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TREE COVER IN THE SURROUNDING LANDSCAPE REDUCES BURROWING OWL (*ATHENE CUNICULARIA*) OCCUPANCY OF BLACK-TAILED PRAIRIE DOG COLONIES IN SOUTH DAKOTA

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ABSTRACT.—Burrowing Owl (*Athene cunicularia*) population declines have led to the owl's designation as a species of conservation concern in South Dakota. Burrowing Owls nest primarily in black-tailed prairie dog (*Cynomys ludovicianus*) colonies, but a significant proportion of colonies in South Dakota are not occupied by owls. We studied the influence of landscape-level habitat variables on colony selection by Burrowing Owls. We used call-playback surveys to document presence or absence of Burrowing Owls at 613 prairie dog colonies throughout western and central South Dakota. We used a geographic information system to calculate the percent cover of prairie dog colonies, grassland, cropland, and tree canopy in the surrounding landscape at four buffer sizes. We modeled Burrowing Owl occupancy of prairie dog colonies using logistic regression, and ranked models using Akaike's Information Criterion. All competitive models contained a tree-canopy-cover variable. Increasing tree canopy cover within 800 m and 1200 m of colony centers was associated with decreasing likelihood of occupancy by Burrowing Owls. Grassland, cropland, and prairie dog colony cover variables did not influence occupancy by Burrowing Owls, and these variables did not improve model fit or discrimination. In landscapes where the presence of nesting burrows is not a limiting factor, as in central and western South Dakota, Burrowing Owls occupied colonies based on the absence of trees. Trees provide habitat for avian and mammalian predators and reduce the available foraging area for Burrowing Owls around prairie dog colonies. Management for Burrowing Owls should include conserving prairie dog colonies in landscapes with few trees and preventing the establishment of trees near occupied colonies.

KEY WORDS: *Burrowing Owl*; Athene cunicularia; *grassland*; *prairie dog colonies*; *site occupancy*; *South Dakota*.

LA COBERTURA DE ÁRBOLES EN EL PAISAJE CIRCUNDANTE REDUCE LA OCUPACIÓN POR PARTE DE *ATHENE CUNICULARIA* DE LAS COLONIAS DE *CYNOMIS LUDOVICIANUS* EN DAKOTA DEL SUR

RESUMEN.—La disminución de las poblaciones de *Athene cunicularia* ha llevado a que la especie sea designada como de preocupación para la conservación en Dakota del Sur. En este estado, *A. cunicularia* anida principalmente en colonias de *Cynomys ludovicianus*, pero una porción significativa de las colonias no está ocupada. Estudiamos la influencia de las variables del hábitat a escala de paisaje en la selección de la colonia por parte de *A. cunicularia*. Usamos muestreos con reclamo para documentar la presencia o ausencia de *A. cunicularia* en 613 colonias de *Cynomis ludovicianus* a lo largo del oeste y el centro de Dakota del Sur. Usamos

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un sistema de información geográfica para calcular el porcentaje de cobertura de colonias de *C. ludovicianus*, de pastizal, de campos agrícolas/heno y del dosel arbóreo en el paisaje circundante considerando cuatro tamaños de amortiguamiento. Modelamos la ocupación por parte de *A. cunicularia* de las colonias de *Cynomis ludovicianus* usando regresión logística y modelos de rango siguiendo el Criterio de Información de Akaike. Todos los modelos adecuados incluyeron una variable de cobertura del dosel arbóreo. El aumento de la cobertura del dosel de árboles dentro de los 800 m y los 1200 m desde el centro de la colonia estuvo asociado con una disminución de la probabilidad de ocupación por parte de *A. cunicularia*. Las variables de cobertura de pastizal, de campos agrícolas/heno y de colonias de *Cynomis ludovicianus* no influyeron en la ocupación de *A. cunicularia*, y estas variables no mejoraron el ajuste o la discriminación de los modelos. En los paisajes donde la presencia de individuos nidificantes de *A. cunicularia* no es un factor limitante, como en el centro y el oeste de Dakota del Sur, *A. cunicularia* ocupa las colonias en base a la ausencia de árboles. Los árboles proporcionan hábitat para aves y mamíferos depredadores y reducen el área de alimentación disponible para *A. cunicularia* alrededor de las colonias de *Cynomis ludovicianus*. Las políticas de gestión para *A. cunicularia* deberían incluir la conservación de las colonias de *Cynomis ludovicianus* en paisajes con pocos árboles y evitar el establecimiento de árboles cerca de las colonias ocupadas.

