The Wilson Journal *of Ornithology*

MULTISCALE NEST SITE SELECTION BY BURROWING OWLS IN WESTERN SOUTH DAKOTA

JASON P. THIELE,[1,3] KRISTEL K. BAKKER,[2,4] AND CHARLES D. DIETER[1]

Published by the
Wilson Ornithological Society

The Wilson Journal of Ornithology 125(4):763–774, 2013

MULTISCALE NEST SITE SELECTION BY BURROWING OWLS IN WESTERN SOUTH DAKOTA

JASON P. THIELE,[1,3] KRISTEL K. BAKKER,[2,4] AND CHARLES D. DIETER[1]

ABSTRACT.—Grassland bird species frequently respond to habitat characteristics at multiple spatial scales when selecting nest sites. The Western Burrowing Owl (*Athene cunicularia hypugaea*) is a grassland bird species of conservation concern across much of its range, but most studies of its habitat needs have been restricted to relatively small geographical areas and have not integrated multiple spatial scales. Our study examined habitat characteristics at three spatial scales—local (near the burrow), colony, and landscape—across western South Dakota. We searched for Burrowing Owls in 107 prairie dog colonies from May to August 2011. We located nest burrows in owl-occupied colonies, and we randomly selected non-nest burrows in colonies that were not occupied by owls for comparison. We collected data for local habitat variables in the field. Ground truthing and aerial imagery were used to calculate colony and landscape variables. We used logistic regression to identify variables that impacted nest site selection. Variables at multiple scales were important, with percent tree cover within 800 m of the burrow and visual obstruction at the burrow having the greatest effect on nest site selection. Burrowing Owls in western South Dakota were most likely to nest in landscapes with little tree cover, perhaps to avoid large avian predators associated with trees. At the local scale, Burrowing Owls were most likely to nest in regions of prairie dog colonies with relatively low visual obstruction. Burrowing Owls may benefit from prairie dogs maintaining vegetation at a short height, which allows the owls to easily detect prey and predators. Maintaining active prairie dog colonies in open landscapes across western South Dakota and preventing the establishment of trees near prairie dog colonies is necessary to ensure preferred breeding habitat remains for Burrowing Owls. *Received 17 January 2013. Accepted 14 June 2013.*

Key words: black-tailed prairie dog, Burrowing Owl, mixed grass prairie, multiscale habitat selection, nesting habitat, South Dakota, western South Dakota.

The Western Burrowing Owl (*Athene cunicularia hypugaea*, hereafter 'Burrowing Owl') is a species of concern throughout much of its North American range, as many populations have shown signs of decline (Johnsgard 2002, Klute et al. 2003, Poulin et al. 2011, Sauer et al. 2011). In South Dakota, the Burrowing Owl has been identified as a Species of Greatest Conservation Need in the South Dakota Wildlife Action Plan (South Dakota Department of Game, Fish, and Parks 2006) and a Level I priority species in the South Dakota All Bird Conservation Plan (Bakker 2005).

Burrowing Owls breed primarily in the western half of South Dakota (Peterson 1995, Tallman et al. 2002). Burrowing Owls nest underground, rarely, if ever, creating their own nest burrows but instead using burrows created by semi-fossorial mammals (Johnsgard 2002, Poulin et al. 2011). In South Dakota, Burrowing Owls are closely associated with colonies of black-tailed prairie dogs (*Cynomys ludovicianus*, hereafter 'prairie dogs'). A strong affinity for prairie dog colonies is typical of Burrowing Owls in regions where prairie dogs are present. Other researchers have surveyed for Burrowing Owls in prairie dog colonies and surrounding uncolonized grasslands and found that most or all Burrowing Owls nested in prairie dog colonies (Butts and Lewis 1982, Thompson 1984, Agnew et al. 1986, Plumpton and Lutz 1993, VerCauteren et al. 2001, Conway and Simon 2003, Winter et al. 2003, Tipton et al. 2008). To our knowledge, only one study of Burrowing Owls nesting within the geographic range of prairie dogs did not find prairie dog colonies to be the predominant source of nest sites (Korfanta et al. 2001).

Loss of prairie dog colonies to poisoning, land conversion, and sylvatic plague (a disease caused by the bacterium *Yersinia pestis*) has been linked to declining populations of Burrowing Owls (Desmond et al. 2000, Holroyd et al. 2001). However, because not all prairie dog colonies are occupied by Burrowing Owls, the loss of potential nest sites cannot completely account for population declines. Orth and Kennedy (2001) commented that the decreasing availability of potential nest sites was probably not a limiting factor for the

[1] Department of Natural Resource Management, South Dakota State University, Box 2104A, Brookings, SD 57007, USA.

[2] College of Arts and Sciences, Dakota State University, 820 N. Washington Avenue, Madison, SD 57042, USA.

[3] Current address: Eagle Valley Nature Preserve, 8411 Duncan Road, Glen Haven, WI 53810, USA.

[4] Corresponding author; e-mail: kristel.bakker@dsu.edu

population of Burrowing Owls in eastern Colorado; many prairie dog colonies were not occupied by owls, implying that competition was not particularly high for nest sites.

Much research has been conducted on habitat use by Burrowing Owls in different regions. Most quantitative studies of their habitat have been conducted at the 'local' or 'microhabitat' scale, examining habitat characteristics immediately around nest burrows and comparing them with those of non-nest burrows. Results have been inconsistent among studies, but some habitat characteristics found to differ between nest and non-nest burrows include vegetation composition (Thompson 1984, MacCracken et al. 1985), vegetation structure (Green and Anthony 1989, Plumpton and Lutz 1993), and density or proximity of prairie dog burrows (Plumpton and Lutz 1993, Desmond et al. 2000, Poulin et al. 2005).

Studies of larger-scale habitat characteristics selected by Burrowing Owls have been less common. Some studies have compared the sizes of prairie dog colonies occupied by Burrowing Owls to colonies that were not occupied by owls, but results were mixed. Griebel and Savidge (2007) found that owl-occupied colonies were larger; in contrast, Plumpton and Lutz (1993), Orth and Kennedy (2001), and Restani et al. (2001) found no size difference between occupied and unoccupied colonies. Few studies have examined landscape-scale habitat characteristics. Orth and Kennedy (2001) found that Burrowing Owls in northeastern Colorado were more likely to occupy prairie dog colonies in patchy landscapes than in unfragmented shortgrass landscapes. In western North Dakota, Restani et al. (2008) found that the number of pairs of Burrowing Owls in a prairie dog colony was positively associated with cover of crops, crested wheatgrass (*Agropyron cristatum*), and prairie dog colonies in the surrounding landscape.

