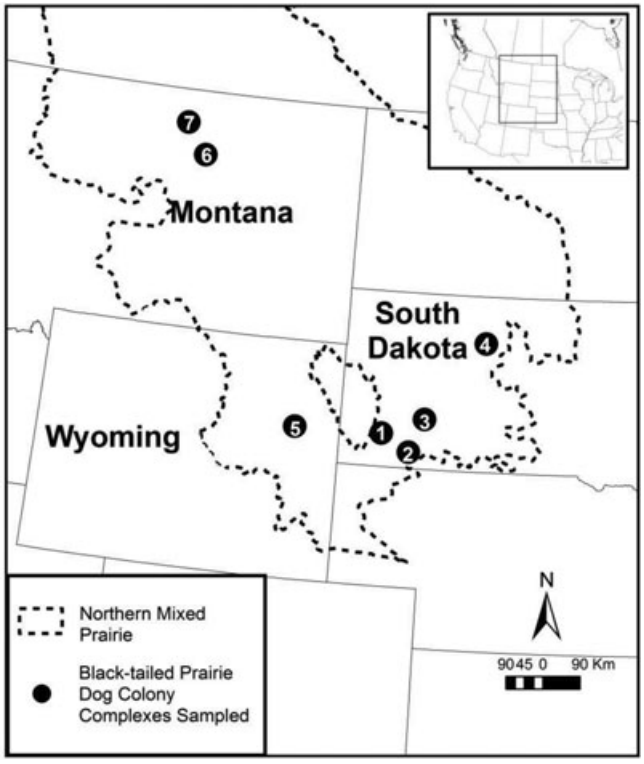

Figure 1. Locations of black-tailed prairie dog complexes sampled in the northern mixed prairie of the North American Great Plains. Numbers correspond to the site names and characteristics listed in Supporting Information.

Grasslands of the Great Plains encompass substantial variation in climate, soils, topography, and vegetation structure. The mixed-grass prairie of the northern Great Plains contains a mixture of midheight C_3 grasses and short C_4 grasses, whereas the southern shortgrass steppe contains mainly short C_4 grasses (Lauenroth et al. 1999). In the southern shortgrass steppe, prairie dogs can reduce vegetation height and alter composition of plant species even though the surrounding vegetation matrix primarily contains short C_4 grasses (Baker et al. 2012). This effect in turn influences the composition of the breeding-bird community (Smith & Lomolino 2004). In northern mixed prairie, prairie dogs affect vegetation structure even more. At 7 different study areas in Montana, Wyoming, and South Dakota (Fig. 1), vegetation height and density was 64–90% lower on colony sites than on off-colony sites (Baker et al. 2012). Prairie dogs also reduced cover of tall shrubs (*Artemisia* spp.) at the 3 study areas in Montana and Wyoming, likely because clipping shrubs increases their ability to detect predators (Baker et al. 2012). In contrast, 4 study areas in South Dakota lacked tall shrubs at on- and off-colony sites (Baker et al. 2012). Regional differences in effects of prairie dogs on vegetation reflect an east-west gradient in mean annual precipitation, plant productivity, and plant composition (Lauenroth et al. 1999) and suggest prairie dogs may have different effects on birds in the eastern versus western regions of the northern mixed-grass prairie.

We examined how black-tailed prairie dogs affect the composition and abundance of breeding birds in the northern mixed prairie. In addition, we evaluated whether the bird community in the eastern and western portions of the northern mixed prairie responded differently to differences in vegetation composition and structure and the effects of prairie dogs. We also present a synthesis of the mechanisms through which black-tailed prairie dogs significantly affect vertebrate species in the Great Plains.

Methods

Field Sampling

We sampled birds on black-tailed prairie dog colony sites and paired off-colony sites at 7 locations in the northern Great Plains (Fig. 1 & Supporting Information). Six locations were selected because they each supported >10 colonies that each occupied areas >20 ha (referred to hereafter as a complex). We also sampled 1 complex of 6 colonies at Wind Cave National Park because seminal studies about the effects of prairie dogs on the northern mixed-grass prairie were conducted there (reviewed by Whicker & Detling 1988). Study sites were in the northern mixed prairie as defined by Lauenroth et al. (1999), where western wheatgrass (*Pascopyrum smithii*) was the dominant grass. However, vegetation differed in the eastern versus western region of the study area (Lauenroth et al. 1999). The 3 western complexes in Montana and Wyoming had tall shrubs (primarily *Artemisia* spp.) and lower mean annual precipitation than the 4 eastern complexes in South Dakota, which were wetter and lacked tall shrubs (Supporting Information; Baker et al. 2012). Grassland bird surveys were conducted from 29 May to 17 July 1996, which coincides with the breeding season. During the survey period, moisture availability was average to above average, as measured by the Palmer Drought Index (http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers.php; Supporting Information). Across all locations, we sampled 137 paired on-colony and off-colony sites (Supporting Information).