[Traducción del equipo editorial]

Many Western Burrowing Owl (*Athene cunicularia hypugaea*; hereafter, Burrowing Owl) populations have declined in North America in recent decades. Declines have been especially severe along the northern and eastern edges of the Burrowing Owl's North American breeding range (Johnsgard 2002, Davies and Restani 2006, Poulin et al. 2011). Populations in some northern Great Plains states and provinces have decreased most significantly (Sauer et al. 2017). Population declines in the region and perceived threats to existing populations and habitats led to the Burrowing Owl being identified as a Species of Greatest Conservation Need in the South Dakota Wildlife Action Plan (South Dakota Department of Game, Fish, and Parks 2014). Burrowing Owls are present in South Dakota only during the breeding season. Most occur in the western half of the state, but breeding pairs are also reported infrequently in eastern counties (Peterson 1995, Tallman et al. 2002, Shaffer and Thiele 2013).

Burrowing Owls generally nest in burrows excavated by semi-fossorial mammals and are primarily associated with colonies of black-tailed prairie dogs (*Cynomys ludovicianus*; hereafter prairie dogs) in South Dakota (Peterson 1995, Johnsgard 2002, Poulin et al. 2011, Shaffer and Thiele 2013). Prairie dog burrows are the main source of Burrowing Owl nest sites where the species co-occur (e.g., Butts and Lewis 1982, Agnew et al. 1986, Plumpton and Lutz 1993, Conway and Simon 2003, Winter et al. 2003, Tipton et al. 2008).

Burrowing Owls face a variety of threats, but habitat loss and degradation are likely the primary reasons for documented declines. Although western and central South Dakota contain some of the largest blocks of native mixed-grass prairie in North America, conversion of grassland to corn and soybeans has expanded westward at an accelerated rate (Wright and Wimberly 2013) resulting in decreased habitat availability for prairie dogs (Hoogland 2006, Poulin et al. 2011). Even in areas where grasslands are not decreasing, habitat suitability is diminished by the presence of planted and encroaching trees. Woody vegetation negatively affects the occurrence, density, and productivity of grassland birds at multiple scales across their range (Bakker et al. 2002, Winter et al. 2006, Thiele et al. 2013, Greer et al. 2016, Herse et al. 2018). Widespread eradication of prairie dogs and other burrowing mammals has further reduced the availability of nest burrows for Burrowing Owls across much of the western United States (Dechant et al. 1999, Desmond et al. 2000, Holroyd et al. 2001). Many ranchers view prairie dogs as vermin that compete with livestock for forage and seek to control them with poisons or by shooting (Butts and Lewis 1982, Sharps and Uresk 1990, Vosburgh and Irby 1998, Knowles et al. 2002, Hoogland 2006). Prairie dog colonies are also subject to elimination by outbreaks of sylvatic plague (Desmond et al. 2000, Antolin et al. 2002, Hoogland 2006).

Despite widespread losses of prairie dog colonies, not all existing colonies in western South Dakota are occupied by Burrowing Owls. This suggests that additional factors are limiting owl populations in the region and that colony selection by Burrowing Owls depends on environmental features other than the presence of potential nest burrows (Berdan and Linder 1973, Knowles 2001, Griebel and Savidge 2007, Bly 2008, Thiele et al. 2013). Characteristics of