Models that incorporate variables from multiple scales are frequently better predictors of grassland bird occurrence and density than single-scale models (Bakker et al. 2002; Fletcher and Koford 2002; Cunningham and Johnson 2006; Winter et al. 2006a, b; Renfrew and Ribic 2008). A literature search revealed only two nesting studies on Burrowing Owls that incorporated local-, colony-, and landscape-level variables—one on the Thunder Basin National Grassland in northeastern Wyoming (Lantz et al. 2007) and the other on the privately-owned Bad River Ranches in central South Dakota (Bly 2008). Results of both studies supported a multiscale approach to modeling habitat selection by Burrowing Owls. Lantz et al. (2007) found that models incorporating local (burrow length, number of burrows, and percent shrub cover), colony (percent prairie dog activity), and landscape (distance to water) variables were the best predictors of presence of Burrowing Owls' nest burrows. Bly (2008) found that prairie dog colony size alone was the best predictor of nest density, but a model incorporating landscape variables (isolation from other colonies and colony habitat type, i.e., upland or lowland) along with colony size was the best predictor of Burrowing Owls' breeding productivity.

Conserving prime habitat for Burrowing Owls requires a better understanding of habitat characteristics that make some potential nest sites more suitable than others. Our objectives were to determine local, colony, and landscape habitat variables that are useful for segregating prairie dog colonies that contain nests of Burrowing Owls from colonies that do not contain nests and to determine the scale/s at which Burrowing Owls respond to habitat changes across a large geographic area. This information is needed by managers seeking to conserve suitable habitat for Burrowing Owls so that a stable population can be maintained. Our study followed the multiscale approach of Lantz et al. (2007) and Bly (2008), but our study area was larger and more ecologically diverse, with many land uses represented. Unlike the previous multiscale studies, our study incorporated land use variables, because we hypothesized that conversion of grasslands to croplands and the incorporation of woody vegetation into the landscape has an effect on Burrowing Owls' nest site selection. Although several authors have commented that Burrowing Owls seem to prefer landscapes with few or no trees (Wedgwood 1976, Clayton and Schmutz 1999, Poulin et al. 2011), only Stevens et al. (2011) quantified tree cover in a Burrowing Owl habitat study.

METHODS

Study Area.—South Dakota is divided approximately in half by the Missouri River. We conducted our study in the western half (Fig. 1), with the exception of the forested Black Hills region, which does not contain habitat for Burrowing Owls (Tallman et al. 2002). Regional

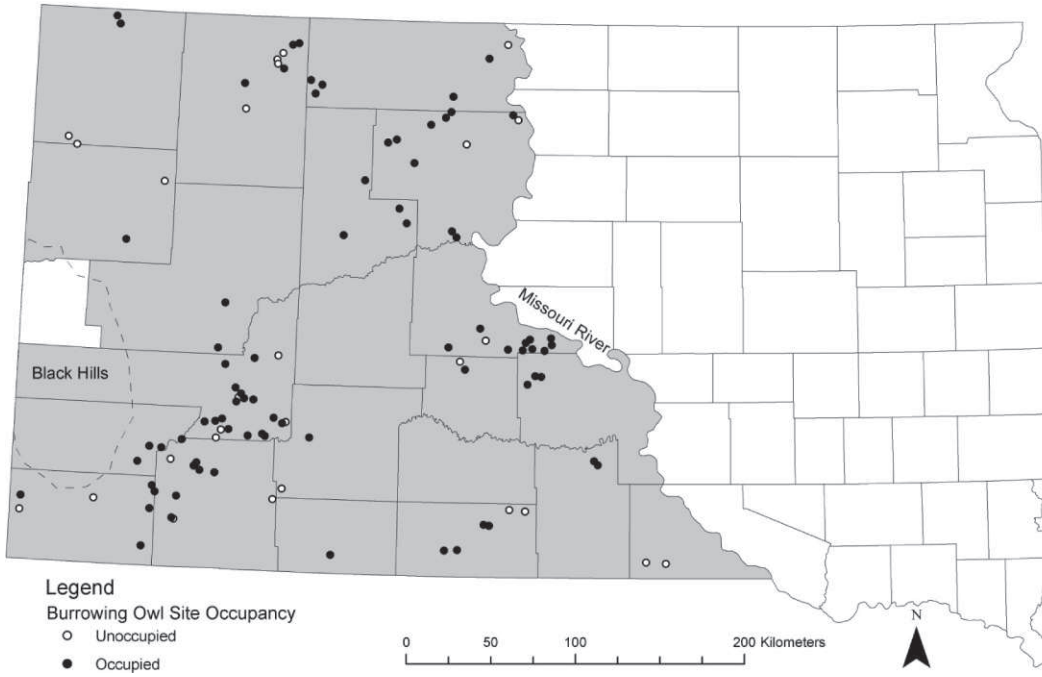

FIG. 1. Map of South Dakota with the study area counties highlighted in gray and prairie dog colonies surveyed for Burrowing Owls represented by black and white circles. Occupied colonies ($n = 80$) contained at least one Burrowing Owl nest, and unoccupied colonies ($n = 27$) contained no nests.

climate is characterized by cold, dry winters and hot summers, with much of the annual precipitation coming in summer thunderstorms. Precipitation generally decreases from east to west across the study area (High Plains Regional Climate Center 2012). Topography consists mostly of flat to rolling plains dissected by drainages. However, badlands formations are abundant in parts of southwestern South Dakota, and buttes and rocky outcrops can be found locally across most of the study area.