All colony sites sampled within each complex were active, as assessed by the presence of prairie dogs or fresh scat present at burrows. Paired off-colony sites were identified by observing colony boundaries and identifying nearby sites approximately 0.5–2.0 km from the colony perimeter) with similar topography, soils, and livestock or bison (*Bison bison*) grazing that were not affected by prairie dogs (Baker et al. 2012). We sampled

all colonies within each complex that met these criteria, except we sampled only half the colonies at the 2 largest complexes (Badlands National Park-Buffalo Gap National Grassland and Thunder Basin National Grassland). We sampled vegetation along a single transect that bisected the longest axis of each colony site and along a transect of the same length at the paired off-colony site (mean transect length = 1150 m [1 SE = 35 m]). Transect length varied with colony size. Visual obstruction of vegetation (VO), a surrogate measure of vegetation volume (Baker et al. 2012); percent canopy cover of grasses, forbs, and shrubs; and percent exposure of bare ground were measured every 100 m along transects. We used these vegetation measurements because vegetation height, density, and cover can strongly affect habitat for grassland bird species (Knopf 1996). Details of vegetation sampling and effects of prairie dogs on vegetation at each complex are described in Baker et al. (2012). All complexes were similar in terms of the direction and magnitude of prairie dog effects on VO, percent cover of grass, and percent exposure of bare ground (Baker et al. 2012).

Birds were surveyed along the same transect lines established to sample vegetation. At each transect a single observer proceeded at a slow pace, stopping every 50 m for 1–2 min. Observers recorded species, group size, and their perpendicular distance to birds at distance categories of 0–40 m, >40–80 m, >80–140 m, >120–200 m, and >200–300 m. We removed birds detected at >300 m from the data set. Transects were surveyed twice by 2 different observers on the same morning. Surveys began near sunrise and lasted about 2 h/transect. On a given morning, each observer surveyed both the transect on the colony site and the paired transect off the colony site. Observers then switched transects and completed a second survey.

Analyses of Bird Density

We used Program Distance (version 6.0) to estimate a detection function (the probability of detecting individuals at different distances from transects) for each bird species that was detected over 60 times (Buckland et al. 2001; Thomas et al. 2009). Program Distance combines the detection function and number of observations to calculate an absolute density (number per square kilometer) and confidence interval for each species. For each species, we fitted (1) a global detection-function model on the basis of conventional distance sampling (CDS), (2) a detection-function model on the basis of multiple-covariate distance sampling (MCDS) with a covariate identifying transects on versus off colony sites, (3) a detection-function model allowing for up to 4 different functions for 4 possible strata (eastern versus western complexes and on versus off colony sites), which we fitted with CDS, and (4) a detection-function model with the 4 previous strata as covariates, which we fitted with MCDS. Models 1 and 3 were fitted with a half-normal key with hermite polynomial expansion, hazard-rate key with cosine expansion, uniform key with cosine expansion, and uniform key with simple polynomial expansion (Buckland et al. 2001). Because models 2 and 4 included a covariate, we considered only half-normal and hazard-rate key functions for these models (Marques & Buckland 2004). For each species, we considered only potential detection functions that were monotonically decreasing, and we selected the detection function that minimized Akaike's information criterion (AIC). We used the selected function to calculate the species' density and associated 95% CI on versus off colony sites in 3 western and 4 eastern complexes. We also calculated densities for each bird species on versus off colony sites at each complex separately (Supporting Information). In addition to the absolute density estimates, we calculated the relative density (percent) on versus off colony sites as the density on colony sites divided by the sum of the density on and off colony sites multiplied by 100.