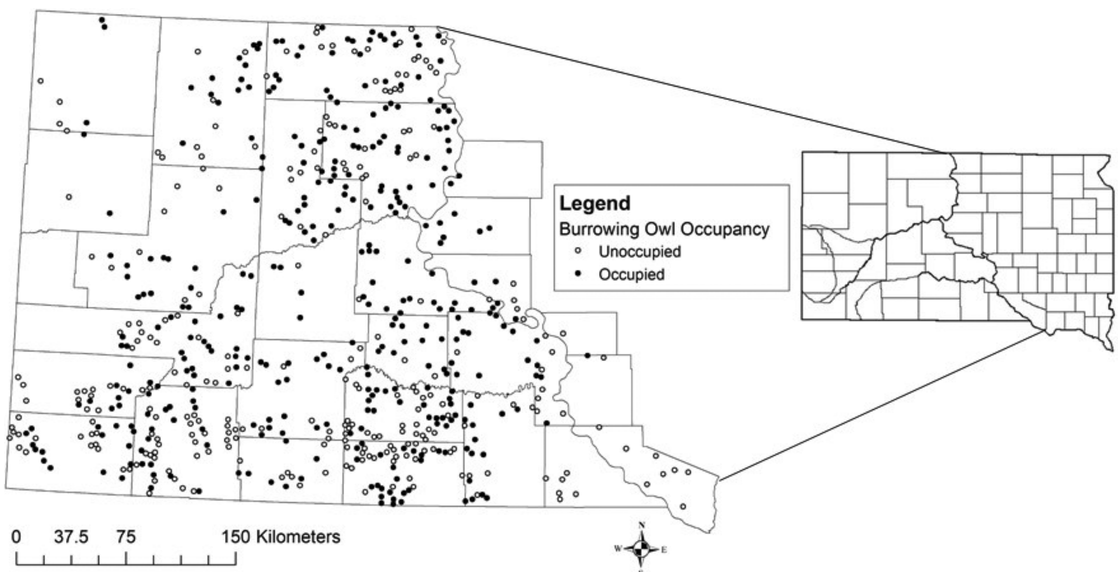

Figure 1. Locations of prairie dog colonies ($n = 613$) in western and central South Dakota South Dakota surveyed for Burrowing Owls in 2010 and 2011. Circles represent the centroids of surveyed colonies. To develop occurrence models, we selected colonies to maintain at least 3200-m spacing between adjacent centroids.

habitat variables at the nest and colony scales for Burrowing Owls are well known (e.g., MacCracken et al. 1985, Green and Anthony 1989, Plumpton and Lutz 1993, Belthoff and King 2002, Poulin et al. 2005, Thiele et al. 2013); however, although such information exists for multiple species of grassland passerines (Bakker et al. 2002, Cunningham and Johnson 2006, Greer et al. 2016), how Burrowing Owls respond to landscape-level habitat characteristics beyond the scale of a nest site or habitat patch is not well known. Our objective was to build on previous work that found landscape variables contributed to the likelihood of Burrowing Owls using prairie dog colonies for nesting (Thiele et al. 2013) by determining if and at what scale landscape-level habitat variables influence the occupancy of prairie dog colonies by Burrowing Owls throughout their range in South Dakota. Land managers require this information to identify priority conservation areas and implement management plans to proactively protect Burrowing Owl habitat across large geographic regions in the face of ongoing land-use change.

METHODS

Study Area. We defined our study area as all South Dakota counties located west of the Missouri River, plus six adjacent counties along the east side of the river that were known to contain prairie dog colonies (Fig. 1). We excluded the forested Black Hills region because it lacks Burrowing Owl habitat (Tallman et al. 2002). Regional climate is characterized by cold, dry winters and hot summers, with much of the annual precipitation coming in summer thunderstorms. The topography of the study area was mostly flat to rolling plains dissected by drainages and dominated by mixed-grass prairie. Both native (e.g., western wheatgrass [*Pascopyrum smithii*], green needlegrass [*Nassella viridula*], and blue grama [*Bouteloua gracilis*]) and introduced grass species (e.g., crested wheatgrass [*Agropyron cristatum*], cheatgrass [*Bromus tectorum*]) were common. Forbs were typically abundant within prairie dog colonies, including native species (e.g., woolly plantain [*Plantago patagonica*], scarlet globemallow [*Sphaeralcea coccinea*]) and exotic species (e.g., field bindweed [*Convolvulus arvensis*], common mullein [*Verbascum thapsus*]). Sagebrush (*Artemisia* spp.) was a major vegetative component in extreme western counties. Tree cover was relatively sparse; most trees were in riparian woodlands (including plains cottonwood [*Populus deltoides*], willow [*Salix* spp.], boxelder [*Acer negundo*], and green ash [*Fraxinus pennsylvanica*]) or in planted shelter belts (including cottonwood, eastern redcedar [*Juniperus virginiana*], and Russian olive [*Elaeagnus angustifolia*]). Eastern redcedar also naturally occurred in some drainages and Ponderosa pine (*Pinus ponderosa*) was locally common near the Black Hills in the west and the Pine Ridge Escarpment in the southwest.