Dominant vegetation within prairie dog colonies varies with factors such as soil type, precipitation, prairie dog density, and livestock grazing pressure. Western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), buffalograss (*Bouteloua dactyloides*), purple threeawn (*Aristida purpurea*), and sedges (*Carex* spp.) were commonly encountered native graminoid species in our study area. Non-native crested wheatgrass has been commonly planted as a forage species and in some areas was the dominant grass species. Another introduced species, cheatgrass (*Bromus tectorum*), was an invasive grass through much of the study area. Common native forbs within and near prairie dog colonies included wooly plantain (*Plantago patagonica*), scarlet globemallow (*Sphaeralcea coccinea*), prickly pear (*Opuntia* spp.), snow on the mountain (*Euphorbia marginata*), western yarrow (*Achillea millefolium* L. var *occidentalis*), fetid marigold (*Dyssodia papposa*), and longbract spiderwort (*Tradescantia bracteata*). Commonly encountered exotic forb species included nodding plumeless thistle (*Carduus nutans*), field bindweed (*Convolvulus arvensis*), common mullein (*Verbascum thapsus*), and sweetclover (*Melilotus* spp.). Sagebrush (*Artemisia* spp., primarily *Artemisia tridentata*) was a major vegetative component in a few areas, but it was usually clipped to the ground by prairie dogs within the boundaries of colonies. Trees encountered throughout the study area were generally species associated with riparian areas such as plains cottonwood (*Populus deltoides*), willow (*Salix* spp.), boxelder (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*) or species planted in shelter belts such as cottonwood, eastern red cedar (*Juniperus virginiana*), and the introduced Russian olive (*Elaeagnus angustifolia*). Eastern red cedar was also a

frequent and increasing species in drainages in some areas. Ponderosa pine (*Pinus ponderosa*) was a locally common species near the Black Hills in the west and the Pine Ridge Escarpment in the southwest.

Private, state, federal, and tribal lands were well represented in the study area. Human population is sparse, and ranching is the most common land use. Most prairie dog colonies were located on pasture land used for grazing by livestock. Prairie dog populations were periodically controlled throughout most of the study area. Many of the colonies surveyed during this study had been poisoned within the previous 1–5 years, and many were also subjected to recreational prairie dog shooting according to local landowners and managers.

Haying of forage crops such as alfalfa (*Medicago sativa*) and some native and introduced grasses was also common. Row crop and/or small grain agriculture was generally restricted to areas with topography suitable for cultivation but could be found in all counties in the study area. Common crops were common wheat (*Triticum aestivum*), corn (*Zea mays*), and soybeans (*Glycine max*).

Local (Nest Site) Habitat Data Collection.— From 25 May 2011 to 9 August 2011, we searched for nest sites of Burrowing Owls in 107 prairie dog colonies selected from across the study area (Fig. 1). Selection was pseudo-random; we divided each county into 'clusters' of prairie dog colonies based on geography and colony density and then randomly selected 1–5 colonies from each cluster in proportion to the number of colonies found in the region. If we could not obtain permission to access a randomly selected colony, we selected the nearest colony that we could access. All selected colonies were ≥1,600 m apart to avoid pseudoreplication of landscape variables. Colonies that lacked prairie dogs (because of poisoning or sylvatic plague outbreaks) were rejected from our sample. We spent a minimum of 20 mins systematically surveying each colony with binoculars and/or a spotting scope. In larger colonies, we spent several hours surveying from multiple vantage points to ensure complete coverage. We noted the locations of all Burrowing Owls and observed them until we were fairly certain of the approximate location of each nest burrow. If multiple pairs of owls were nesting within the colony, we assigned a number to each pair and used a random number generator to determine which nest would be used for data collection.

We identified a nest burrow by the presence of at least two of the following signs: owl at burrow entrance, entrance lined with shredded manure of cattle or other grazing mammals, owl droppings, and regurgitated pellets or other prey remains (Thompson 1984, Griebel and Savidge 2007, Lantz et al. 2007). Burrowing Owls often line the nest burrow entrance with shredded manure (Butts and Lewis 1982, Levey et al. 2004, Smith and Conway 2007), and we used the presence of shredded manure as the deciding factor for identifying the nest burrow if several burrows in a small area contained signs of owls.

If the prairie dog colony did not contain any Burrowing Owls, we chose a random burrow within the visible colony boundaries. We used a method described by Restani et al. (2001) where we broke the colony down into progressively smaller quadrants selected at random. We continued to select quadrants until a single suitable burrow remained. Only burrows ≥5 cm in diameter (Lantz et al. 2007) and unobstructed for ≥0.5 m were selected. Virtually all prairie dog burrows in our study area exceeded the minimum diameter criterion, but some randomly selected burrows were rejected because they had collapsed.

To evaluate the vegetative composition around the burrow, we placed pin flags at 2 m and 4 m from the burrow in each cardinal direction. We centered a 1-m^2 Daubenmire frame (Daubenmire 1959) over each flag and recorded the cover class for bare ground (i.e., exposed soil), grass, forb, and tree/shrub. Cover classes were defined as Class 1, 0–5%; Class 2, 5–25%; Class 3, 25–50%; Class 4, 50–75%; Class 5, 75–95%; and Class 6, 95–100%. Total coverage for all cover types could sum to >100%, because vegetation frequently grows in overlapping layers. We calculated the mean value for percent cover of each cover type near a selected burrow using the midpoint for each recorded cover class (Daubenmire 1959).

We obtained a visual obstruction reading using a modified Robel pole (Robel et al. 1970) marked in increments of 0.5 dm. The pole was placed 5 m north of the burrow and viewed from a height of 1 m at a distance of 4 m in each cardinal direction. The lowest mark on the pole that was not completely obstructed by vegetation was recorded. This process was repeated with the pole placed 5 m east, south, and west of the burrow. We

calculated the mean value of the 16 visual obstruction readings taken around each burrow.

We measured the distance to the nearest active burrow, or burrow currently being used by prairie dogs, and the nearest inactive burrow. An active burrow was identified by the presence of fresh scat, fresh digging, clipped vegetation, or a prairie dog at the burrow entrance; an inactive burrow had unclipped vegetation in or near the burrow entrance, had spider webs growing across the burrow entrance, and/or lacked fresh scat (Desmond et al. 1995, Desmond and Savidge 1996, Lantz et al. 2007). We also counted the total number of active and inactive burrows within 10 m of the selected burrow.

We measured the distance to the nearest vegetational edge. The edge was defined as the zone where prairie dogs were no longer modifying the vegetation by grazing or clipping it. The nearest edge was often the outer perimeter of the colony, but occasionally prominent vegetational edges were found within the boundaries of the colony, often because saturated soil excluded prairie dogs and caused a different plant community to develop.

Distance to the nearest perch was measured. We considered a perch to be any object ≥0.5 m tall that could support a Burrowing Owl (Lantz et al. 2007). We did not consider prairie dog mounds to be perch sites since they were abundant at almost all sites and burrow density and distance to burrows were already measured.

Colony- and Landscape-Level Data Collection.—We quantified colony- and landscape-level metrics using a geographic information system (GIS; ArcMAP version 9.3, Esri, Redlands, California, USA). We used 2010 National Agriculture Imagery Program (NAIP) aerial photographs and ground truthing to digitize the boundaries of the prairie dog colonies. The GIS calculated the area of each colony.