Analyses of Bird Communities

We used nonmetric multidimensional scaling (NMS) ordination to examine variation in the bird community relative to variation in vegetation structure (VO, percent cover of grasses and shrubs, percent bare ground exposure), to presence versus absence of prairie dogs, and to geographic region (eastern [South Dakota] versus western [Wyoming and Montana]). We used NMS ordination because it is well-suited for non-normal data (McCune & Grace 2002). We used the Sorensen distance measure (implemented with PC-ORD [version 6.0]) and related the first 2 axes of the NMS ordination to a secondary matrix of vegetation variables. We used the multi-response permutation procedure (MRPP) (McCune & Grace 2002) with the Sorensen distance measure implemented in PC-ORD to test whether composition of bird communities differed on versus off colony sites and for eastern versus western complexes. The MRPP provides a statistic (A) that measures the degree of within-group homogeneity relative to the overall sample (McCune & Grace 2002). Values for A vary from 1.0 (all samples within a group are identical) to < 0.0 (less within-group agreement than expected by chance). In community ecology, values for A often range from 0.05 to 0.1 even for groups that are significantly more homogenous than the overall sample (McCune & Grace 2002).

Results

Prairie Dog Effects on Bird Density

We found distinct patterns of bird composition and density on and off colony sites (Fig. 2). At western

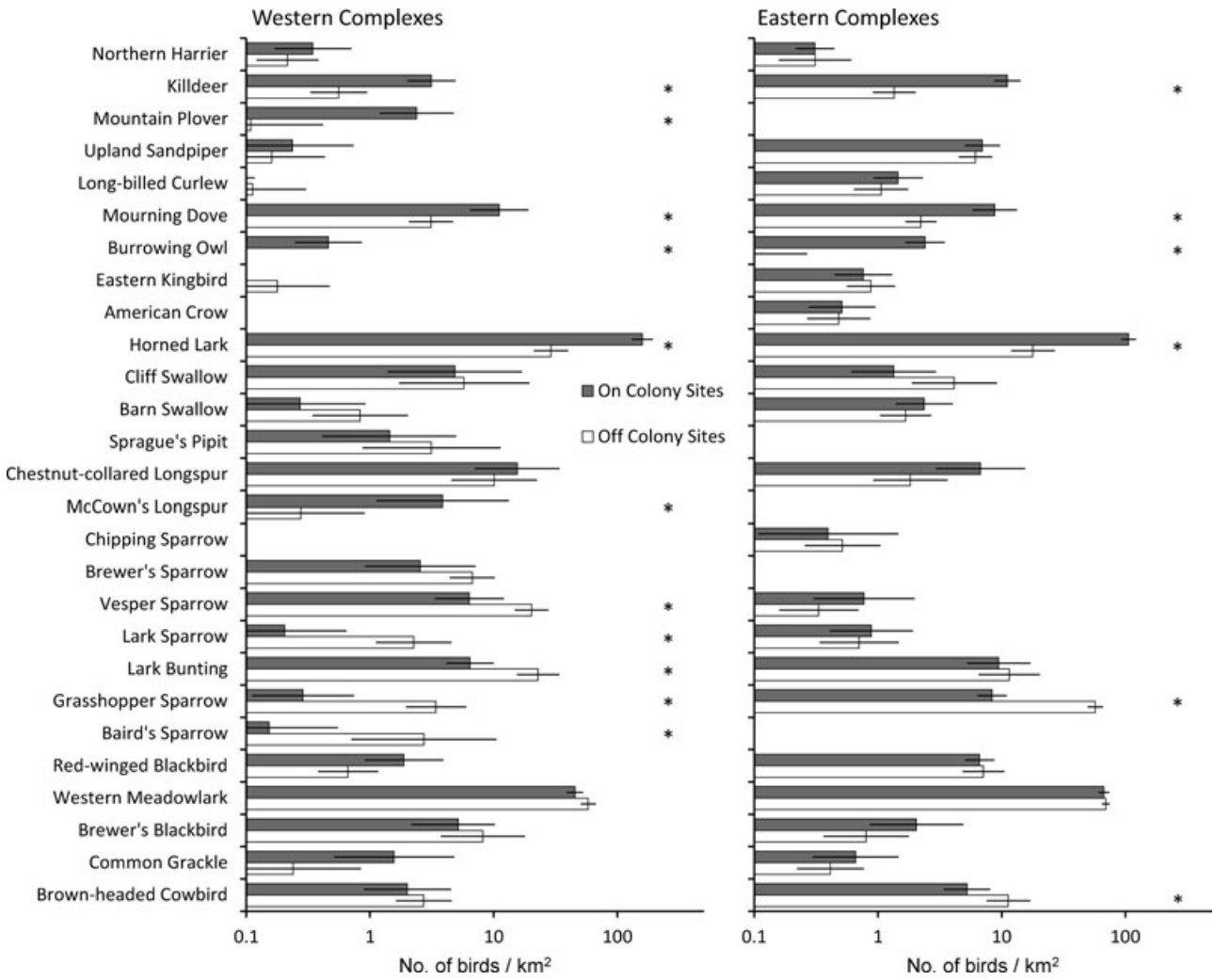

*Figure 2. Comparison of absolute bird density (species listed in taxonomic order) on versus off black-tailed prairie dog colony sites at 3 western complexes in Wyoming and Montana (25 species) and 4 eastern complexes in South Dakota (22 species) (error bars, 95% CI; *, significant difference at the 95% confidence level; x-axis has logarithmic scale).*