Ranching was the most common land use in the study area. Haying of forage crops such as alfalfa (*Medicago sativa*) and some native and introduced grasses also was widespread. Some cropland was found throughout the study area where topography was suitable for farming. Common crops were wheat (*Triticum aestivum*), corn (*Zea mays*), and soybeans (*Glycine max*); dryland farming was predominant, but there were isolated regions of irrigated farmland, mostly in the southern counties. Most prairie dog colonies were in pastures, but a few colonies (or portions of them) were in crop and hay fields.

Burrowing Owl Surveys. To determine presence or absence of Burrowing Owls, we conducted point-count surveys primarily from roadways throughout the study area using a protocol adapted from Conway and Simon (2003). To obtain a spatially representative sample, we used a map of prairie dog distribution in South Dakota (Kempema et al. 2009) to establish road survey routes. Our objective was to survey approximately 50% of all prairie dog colonies within 800 m of public roads in each county. Poor road conditions and private-property restrictions necessitated modification of some routes in the field.

We conducted surveys during favorable conditions between 0.5 hr before sunrise and 0.5 hr after sunset from 2 May to 21 July 2010 and from 30 April to 9 August 2011. Each survey was conducted once during a single breeding season. We did not survey in the rain, when high winds (>29 km/hr) inhibited our ability to hear owls, nor when hazy conditions noticeably decreased visibility. Each point-count lasted 6 min, divided into two 3-min segments. During the first segment, we searched for owls aurally and visually using 10× binoculars and a 15–45× spotting scope. During the second segment, we broadcast recorded Burrowing Owl calls using the vehicle's sound system while we continued scanning for owls. The recording consisted of the following sequence: 30 sec of male owl's primary call (or *coo-coo* call), 30 sec of silence, 30 sec of primary call, 30 sec of silence, 30 sec of alarm calls, and 30 sec of silence. We recorded the number of adult Burrowing Owls seen or heard in each prairie dog colony and noted owl behaviors, particularly in response to the recorded calls.

We conducted point counts at all locations where burrows were visible along a survey route, using the Kempema et al. (2009) colony map as a guide. We surveyed both active and inactive prairie dog colonies. We obtained location data of survey points with a handheld GPS unit (Trimble Juno SB, Trimble, Sunnyvale, CA, USA). We could adequately survey many colonies from a single point, but the large size and variable topography of some colonies required multiple survey points and periodic deviations from primary roadways to gain additional vantage points. We sought to maintain sufficient spacing (approximately 800 m) between points to minimize double counting of individual owls, and we did not recount owls that flew from the direction of a previous detection. A few colonies could be accessed only on foot; in these cases (<1% of all colonies surveyed), we did not use call-playback methods, but observed and listened for owls for a longer 20-min period at each vantage point.

After surveying a prairie dog colony, we classified it as unoccupied (no owls recorded) or occupied (one or more owls observed). We considered observation of a single owl indicative of a breeding pair because the proportion of unpaired owls is low in most breeding populations (e.g., <10%, Conway and Simon 2003; 0%, Desmond et al. 2000 and Bayless and Beier 2011).