The GIS was used to measure the distance to the nearest road. Roads varied from minimum-maintenance trails to paved highways, but we only considered roads with bare surfaces (i.e., we did not include infrequently used pasture access trails with vegetated wheel tracks). If the nearest road was ≥600 m away, we recorded the distance as 600 m. This maximum distance approximated the home range size of Burrowing Owls calculated by previous studies (Green and Anthony 1989, Haug and Oliphant 1990, Sissons et al. 2001, Gervais et al. 2003).

Buffers with radii of 400 m and 800 m were created around each selected burrow. These buffer sizes were based on home ranges of Burrowing Owls and typical scales of land management (e.g., crop field sizes). Within each buffer, we digitized trees, grassland, cropland (i.e., row crops and small grains), and hayland using NAIP photographs and ground truthing. We used GIS to calculate percent cover of trees, grassland, cropland, and hayland within each buffer. Only colonies with non-overlapping buffers were used in analyses.

Statistical Analyses.—We used logistic regression and the information-theoretic approach to evaluate the influence of local, colony, and landscape variables (Appendix 1) on nest site selection by Burrowing Owls. We developed *a priori* models in three single-scale subsets—local, colony, and landscape—using combinations of variables based on existing literature and prior observations of nest sites in western South Dakota (Appendix 2). We did not include two variables in the same model if they had a Spearman rank correlation ≥0.5. For models in the landscape subset, we followed the approach of Cunningham and Johnson (2006) and created separate models at both buffer sizes for the same variable (e.g., if a model contained percent tree cover within 400 m of the burrow, we also included another version of the same model but substituted percent tree cover within 800 m of the burrow). The response variable for binary logistic regression was nest presence/absence.

We used the program SYSTAT (2007) for all modeling and statistical analyses. Akaike's Information Criterion, corrected for small sample sizes (AIC_c; Burnham and Anderson 2002), was used to rank the models in each subset according to the level of support. We calculated the AIC_c difference (ΔAIC_c) between the model with the lowest AIC_c value in each subset and all other models in the subset. According to Burnham and Anderson (2002), models with $\Delta AIC_c < 2$ have 'substantial' support for being the best model in a set. Models with $\Delta AIC_c < 2$ were retained from each subset and combined in four multiscale model subsets—local + colony, local + landscape, colony + landscape, and local + colony + landscape. We ranked the retained single-scale models and the multiscale models by ΔAIC_c and considered any model with $\Delta AIC_c < 2$ to be competitive as the best model in the entire set unless it differed from the top model only by the

TABLE 1. Competitive nest site selection models (ΔAIC_c <2) for Burrowing Owls, the lowest ΔAIC_c model from each model subset, and the null model (intercept only). Data were collected during the summer of 2011 at Burrowing Owls' nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota. ROC is the area under the receiver operating characteristic curve, and ρ^2 is the McFadden's rho-squared value. Variable descriptions are found in Appendix 1.

Model	Model subset	ΔAIC_c	ρ^2	ROC
FORB + BARE + ROBEL + TREE_800	Local + Landscape	0	0.297	0.822
FORB + ROBEL + TREE_800	Local + Landscape	1.137	0.269	0.812
FORB + ROBEL + COL_AREA + TREE_800	Local + Colony + Landscape	2.874	0.273	0.816
ROAD + TREE_800	Landscape	12.781	0.155	0.721
COL_AREA + ROAD + TREE_800	Colony + Landscape	13.557	0.166	0.731
FORB + BARE + ROBEL	Local	14.701	0.157	0.738
FORB + BARE + ROBEL + COL_AREA	Local + Colony	15.961	0.165	0.750
COL AREA	Colony	26.470	0.024	0.638
Null	–	27.307	–	–

presence of an additional variable (Burnham and Anderson 2002, Arnold 2010). We calculated Akaike model weights to evaluate the relative support for each model (Burnham and Anderson 2002).

AIC values only indicate the relative strength of models in a set (Burnham and Anderson 2002, Cunningham and Johnson 2006), so 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 is a metric of model fit; values from 0.2–0.4 are considered highly satisfactory (Tabachnick and Fidell 2007). We used ROC curves to evaluate the ability of each model to discriminate between nest burrows and non-nest burrows. Hosmer and Lemeshow (2000) considered models with area under ROC curve values between 0.7–0.8 to have 'acceptable discrimination' and those with values between 0.8–0.9 to have 'excellent discrimination.'

We also evaluated the effects of variables within competitive models. We calculated a relative importance value for each variable that appeared in one or more competitive models by summing the Akaike weights of models that contained the variable (Burnham and Anderson 2002). Because models containing landscape variables were duplicated at different scales, importance values for landscape variables are not directly comparable to those for local and colony variables. We calculated 85% confidence intervals for the coefficient of each variable in competitive models (Arnold 2010). If the confidence interval overlapped zero, the variable had no significant effect.

RESULTS

Within our sample of 107 prairie dog colonies, 80 were occupied by Burrowing Owls and 27 were unoccupied. Fifty-three occupied colonies contained two or more nests.

Two *a priori* models, both from the local + landscape subset, were considered competitive by having ΔAIC_c <2 (Table 1). The competitive models had highly satisfactory fit and excellent discrimination (Table 1), but model weights were relatively low (0.209 and 0.119). All variables in competitive models had significant effects.

Probability of a site being chosen for nesting dropped from >80% with 0% tree cover within 800 m to below 50% with an increase to 3.5% tree cover (Fig. 2). Both competitive models contained percent tree cover within 800 m of the burrow (TREE_800). Models at the 400 m scale were not competitive. The importance value for TREE_800 was 0.906.

Burrowing Owls were most likely to nest where visual obstruction was low and percent cover of forbs and bare ground was relatively high (Fig. 2). Average visual obstruction reading (ROBEL) occurred in both competitive models. ROBEL had an importance value of 0.998. Average forb cover (FORB) appeared in both competitive models and average bare ground cover (BARE) appeared in the top model, but both FORB and BARE were considerably less important (importance values of 0.574 and 0.373, respectively) than TREE_800 and ROBEL, and they had relatively weak effects (Fig. 2).

