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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.
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 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, Yosburgh 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...
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 \( \text{Juniperus virginiana} \), and Russian olive \( \text{Elaeagnus angustifolia} \). Eastern redcedar also naturally occurred in some drainages and Ponderosa pine \( \text{Pinus ponderosa} \) 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 \( \text{Medicago sativa} \) 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 \( \text{Triticum aestivum} \), corn \( \text{Zea mays} \), and soybeans \( \text{Glycine max} \); 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, 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 depicts in the state GIS layer that had been fragmented or dramatically
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, 800 m, 1200 m, and 1600 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.

<table>
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<th>PREDICTOR VARIABLES</th>
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<th>WIC</th>
<th>rho²</th>
<th>ROC</th>
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1 PDOG = percent cover of prairie dog colonies within radial buffer distance; GRASS = percent cover of grassland within radial buffer distance; CROP = percent cover of cultivated field within radial buffer distance.
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 $\rho^2$ 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, ≥95% of colonies had <50% cropland in the surrounding landscape, and ≥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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**Literature Cited**


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