Landscape Analyses. Because we did not know the exact location of each owl pair's nest site within a colony, we used the centroid of each prairie dog colony as the focal point for landscape analysis. We used ArcGIS 9.3 (ESRI, Redlands, CA, USA) to calculate the centroid of each surveyed colony depicted in the South Dakota map of prairie dog colonies (Kempema et al. 2009). Some colonies were represented by multiple polygons in this GIS layer. Before calculating colony centroids, we merged adjacent polygons separated by <50 m because it was difficult to distinguish individual colony units at that scale in the field. In the rare circumstance when we surveyed a colony that was not depicted in the state GIS layer, we digitized the boundary of the missing colony using imagery from 2010 provided by the National Agriculture Imagery Program (NAIP, Aerial Photography Field Office, USDA Farm Services Agency, Salt Lake City, UT, USA). We also used the NAIP imagery to digitize into separate colony units some large colonies depicted in the state GIS layer that had been fragmented or dramatically

Table 1. Percent cover of grassland (GRASS), cropland/hayland (CROP), tree canopy (TREE), and prairie dog colonies (PDOG) within 400-m, 800-m, 1200-m, and 1600-m radii of the centroids of individual prairie dog colonies ($n = 613$) in western and central South Dakota surveyed for Burrowing Owls in 2010 and 2011.

Landscape Variable and Buffer Radius	Percent Cover		
	Mean	Standard Deviation	Range
GRASS_400	86.6	16.8	0.0–100.0
GRASS_800	80.8	18.5	0.0–100.0
GRASS_1200	77.7	19.0	0.7–100.0
GRASS_1600	76.3	18.9	1.3–99.6
CROP_400	7.2	15.0	0.0–98.3
CROP_800	11.5	17.1	0.0–95.2
CROP_1200	13.7	18.0	0.0–95.1
CROP_1600	14.5	17.9	0.0–90.4
TREE_400	1.2	3.2	0.0–26.8
TREE_800	2.5	5.1	0.0–55.7
TREE_1200	3.2	5.7	0.0–63.3
TREE_1600	3.4	5.6	0.0–62.5
PDOG_400	42.1	29.8	0.1–100.0
PDOG_800	18.7	18.8	0.0–97.7
PDOG_1200	11.3	12.7	0.0–86.1
PDOG_1600	8.5	10.1	0.0–84.4

reduced in size since the publication of Kempema et al. (2009); these infrequent scenarios were primarily the result of local sylvatic plague outbreaks in the southern counties.

For each colony unit, we used GIS tools to create buffers with radii of 400 m, 800 m, 1200 m, and 1600 m around the colony centroid. These buffers represented typical scales of land management (e.g., pasture sizes and field sizes) and approximated the lower and upper ends of Burrowing Owl home range sizes noted in previous studies (e.g., Butts 1973, Green and Anthony 1989, Haug and Oliphant 1990, Gervais et al. 2003). Many of the prairie dog colonies were located relatively close to one another. Colonies with overlapping buffers could not be considered independent samples (Cunningham and Johnson 2006). Therefore, if two or more colonies had overlapping 1600-m buffers, we randomly selected only one colony from the group to include in the analyses.

We calculated additional landscape variables from remotely sensed data (Table 1). To calculate the cover of cropland (defined as row crops, small grains, and hay) and grassland, we used the 2006 National Land Cover Database (NLCD, USGS Earth Resources Observation and Science Center, Sioux Falls, SD, USA). The best available tree canopy layer was obtained from the 2001 NLCD; this dataset displayed a combined canopy layer that was more representative of actual tree cover than combining the separately classified deciduous, evergreen, and mixed forest types in the 2006 NLCD, based on a comparison of both layers with the 2010 aerial imagery. Using this combination of layers and the compiled prairie dog colony layer, we calculated the percent cover of trees, cropland, grassland, and prairie dog colonies surrounding each colony centroid at the four buffer levels. Tree canopy, grassland, and cropland cover were mutually exclusive classifications; however, prairie dog colonies were located within other cover types (predominantly grassland), such that measures of colony cover overlapped with those cover types.