DISCUSSION

Our results indicate that Burrowing Owls' nest site selection in prairie dog colonies is related to

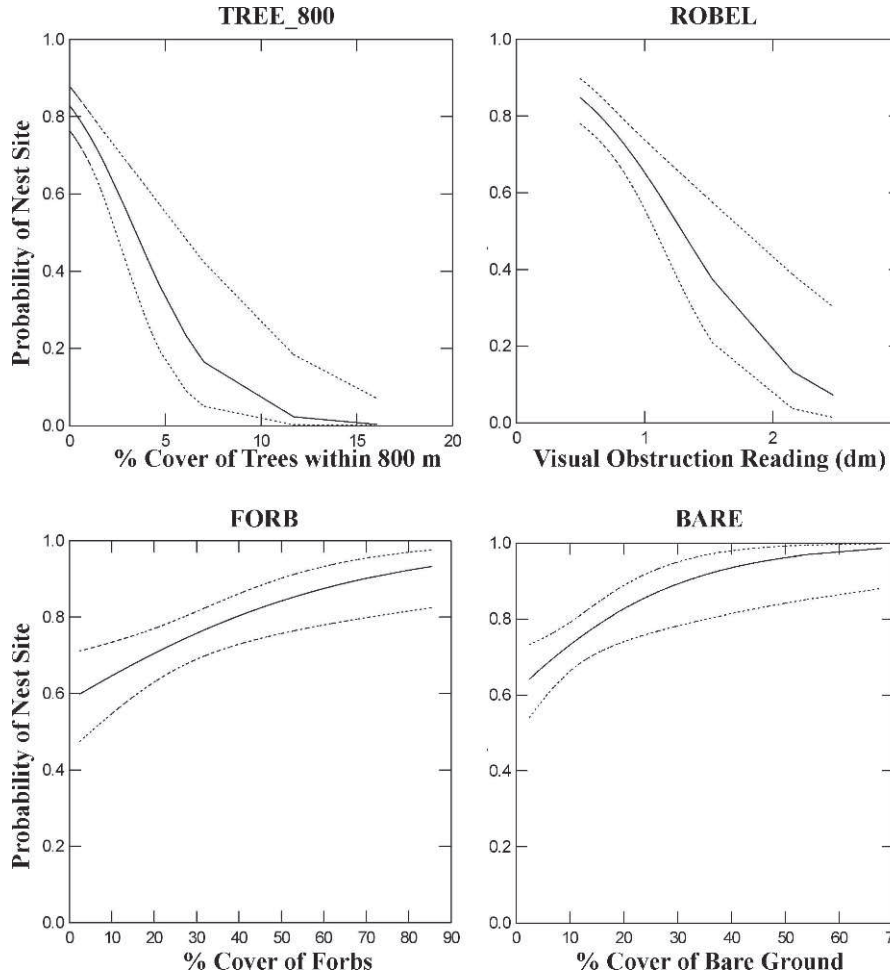

FIG. 2. Effects of variables included in the top model for nest site selection by Burrowing Owls in western South Dakota. Dotted lines represent 85% confidence intervals. Data were collected during the summer of 2011 at Burrowing Owls' nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

both local and landscape habitat characteristics. Single-scale models were not competitive with multiscale models, suggesting that Burrowing Owls may seek out prairie dog colonies in suitable landscapes before searching for specific local vegetative characteristics around potential nest burrows.

Burrowing Owls in western South Dakota avoid trees when selecting prairie dog colonies to nest within. Prairie dogs typically establish colonies in upland areas that are relatively free of trees (Hygnstrom and Virchow 1994), so tree cover is generally absent within and near colonies. However, Burrowing Owls in our study avoided selecting colonies for nest sites where trees were more abundant outside of the colony. Although Burrowing Owls frequently hunt within their selected prairie dog colonies, their home ranges often extend beyond the boundaries of prairie dog colonies, where other prey are available (Butts 1973; Orth and Kennedy 2001; JPT, pers. obs.). The better performance of models at the 800 m scale over models at the 400 m scale indicates that Burrowing Owls select against trees within their home ranges and perhaps beyond.

Our results indicate that even small increases in tree cover can have disproportionately negative effects on Burrowing Owl nest site selection. A variety of grassland birds respond negatively to the presence of trees (Bakker 2003), but our study

is the first to demonstrate a negative relationship between trees and Burrowing Owls. Stevens et al. (2011) also looked at the effects of tree cover but did not find it to be an important predictor of Burrowing Owls' home ranges in southeastern Alberta and southern Saskatchewan; however, tree cover was much lower in their study area (mean of 0.3% within 1,200 m) than in our study area (mean of 1.0% within 800 m). Burrowing Owls may avoid trees in the landscape because trees provide perch sites and nest sites for larger species of raptors. We did not witness any predation events, but we did find remains of Burrowing Owls that had been killed by avian predators. The most abundant large raptors observed near prairie dog colonies in our study area were Red-tailed Hawks (*Buteo jamaicensis*), Swainson's Hawks (*B. swainsonii*), Ferruginous Hawks (*B. regalis*), and Great Horned Owls (*Bubo virginianus*). Habitat for these raptors includes wooded draws or other patches of trees surrounded by upland prairie (Faanes 1983; Johnsgard 1990, 2002), and all of these species are known or suspected predators of Burrowing Owls (Konrad and Gilmer 1984, Clayton and Schmutz 1999, Leupin and Low 2001, Todd 2001, Davies and Restani 2006, Poulin et al. 2011). Birds should be expected to select breeding sites that minimize predation risk for themselves and their offspring (Lima 2009), and trees increase the risk to Burrowing Owls.

The amount of grassland in the surrounding landscape had no influence on nest site selection by Burrowing Owls in our study, suggesting that, at current levels, the conversion of grassland to cropland or hayland is not limiting Burrowing Owls' nest site selection. The landscape in western South Dakota still consists of predominantly intact grasslands, especially in areas where prairie dog colonies remain. The local vegetation variables included in competitive models suggest that Burrowing Owls may nest in areas of high prairie dog activity within colonies. The digging, scratching, grazing, and clipping behaviors of prairie dogs reduce visual obstruction by favoring short, grazing-tolerant grasses, create more patches of bare ground, and promote annual forbs (Agnew et al. 1986, Archer et al. 1987, Whicker and Detling 1988, Winter et al. 2002). Selection of nest sites with short, sparse vegetation is consistent with results of previous studies that have recorded visual obstruction measurements (Green and Anthony 1989, Clayton and Schmutz 1999). Several factors may explain why Burrowing Owls tend to nest in areas with low visual obstruction. Unlike more nocturnal owl species that rely heavily on their sense of hearing to locate prey, Burrowing Owls are primarily visual hunters (Johnsgard 2002). Burrowing Owls use a variety of hunting methods, including running after prey on the ground, flying from a perch, and hovering (Butts 1973, Clayton and Schmutz 1999, Johnsgard 2002, Poulin et al. 2011). These hunting methods are more likely to be successful when vegetation is short and relatively sparse. Burrowing Owls may have difficulty locating prey at ground level if visual obstruction is high, which could have particularly strong implications for juvenile owls, since they often hunt for insects from the ground (JPT, pers. obs.). Low visual obstruction near the nest burrow may also be important for predator detection (Green and Anthony 1989).