complexes, 6 species were more abundant on colony sites: 3 species designated by state wildlife agencies (Colorado, Wyoming, and Montana) and federal land management agencies (U.S. Forest Service, U.S. Fish and Wildlife Service, Bureau of Land Management) as species of conservation concern (Mountain Plover [*Charadrius montanus*]; McCown's Longspur [*Rhynchophanes mccownii*], and Burrowing Owl), 1 game species (Mourning Dove [*Zenaida macroura*]), and 2 other species (Killdeer [*Charadrius vociferous*] and Horned Lark [*Eremophila alpestris*]). Conversely, 5 species were more abundant at off-colony sites: 2 species of conservation concern (Grasshopper Sparrow, [*Ammodramus savannarum*] and Baird's Sparrow [*Ammodramus bairdii*]), and 3 other species (Lark Bunting [*Calamospiza melanocorys*], Vesper Sparrow [*Pooecetes gramineus*], and Lark Sparrow [*Chondestes grammacus*]).

At the eastern complexes, 4 species were more abundant on colony sites: Burrowing Owl, Mourning Dove, Horned Lark, and Killdeer. Conversely, 2 species were more abundant off colony sites: Grasshopper Sparrow and Brown-headed Cowbird (*Molothrus ater*).

Relative densities of bird species at on- and off-colony sites were symmetrical, especially at the western complexes (Fig. 3). In other words, for each species that was positively associated with prairie dog colonies, there was another species that was positively associated with uncolonized prairie to a similar degree.

Prairie Dogs, Vegetation Structure, and Avian Community Composition

Prairie dogs and geographic location of complexes affected the avian community through their effects on