Data Analyses. We used logistic regression and the information-theoretic approach (Burnham and Anderson 2002) to evaluate the influence of grassland, cropland, tree canopy, and prairie dog colony coverage on Burrowing Owl occupancy of prairie dog colonies. We checked for correlations between pairs of variables before developing models. Crop cover and grassland cover were strongly negatively correlated at all buffer levels (Spearman rank correlation –0.68 to –0.75) and were not included together in any models. We created nine candidate models to evaluate based on existing literature and field observations. A version of each candidate model was created for all four buffer levels (400 m,

Table 2. Binary logistic regression models analyzed to evaluate the influence of landscape variables on Burrowing Owl occupancy of prairie dog colonies ($n = 613$) surveyed throughout western and central South Dakota in 2010 and 2011. Each model was run at the 400-m, 800-m, 1200-m, and 1600-m scales for 36 total candidate models.

PREDICTOR VARIABLES[1]
PDOG
GRASS
TREE
PDOG + TREE
PDOG + CROP
TREE + GRASS
TREE + CROP
PDOG + TREE + GRASS
PDOG + TREE + CROP

[1] PDOG = percent cover of prairie dog colonies within radial buffer distance; GRASS = percent cover of grassland within radial buffer distance; etc.

800 m, 1200 m, and 1600 m) for a total of 36 models in the set (Table 2).

We used Akaike's Information Criterion (AIC) to rank candidate models. We considered $\Delta AIC < 2$ as indicative of similarly competitive top models and calculated Akaike model weights to evaluate the probability of any model being the best model in the set (Burnham and Anderson 2002). AIC values only indicate the relative strength of models in a set (Burnham and Anderson 2002, Cunningham and Johnson 2006). We also considered McFadden's ρ^2 and area under receiver operating characteristic (ROC) curve as metrics of model fit and performance when evaluating competitive models. McFadden's ρ^2 values from 0.2 to 0.4 are considered a highly satisfactory indicator of model fit (Tabachnick and Fidell 2007). We used ROC curves to evaluate the ability of each model to discriminate between occupied and unoccupied colonies. Hosmer and Lemeshow (2000) considered models with area under ROC curve values between 0.7 and 0.8 to have acceptable discrimination and those with values between 0.8 and 0.9 to have excellent discrimination. We also calculated 85% confidence intervals for coefficients of variables in competitive models. We considered a variable to have a significant effect if the 85% confidence interval for the coefficient did not include zero (Arnold 2010).

RESULTS

In 2010, we surveyed 776 prairie dog colonies; 405 (52%) were unoccupied and 371 (48%) were occupied. In 2011, we surveyed 460 colonies; 187 (41%) were unoccupied and 273 (59%) were occupied. After eliminating those with overlapping 1600-m buffers, 613 surveyed prairie dog colonies (350 occupied, 263 unoccupied) remained as the basis for modelling Burrowing Owl occurrence (Fig. 1).

Based on $\Delta AIC < 2$ and Akaike model weight criteria, seven of the 36 candidate models were similarly competitive as top models (Table 3). All of the top models contained a tree cover variable reflecting influences at the 800-m or 1200-m buffer scales. Tree cover variables were the only variables with significant coefficients. The probability of Burrowing Owl occurrence decreased as the proportion of tree cover increased, whether evaluated at the 800-m or 1200-m buffer scale (Fig. 2 and 3). The

Table 3. Top binary logistic regression models ($\Delta AIC < 2$) portraying the influence of land-cover variables on Burrowing Owl occupancy of prairie dog colonies ($n = 613$) surveyed throughout western and central South Dakota in 2010 and 2011.