We suspect that the strong influence of visual obstruction on nest site selection may have been, at least in part, a result of above-average precipitation in western South Dakota during our study. Precipitation may influence the heterogeneity of vegetation within prairie dog colonies. Vegetation will grow faster and taller in wet years, causing more dramatic differences between clipped and unclipped vegetation (Plumpton and Lutz 1993, Lomolino and Smith 2003, Tipton et al. 2008). The presence of prairie dogs may be especially important for Burrowing Owls seeking nest sites in wet years, when unclipped vegetation would exclude Burrowing Owls from otherwise suitable burrows.

Nest sites of Burrowing Owls in western South Dakota are associated with a relatively high abundance of forbs and bare ground. Despite the comparatively weak effects of these variables, their presence in competitive models may indicate biological significance. Thompson (1984) and MacCracken et al. (1985) found that forb cover was greater around nest burrows than around random burrows in central Wyoming and southwestern South Dakota, respectively, but bare ground cover did not differ between nest burrows and random burrows in either study area. In contrast, Plumpton and Lutz (1993) found no differences in forb cover around nest burrows and random burrows in north-central Colorado, but nest burrows were surrounded by more bare ground than random burrows.

Our findings improve the understanding of how landscape scale habitat features influence nest site

selection by Burrowing Owls. Conservation of the Burrowing Owl in western South Dakota, and elsewhere in the Great Plains, may depend on preserving open landscapes with few trees in order to provide suitable habitat. Even low levels of tree cover in the landscape can make a prairie dog colony unsuitable for nesting by Burrowing Owls, regardless of local vegetation characteristics. Land managers should avoid planting trees in or near areas occupied by Burrowing Owls or by areas with high potential as habitat for Burrowing Owls. Managers should also prevent the colonization of upland habitats by trees such as eastern red cedar. Promoting the persistence of active prairie dog colonies, which provide the vegetative characteristics selected by Burrowing Owls, is critical to maintaining the Burrowing Owl as a relatively common component of the Great Plains' avifauna.

ACKNOWLEDGMENTS

This study was funded by the South Dakota Department of Game, Fish, and Parks through State Wildlife Grant T2-5-R-1, study # 2446. Our manuscript benefitted greatly from reviews by C. Ribic and two anonymous reviewers. We thank C. Loney and A. Kunkel for their assistance with fieldwork and S. Kempema, C. Marsh, E. Childers, R. Hodorff, R. Griebel, R. Mares, P. Drayton, T. LeFaive, L. Sweikert, T. Ecoffey, R. Long, and E. Boyd for their help in finding study sites. We are very grateful to the dozens of private landowners across western South Dakota who gave us access to their properties to search for nests of Burrowing Owls.

LITERATURE CITED

AGNEW, W. D., D. W. URESK, AND R. M. HANSEN. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. Journal of Range Management 39:135–139.

ARCHER, S., M. G. GARRETT, AND J. K. DETLING. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio 72:159–166.

ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

BAKKER, K. K., D. E. NAUGLE, AND K. F. HIGGINS. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638–1646.

BAKKER, K. K. 2003. A synthesis of the effect of woody vegetation on grassland nesting birds. Proceedings of the South Dakota Academy of Science 82:119–141.

BAKKER, K. K. 2005. South Dakota all bird conservation plan. South Dakota Department of Game, Fish and Parks, Pierre, South Dakota, USA.

BLY, K. L. S. 2008. Influence of local and landscape characteristics of prairie dog colonies on Burrowing Owl nest ecology in South Dakota. Thesis. Montana State University, Bozeman, USA.

BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer, New York, USA.

BUTTS, K. O. 1973. Life history and habitat requirements of Burrowing Owls in western Oklahoma. Thesis. Oklahoma State University, Stillwater, USA.

BUTTS, K. O. AND J. C. LEWIS. 1982. The importance of prairie dog towns to Burrowing Owls in Oklahoma. Proceedings of the Oklahoma Academy of Science 62:46–52.

CLAYTON, K. M. AND J. K. SCHMUTZ. 1999. Is the decline of Burrowing Owls *Speotyto cunicularia* in prairie Canada linked to changes in Great Plains ecosystems? Bird Conservation International 9:163–185.

CONWAY, C. J. AND J. C. SIMON. 2003. Comparison of detection probability associated with Burrowing Owl survey methods. Journal of Wildlife Management 67:501–511.

CUNNINGHAM, M. A. AND D. H. JOHNSON. 2006. Proximate and landscape factors influence grassland bird distributions. Ecological Applications 16:1062–1075.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Scientist 33:43–64.

DAVIES, J. M. AND M. RESTANI. 2006. Survival and movements of juvenile Burrowing Owls during the postfledging period. Condor 108:282–291.

DESMOND, M. J. AND J. A. SAVIDGE. 1996. Factors influencing Burrowing Owl (*Speotyto cunicularia*) nest densities and numbers in western Nebraska. American Midland Naturalist 136:143–148.

DESMOND, M. J., J. A. SAVIDGE, AND K. M. ESKRIDGE. 2000. Correlations between Burrowing Owl and black-tailed prairie dog declines: a 7-year analysis. Journal of Wildlife Management 64:1067–1075.

DESMOND, M. J., J. A. SAVIDGE, AND T. F. SEIBERT. 1995. Spatial patterns of Burrowing Owl (*Speotyto cunicularia*) nests within black-tailed prairie dog (*Cynomys ludovicianus*) towns. Canadian Journal of Zoology 73:1375–1379.

FAANES, C. A. 1983. Breeding birds of wooded draws in western North Dakota. Prairie Naturalist 15:173–187.

FLETCHER JR., R. J. AND R. R. KOFORD. 2002. Habitat and landscape associations of breeding birds in native and restored grasslands. Journal of Wildlife Management 66:1011–1022.

GERVAIS, J. A., D. K. ROSENBERG, AND R. G. ANTHONY. 2003. Space use and pesticide exposure risk of male Burrowing Owls in an agricultural landscape. Journal of Wildlife Management 67:155–164.

GREEN, G. A. AND R. G. ANTHONY. 1989. Nesting success and habitat relationships of Burrowing Owls in the Columbia Basin, Oregon. Condor 91:347–354.