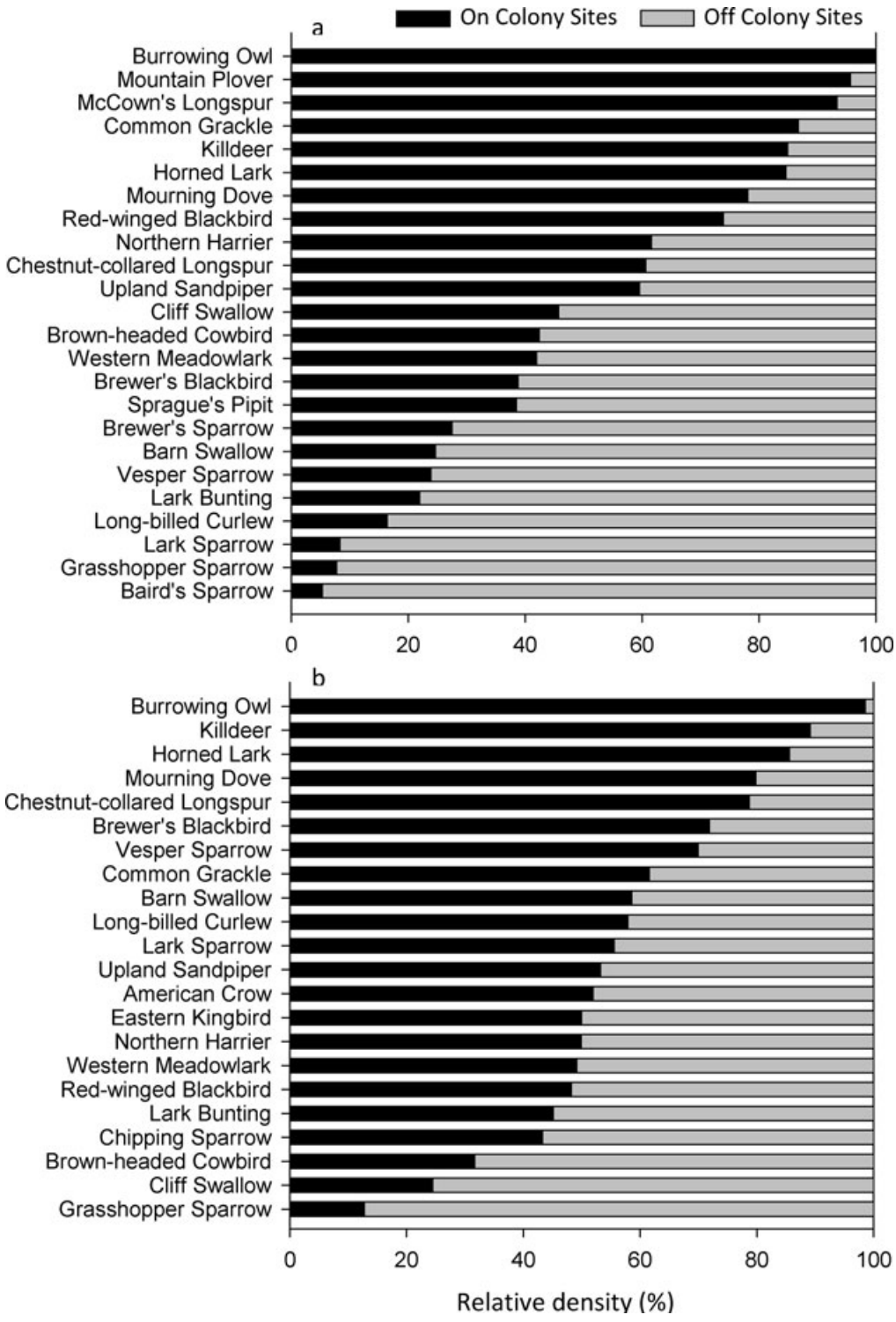

Figure 3. Comparison of relative bird density (%) on versus off black-tailed prairie dog colony sites at (a) 3 western complexes in Wyoming and Montana and 4 (b) eastern complexes in South Dakota. Species are listed according to the strength of their association with prairie dog colony sites.

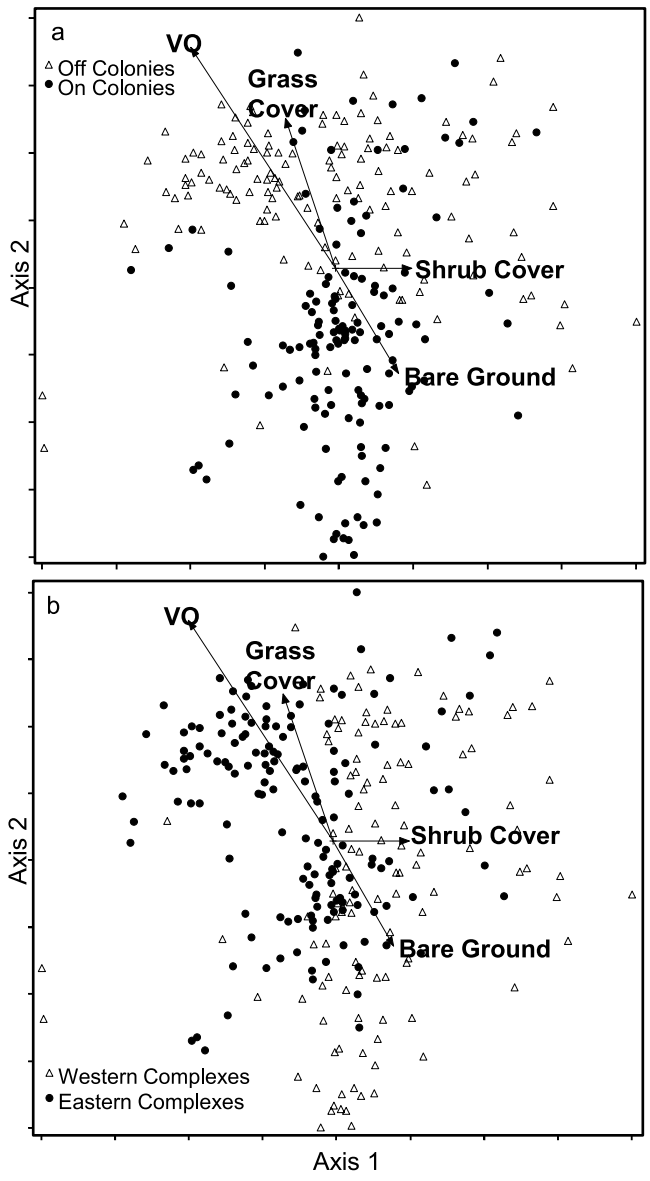

Figure 4. Nonmetric multidimensional scaling ordination of bird communities (a) on and off 137 black-tailed prairie dog colony sites at (b) 3 western and 4 eastern complexes in northern mixed prairie (arrows, direction and strength of correlations between axes 1 and 2 and vegetation attributes [visual obstruction (VO) and cover of grasses, shrubs, and bare ground]). Visual obstruction is a measure that integrates vegetation height and density.