MODEL[a]	ΔAIC[b]	W_i[c]	ρ^2[d]	ROC[e]
CONSTANT − **TREE_1200**	0	0.168	0.048	0.656
CONSTANT − **TREE_1200** + GRASS_1200	0.158	0.155	0.050	0.647
CONSTANT − **TREE_800**	0.645	0.121	0.047	0.672
CONSTANT − **TREE_800** + GRASS_800	1.038	0.100	0.049	0.659
CONSTANT − **TREE_1200** + GRASS_1200 − PDOG_1200	1.466	0.081	0.051	0.646
CONSTANT − **TREE_1200** − PDOG_1200	1.726	0.071	0.048	0.656
CONSTANT − **TREE_1200** − CROP_1200	1.733	0.070	0.048	0.652

[a] Consult Table 1 for additional information about variables considered in the models. Variables in bold had coefficients with 85% confidence intervals that did not contain zero.
[b] Difference in the Akaike Information Criterion score between the evaluated model and the top model.
[c] Akaike weight.
[d] McFadden's rho-squared.
[e] Area under receiver operating characteristics curve.

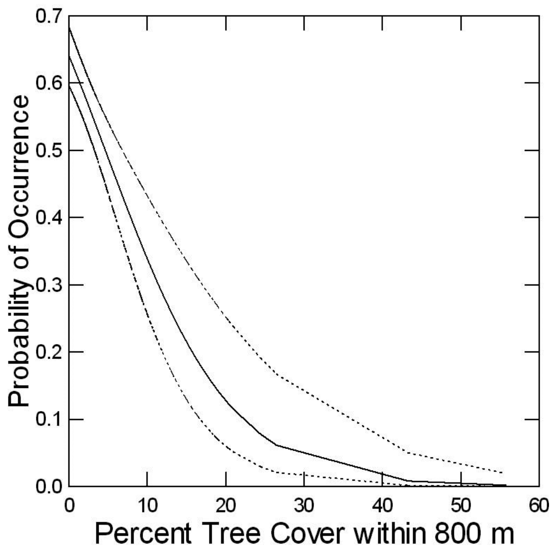

Figure 2. Probability of Burrowing Owl occurrence in prairie dog colonies surveyed throughout western and central South Dakota in 2010 and 2011 in relation to percent tree cover within 800 m of colony centroids. Dotted lines represent upper and lower 95% confidence limits.

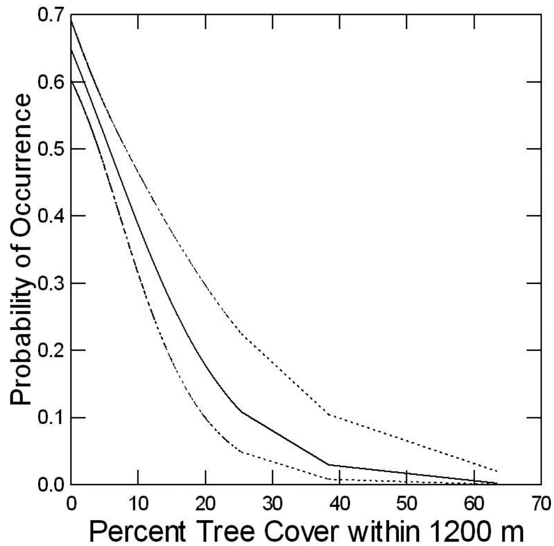

Figure 3. Probability of Burrowing Owl occurrence in prairie dog colonies surveyed throughout western and central South Dakota in 2010 and 2011 in relation to percent tree cover within 1200 m of colony centroids. Dotted lines represent upper and lower 95% confidence limits.

probability of owl occurrence was 64–65% in prairie dog colonies that had no tree cover within 800 m or 1200 m of the colony centroid. With 20% tree cover, the probability of owl occurrence dropped to 12.5% at the 800-m buffer scale and to 16.5% at the 1200-m buffer scale. Variables indicating a positive relationship to grassland coverage and a negative relationship to cropland and prairie dog colony coverage also contributed to the top models, but the coefficients for these variables were not significant and their inclusion did not improve model discrimination or fit. Area under ROC values (0.646–0.672) for all top models indicated marginal ability to discriminate between occupied and unoccupied colonies (Hosmer and Lemeshow 2000). Similarly, low McFadden's ρ^2 values (0.047–0.051) indicated poor goodness-of-fit (Tabachnick and Fidell 2007).