GRIEBEL, R. L. AND J. A. SAVIDGE. 2007. Factors influencing Burrowing Owl reproductive performance in contiguous shortgrass prairie. Journal of Raptor Research 41:212–221.

HAUG, E. A. AND L. W. OLIPHANT. 1990. Movements, activity patterns, and habitat use of Burrowing Owls in Saskatchewan. Journal of Wildlife Management 54:27–35.

HIGH PLAINS REGIONAL CLIMATE CENTER. 2012. Historical climate data summaries. High Plains Regional Climate Center, Lincoln, Nebraska, USA. www.hprcc.unl.edu/data/historical/ (accessed 24 May 2012).

HOLROYD, G. L., R. RODRÍGUEZ-ESTRELLA, AND S. R. SHEFFIELD. 2001. Conservation of the Burrowing Owl in western North America: issues, challenges, and recommendations. Journal of Raptor Research 35:399–407.

HOSMER, D. W. AND S. LEMESHOW. 2000. Applied logistic regression. Second edition. John Wiley & Sons, Hoboken, New Jersey, USA.

HYGNSTROM, S. E. AND D. R. VIRCHOW. 1994. Prairie dogs. Pages B85–B92 *in* Prevention and control of wildlife damage (S. E. Hyngstrom, R. M. Timm, and G. E. Larson, Editors). University of Nebraska Cooperative Extension, Lincoln, USA.

JOHNSGARD, P. A. 1990. Hawks, eagles, and falcons of North America: biology and natural history. Smithsonian Institution Press, Washington, D.C., USA.

JOHNSGARD, P. A. 2002. North American owls: biology and natural history. Second Edition. Smithsonian Institution Press, Washington, D.C., USA.

KLUTE, D. S., L. W. AYERS, M. T. GREEN, W. H. HOWE, S. L. JONES, J. A. SHAFFER, S. R. SHEFFIELD, AND T. S. ZIMMERMAN. 2003. Status assessment and conservation plan for the western Burrowing Owl in the United States. USDI, Fish and Wildlife Service, Biological Technical Publication FWS/BTP-R6001-2003. Washington, D.C., USA.

KONRAD, P. M. AND D. S. GILMER. 1984. Observations on the nesting ecology of Burrowing Owls in central North Dakota. Prairie Naturalist 16:129–130.

KORFANTA, N. M., L. W. AYERS, S. H. ANDERSON, AND D. B. MCDONALD. 2001. A preliminary assessment of Burrowing Owl population status in Wyoming. Journal of Raptor Research 35:337–343.

LANTZ, S. J., C. J. CONWAY, AND S. H. ANDERSON. 2007. Multiscale habitat selection by Burrowing Owls in black-tailed prairie dog colonies. Journal of Wildlife Management 71:2664–2672.

LEUPIN, E. E. AND D. J. LOW. 2001. Burrowing Owl reintroduction efforts in the Thompson-Nicola region of British Columbia. Journal of Raptor Research 35:392–398.

LEVEY, D. J., R. S. DUNCAN, AND C. F. LEVINS. 2004. Use of dung as a tool by Burrowing Owls. Nature 431:39.

LIMA, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485–513.

LOMOLINO, M. V. AND G. A. SMITH. 2003. Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. Biological Conservation 115:89–100.

MACCRACKEN, J. G., D. W. URESK, AND R. M. HANSEN. 1985. Vegetation and soils of Burrowing Owl nest sites in Conata Basin, South Dakota. Condor 87:152–154.

ORTH, P. B. AND P. L. KENNEDY. 2001. Do land-use patterns influence nest-site selection by Burrowing Owls (*Athene cunicularia hypugaea*) in northeastern Colorado? Canadian Journal of Zoology 79:1038–1045.

PETERSON, R. A. 1995. The South Dakota breeding bird atlas. South Dakota Ornithologists' Union, Aberdeen, USA.

PLUMPTON, D. L. AND R. S. LUTZ. 1993. Nesting habitat use by Burrowing Owls in Colorado. Journal of Raptor Research 27:175–179.

POULIN, R. G., L. D. TODD, K. M. DOHMS, R. M. BRIGHAM, AND T. I. WELLICOME. 2005. Factors associated with nest- and roost-burrow selection by Burrowing Owls (*Athene cunicularia*) on the Canadian prairies. Canadian Journal of Zoology 83:1373–1380.

POULIN, R., L. D. TODD, E. A. HAUG, B. A. MILLSAP, AND M. S. MARTELL. 2011. Burrowing Owl (*Athene cunicularia*). The birds of North America. Number 61.

RENFREW, R. B. AND C. A. RIBIC. 2008. Multi-scale models of grassland passerine abundance in a fragmented system in Wisconsin. Landscape Ecology 23:181–193.

RESTANI, M., J. M. DAVIES, AND W. E. NEWTON. 2008. Importance of agricultural landscapes to nesting Burrowing Owls in the northern Great Plains, USA. Landscape Ecology 23:977–987.

RESTANI, M., L. R. RAU, AND D. L. FLATH. 2001. Nesting ecology of Burrowing Owls occupying black-tailed prairie dog colonies in southeastern Montana. Journal of Raptor Research 35:296–303.

ROBEL, R. J., J. N. BRIGGS, A. D. DAYTON, AND L. C. HULBERT. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295–297.

SAUER, J. R., J. E. HINES, J. E. FALLON, K. L. PARDIECK, D. J. ZIOLKOWSKI JR., AND W. A. LINK. 2011. The North American Breeding Bird Survey, results and analysis 1966–2009. Version 12.07.2011. USGS, Patuxent Wildlife Research Center, Laurel, Maryland, USA. www.mbr-pwrc.usgs.gov/bbs (accessed 24 May 2012).

SISSONS, R. A., K. L. SCALISE, AND T. I. WELLICOME. 2001. Nocturnal foraging and habitat use by male Burrowing Owls in a heavily-cultivated region of southern Saskatchewan. Journal of Raptor Research 35:304–309.

SMITH, M. D. AND C. J. CONWAY. 2007. Use of mammal manure by nesting Burrowing Owls: a test of four functional hypotheses. Animal Behaviour 73:65–73.

SOUTH DAKOTA DEPARTMENT OF GAME, FISH, AND PARKS. 2006. South Dakota wildlife action plan. South Dakota Department of Game, Fish, and Parks, Wildlife Division Report 2006–2008. Pierre, South Dakota, USA.

STEVENS, A. F. J., E. M. BAYNE, AND T. I WELLICOME. 2011. Soil and climate are better than biotic land cover for predicting home-range habitat selection by endangered Burrowing Owls across the Canadian Prairies. Biological Conservation 144:1526–1536.