vegetation structure (Fig. 4). The first 2 NMS ordination axes showed significant differences in bird community composition on and off colony sites (MRPP test: $T = -71.23$, $p < 0.001$) (Fig. 4a) and between western and eastern complexes (MRPP test: $T = -40.65$, $p < 0.001$) (Fig. 4b). Within-cluster homogeneity was greater when transects were clustered on the basis of being on versus off prairie dog colonies ($A = 0.085$) than when they were clustered on the basis of being in western versus eastern regions ($A = 0.049$). Axis 1 was most strongly correlated negatively with VO ($r = -0.41$) and positively with percent exposure of bare ground ($r = 0.26$) and percent cover of shrubs ($r = 0.29$). Axis 2 was negatively correlated with percent exposure of bare ground ($r = -0.35$) and positively with percent cover of grass ($r = 0.41$) and VO ($r = 0.50$). Differences in avian community composition on versus off colony sites were primarily associated with variation in VO, percent cover of grass, and percent exposure of bare ground (Fig. 4a). Eastern versus western complexes were separated along axis 1 (eastern complexes with low values; western complexes with high values), which was most strongly associated with greater percent cover of shrubs in western complexes and to a lesser degree with greater percent cover of bare soil and lower VO (Fig. 4b).

Discussion

Prairie dog conservation and management is controversial due to uncertainty in the degree to which prairie dogs enhance populations of species of conservation concern and negatively affect livestock production (Vermeire et al. 2004; Derner et al. 2006; Miller et al. 2007). On one hand, depending on their abundance, the presence of black-tailed prairie dogs can significantly reduce livestock weight gain (Derner et al. 2006). On the other hand, prairie dogs historically coexisted with a diverse and abundant community of native grazing ungulates and forage growing on prairie dog colonies can have relatively higher digestibility and protein concentrations and thus provide a valuable resource for both native and domestic grazers under some conditions (Detling 2006). Studies of how prairie dogs affect the conservation of associated species have focused primarily on the black-footed ferret as an obligate prairie dog predator (Roelle et al. 2006) and on the importance of prairie dog burrows for coexisting mammals, reptiles, and amphibians (Kretzer & Cully 2001; Stapp 2007; Van Nimwegen et al. 2008). Our findings show that the unique vegetation structure created by prairie dogs at their colony sites supported a breeding bird community that differed substantially from grasslands lacking prairie dogs. Bird communities on prairie dog colony sites were characterized by significantly greater densities of 4 species of conservation concern. These effects were consistent across a broad geographic region in the northern Great Plains. We attribute this consistency to similar effects of prairie dogs on vegetation structure across sites in the northern Great Plains (Baker et al. 2012).

Prairie dog effects on vegetation structure may influence the pattern and intensity of nest predation on versus off colony sites (Baker et al. 2000). Aside from the

Mourning Dove, species with increased densities on colony sites had nesting and foraging traits that allow them to avoid predators in short, sparse vegetation (Beason 1995; Knopf & Wunder 2006; With 2010). The bird community on colony sites was characterized by omnivores consisting of Horned Larks and Longspurs, and larger-bodied carnivores consisting of Burrowing Owls, Mountain Plovers, and Killdeer. In contrast, off-colony communities were dominated by omnivores consisting of Lark Buntings, Lark Sparrows, and Vesper Sparrows, and small-bodied insectivorous sparrows. These differences in body size and type of insectivorous bird species may lead to different patterns of predation on the arthropod community at on versus off colony sites and thereby affect the overall structure of the food web.

We found significantly greater densities of 6 breeding bird species on colony sites in northern mixed prairie, whereas Smith and Lomolino (2004) found 4 species with significantly greater densities on colony sites in shortgrass steppe. Western Meadowlarks (*Sturnella neglecta*) were 1 of 4 species Smith and Lomolino (2004) found more abundant on colony sites in shortgrass steppe. In contrast, we found they occurred at similar densities at on and off colony sites in northern mixed prairie. Excluding this widespread and abundant species, we found that prairie dogs significantly affected the abundance of twice as many breeding bird species in northern mixed prairie as was reported by Smith and Lomolino (2004) for shortgrass steppe. This difference may be due to a stronger effect of prairie dogs on vegetation structure in northern mixed prairie, which has higher plant productivity and taller dominant grasses (e.g., *Pascopyrum smithii*) that are less tolerant of grazing. Farther south, aridity and the grazing tolerance of dominant grasses (e.g., *Bouteloua gracilis*) can interact to reduce prairie dog effects on vegetation structure (Baker et al. 2012). However, prairie dog colonies in shortgrass steppe may be an important prey resource for overwintering raptors (Smith & Lomolino 2004), a factor we did not examine for northern mixed-prairie complexes.