DISCUSSION

The ability of our models to discriminate between occupied and unoccupied colonies was marginal, indicating landscape variables do not account for all of the existing variation in colony use by Burrowing Owls. Burrowing Owl habitat requirements span scales from the nest burrow to the home range and beyond (Lantz et al. 2007, Restani et al. 2008, Thiele et al. 2013). Although collecting finer-scale habitat variables for all colonies was not feasible due to the scale of our study, their inclusion likely would have improved model fit and discrimination. In fact, previous work on a smaller scale in western South Dakota found the best models for predicting Burrowing Owl nest-site selection incorporated local and landscape-scale habitat variables, and model fit and discrimination were excellent (Thiele et al. 2013).

Our results suggested that in landscapes where the presence of potential nest burrows is not a limiting factor, as in central and western South Dakota, Burrowing Owls occupy colonies based on the absence of trees. Previous research found Burrowing Owls nested in prairie dog colonies with decreased tree cover within 800 m in western South Dakota (Thiele et al. 2013). Our study indicated this relationship extends to Burrowing Owl occupancy of colonies across their range in central and western South Dakota and supported the use of landscape models to prioritize landscapes for conservation of Burrowing Owl habitat.

For Burrowing Owls, selection of landscapes with few trees may minimize predation risk and maximize foraging opportunities. Trees provide perches and nest sites for large raptors such as Red-tailed Hawks (*Buteo jamaicensis*), Swainson's Hawks (*B. swainsoni*), Ferruginous Hawks (*B. regalis*), and Great Horned Owls (*Bubo virginianus*), species frequently observed in our study area and known predators of Burrowing Owls (Poulin et al. 2011). An alternative hypothesis, though not mutually exclusive, is that trees reduce the available foraging area within a Burrowing Owl pair's home range. Burrowing Owls often hunt by hovering above the ground to scan for insects, rodents, or other prey below (Butts 1973, Johnsgard 2002, Poulin et al. 2011). We know of no instances where Burrowing Owls have gleaned prey from trees, so trees effectively make an area unsuitable as foraging habitat by replacing grassland and creating a visual barrier that reduces the area an owl can see while hunting. The scale of variables (800–1200 m) in our competitive models approximate the maximum distance Burrowing Owls will travel in search of prey (Butts 1973, Green and Anthony 1989, Haug and Oliphant 1990, Gervais et al. 2003).

Our results did not provide definitive insight about the effects of grassland conversion on Burrowing Owl occupancy. Several of the competitive models included variables indicating decreased occurrence in colonies with less grassland or more cropland in the landscape, but the coefficients for these variables were not significant and their inclusion did not notably improve the models' ability to discriminate between occupied and unoccupied colonies. Western South Dakota is relatively unfragmented, and areas with more intensive cultivation generally lack prairie dog colonies (Kempema et al. 2009). Therefore, it is rare to find prairie dogs occupying cropland-dominated landscapes and such colonies were uncommon in our sample. At all buffer levels, $\geq$95% of colonies had $<$50% cropland in the surrounding landscape, and $\geq$55% of colonies had $<$10% cropland in the surrounding landscape. Therefore, although it is conceivable that at some threshold level of grassland conversion to cropland the effect on Burrowing Owl occupancy could become detrimental, we were not able to detect such a relationship, probably because of the scarcity of colonies within more severely fragmented landscapes.

Our results indicated that landscape analyses may be used to identify priority areas for conservation of Burrowing Owl habitat across large geographic regions (e.g., a state). Proactive management for Burrowing Owls should include conserving prairie dog colonies in landscapes with few trees and preventing the establishment of trees near occupied colonies. Suitable Burrowing Owl habitat could be increased by removing trees near prairie dog colonies or by reintroducing prairie dogs to relatively treeless landscapes where these management actions are technically and politically feasible. We did not find that the current level of grassland conversion in prairie dog landscapes is significantly affecting occupancy by Burrowing Owls. However, we recommend monitoring Burrowing Owl and prairie dog populations to assess potential changes in these species' distributions in relation to management actions and ongoing land-use changes in South Dakota.

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