SYSTAT. 2007. Statistics for Windows. Version 12. Systat Software Inc., Richmond, California, USA.

TABACHNICK, B. G. AND L. S. FIDELL. 2007. Using multivariate statistics. Fifth Edition. Allyn and Bacon, Boston, Massachusetts, USA.

TALLMAN, D. A., D. L. SWANSON, AND J. S. PALMER. 2002. Birds of South Dakota. Third Edition. South Dakota Ornithologists' Union, Aberdeen, USA.

THOMPSON, C. D. 1984. Selected aspects of Burrowing Owl ecology in central Wyoming. Thesis. University of Wyoming, Laramie, USA.

TIPTON, H. C., V. J. DREITZ, AND P. F. DOHERTY JR. 2008. Occupancy of Mountain Plover and Burrowing Owl in Colorado. Journal of Wildlife Management 72:1001–1006.

TODD, L. D. 2001. Dispersal patterns and post-fledging mortality of juvenile Burrowing Owls in Saskatchewan. Journal of Raptor Research 35:282–287.

VERCAUTEREN, T. L., S. W. GILLIHAN, AND S. W. HUTCHINGS. 2001. Distribution of Burrowing Owls on public and private lands in Colorado. Journal of Raptor Research 35:357–361.

WEDGWOOD, J. A. 1976. Burrowing Owls in south-central Saskatchewan. Blue Jay 34:26–44.

WHICKER, A. D. AND J. K. DETLING. 1988. Ecological consequences of prairie dog disturbances. BioScience 38:778–785.

WINTER, S. L., J. F. CULLY JR., AND J. S. PONTIUS. 2002. Vegetation of prairie dog colonies and non-colonized shortgrass prairie. Journal of Range Management 55:502–508.

WINTER, S. L., J. F. CULLY JR., AND J. S. PONTIUS. 2003. Breeding season avifauna of prairie dog colonies and non-colonized area in shortgrass prairie. Transactions of the Kansas Academy of Science 106:129–138.

WINTER, M., D. H. JOHNSON, AND J. A. SHAFFER. 2006a. Does body size affect a bird's sensitivity to patch size and landscape structure? Condor 108:808–816.

WINTER, M., D. H. JOHNSON, J. A. SHAFFER, T. M. DONOVAN, W. D. SVEDARSKY. 2006b. Patch size and landscape effects on density and nesting success of grassland birds. Journal of Wildlife Management 70:158–172.

APPENDIX 1. Habitat variables collected in 2011 at Burrowing Owls' nest burrows and random non-nest burrows in prairie dog colonies in western South Dakota for use in nest site selection models. Variables with the same superscripts were correlated (Spearman rank correlation ≥0.5) and were not used together in the same model. Variables marked with an asterisk (*) were not used in any *a priori* models because of correlations with other variables predicted to be more important based on the available literature.

Variable	Description	Mean	SE	Range
ACTIVE[a,b]	Number of active prairie dog burrows within 10 m	2.551	0.215	0–9
INACTIVE[c,d]*	Number of inactive prairie dog burrows within 10 m	2.963	0.267	0–13
TOTAL_BURROWS[a,c,e]	Total number of prairie dog burrows within 10 m	5.514	0.342	0–19
NEAR_ACTIVE[b]	Distance in m to the nearest active prairie dog burrow	11.093	1.650	1.2–100
NEAR_INACTIVE[d,e]*	Distance in m to the nearest inactive prairie dog burrow	6.897	0.431	1.2–30.1
GRASS[f]*	Estimated % cover for grass	59.229	1.812	8.75–91.25
FORB[f]	Estimated % cover for forbs	31.352	2.194	2.50–85.31
BARE	Estimated % cover for bare ground	13.817	1.300	2.50–67.81
ROBEL	Average visual obstruction reading in dm	0.756	0.037	0.50–2.47
EDGE	Distance in m to the nearest vegetational edge	33.223	3.195	0–181.4
PERCH	Distance in m to the nearest potential elevated perch site	125.779	11.325	0–600
COL_AREA	Area of the prairie dog colony in ha	37.154	6.284	0.48–426.69
ROAD	Distance in m to the nearest road	301.636	18.014	2–600
GRASS_400[g,h]	% cover of grassland within 400 m	89.002	1.316	44.22–100.04
GRASS_800[g,i,j]	% cover of grassland within 800 m	81.172	1.803	30.75–99.85
CROP_400[h,i,k]	% cover of cropland within 400 m	4.578	1.049	0–48.30
CROP_800[j,k]	% cover of cropland within 800 m	8.133	1.433	0–55.12
HAY_400[l]	% cover of hayland within 400 m	0.947	0.476	0–40.73
HAY_800[l]	% cover of hayland within 800 m	2.504	0.678	0–53.34
TREE_400[m]	% cover of trees within 400 m	0.619	0.173	0–10.75
TREE_800[m]	% cover of trees within 800 m	1.000	0.230	0–16.06

APPENDIX 2. Single-scale *a priori* nest site selection models for Burrowing Owls in western South Dakota, 2011. Models are in three subsets representing different spatial scales—local, colony, and landscape. Models in bold typeface had $\Delta AIC_C < 2$ within the subset and were retained in multiscale models. Variable descriptions are found in Appendix 1.

Local subset	**Colony subset**	Landscape subset
FORB	**COL_AREA**	ROAD
BARE		GRASS_400
ROBEL		GRASS_800
ACTIVE + ROBEL		**TREE_400**
TOTAL_BURROWS + ROBEL		**TREE_800**
TOTAL_BURROWS + EDGE		ROAD + CROP_400
FORB + ROBEL		ROAD + CROP_400
BARE + ROBEL		ROAD + HAY_400
ROBEL + PERCH		ROAD + HAY_800
ACTIVE + FORB + ROBEL		**ROAD + TREE_400**
TOTAL_BURROWS + ROBEL + PERCH		**ROAD + TREE_800**
TOTAL_BURROWS + EDGE + PERCH		GRASS_400 + TREE_400
NEAR_ACTIVE + FORB + EDGE		GRASS_800 + TREE_800
NEAR_ACTIVE + BARE + EDGE		CROP_400 + TREE_400
FORB + BARE + ROBEL		CROP_800 + TREE_800
		HAY_400 + TREE_400
		HAY_800 + TREE_800
		CROP_400 + HAY_400 + TREE_400
		CROP_800 + HAY_800 + TREE_800