Prairie dog colonies also increase landscape heterogeneity, which can benefit species that use different habitats for foraging, nesting, or brood rearing (Knopf 1996; Fuhlendorf et al. 2006). For example, Mourning Doves, Upland Sandpipers (*Bartramia longicauda*), and Long-billed Curlews (*Numenius americanus*) can use several different habitats during the same breeding season. Mourning Doves occurred at substantially higher densities on prairie dog colonies, where sparse vegetation and increased forb abundance may facilitate foraging for seeds. However, Mourning Doves nest in more dense vegetation that is more typical of uncolonized grassland (Otis et al. 2008). Upland Sandpipers and Long-billed Curlews occurred at similar densities on and off colony sites; both are species of conservation concern in Great Plains and both are associated with landscapes containing variable vegetation structure (Derner et al. 2009). Upland Sandpipers typically nest in dense vegetation for concealment, but forage in areas with short vegetation, including recently burned areas, areas grazed intensively by livestock, and prairie dog colonies (Dechant et al. 2002). Long-billed Curlews can nest in extremely short vegetation in the Great Plains, but forage in both short and tall vegetation and move their broods to areas with taller vegetation after nesting (Dugger & Dugger 2002; Derner et al. 2009). Landscape heterogeneity associated with the interspersion of short, sparse vegetation on prairie dog colonies and tall, dense vegetation off colony sites may benefit all 3 species (Fig. 5). We did not test this hypothesis, but we suggest the abundance and reproduction of Upland Sandpipers, Long-billed Curlews, and Mourning Doves in large expanses of northern mixed prairie lacking versus supporting prairie dogs be examined.

Our results indicate large complexes of prairie dog colonies in the northern Great Plains contribute to a substantially more diverse bird community than would occur in landscapes lacking prairie dogs. Our findings are consistent with those of other studies concerning the effects of prairie dogs on vertebrate fauna. Together these results provide strong quantitative evidence that prairie dogs play an important role in sustaining a diverse community of vertebrate fauna in the Great Plains of North America (Fig. 5). These effects may extend to plant and arthropod species as well (e.g., Davidson & Lightfoot 2007). These relations provide a basis for assessing tradeoffs between conservation benefits and agricultural costs associated with sustaining prairie dog complexes in the northern Great Plains.

Density estimates of rare bird species, particularly those of conservation concern, may provide guidance on the area of prairie dog colonies needed to support a desired minimum population level of rare species. Such areas may also provide adequate space for species with smaller area requirements. For example, we estimated that Mountain Plovers occurred at a density of 2.4 birds/km^2 (95% CI 1.2–4.8) on colony sites in the western complexes; thus, a complex may need 2083–8333 ha of prairie dog colonies to support 100 Mountain Plovers. However, species densities can vary among locales (e.g., see Childers and Dinsmore (2008) and Augustine (2011) for Mountain Plovers). Furthermore, use of colony sites may depend on the size and landscape position of the colonies. In New Mexico, Mountain Plovers selectively used only the largest colony sites (Gougen 2012). Estimates of local densities of species of conservation concern and an understanding of how colony-site attributes affect their use are both needed to guide the conservation and management of prairie dog complexes to sustain grassland bird communities.

Other species of colonial burrowing herbivores occur in rangeland ecosystems throughout the world and like prairie dogs many are considered ecosystem

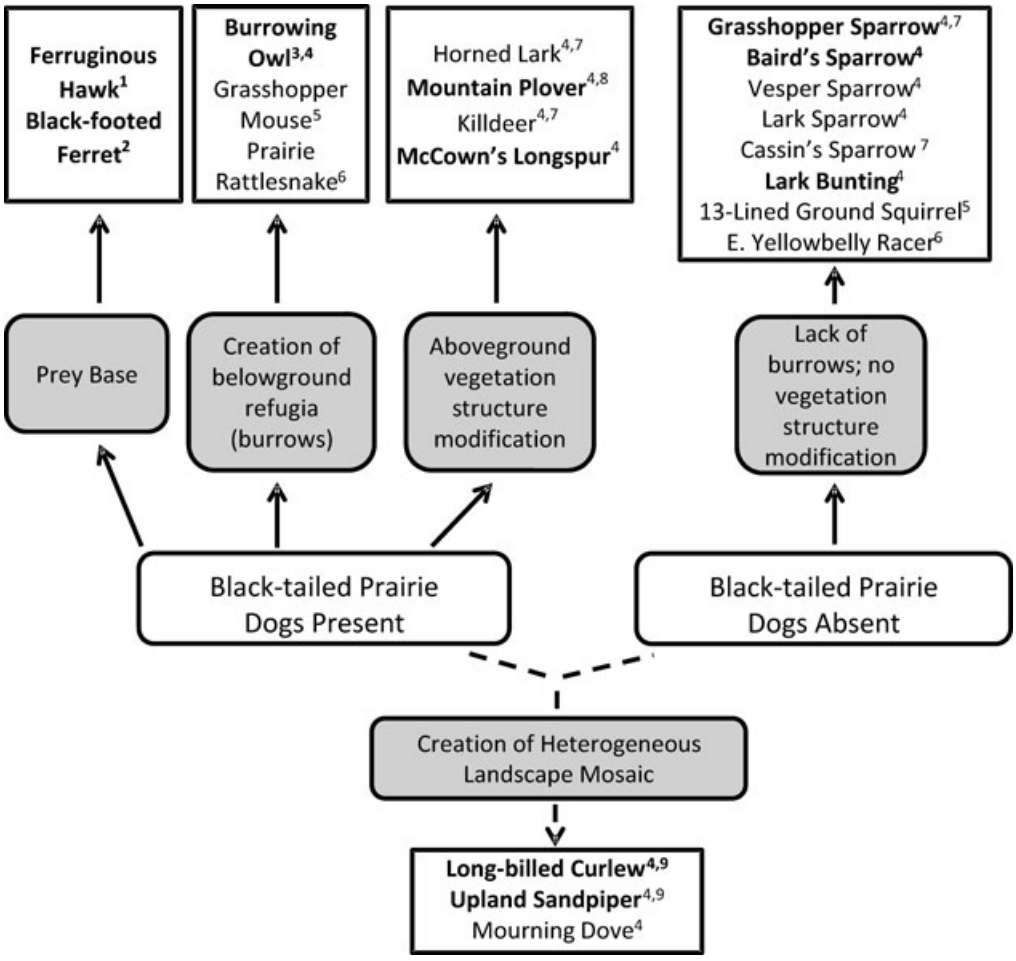

Figure 5. Illustration of how black-tailed prairie dogs affect vertebrate species composition in Great Plains grasslands (solid arrows, relations of species documented to occur at significantly greater or lesser abundance on black-tailed prairie dog colonies in one or more complexes in the western Great Plains; dashed arrows, hypothesized responses to prairie dogs consistent with existing literature; names in bold type, species considered of conservation concern in the western Great Plains by the U.S. Fish and Wildlife Service, U.S. Forest Service, or Bureau of Land Management; 1, Plumpton & Andersen 1997 and Bak et al. 2001; 2, Roelle et al. 2006; 3, Desmond et al. 2000, Sidle et al. 2001, and Lantz & Conway 2009; 4, this study; 5, Stapp 2007, Van Nimwegen et al. 2008, and Cully et al. 2010; 6, Kretzer & Cully 2001; 7, Smith & Lomolino 2004; 8, Childers & Dinsmore 2008 and Augustine 2011; 9, Derner et al. 2009).

engineers, keystone species, and agricultural pests. Examples include European rabbits (*Oryctolagus cuniculus*) in the Iberian peninsula (Galvez-Bravo et al. 2009, 2011), plateau pikas (*Ochotona curzoniae*) and zokors (*Myospalax fontanierii*) on the Tibetan plateau (Zhang et al. 2003), marmots (*Marmota sibirica*) in Mongolian steppe (Yoshihara et al. 2010), burrowing bettongs (*Bettongia lesueur*) in Australia (Baker & Noble 1999; Noble et al. 2007), and plains vizcacha (*Lagostomus maximus*) in South America (Villarreal et al. 2008). Studies have addressed effects of these species on soils, plant community dynamics, belowground refugia, and vegetation heterogeneity. Our findings suggest that vegetation modification by burrowing herbivores may also create unique habitats for grassland birds in other ecosystems. Our findings are consistent with those of Delibes-Mateos et al. (2011), which suggest rangeland managers should consider not only the effects of burrowing herbivores on livestock production, but also recognize the multiple pathways by which they influence native fauna.

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Supporting Information

Characteristics of the 7 complexes of black-tailed prairie dog colonies (Appendix S1) and densities of bird species measured on and off colony sites at each complex (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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