BURROWING OWL DISTRIBUTION AND NEST SITE SELECTION

IN WESTERN SOUTH DAKOTA

By

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This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ABSTRACT

BURROWING OWL DISTRIBUTION AND NEST SITE SELECTION

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The burrowing owl (*Athene cunicularia*) is a species of conservation concern in South Dakota. The species' range in the state is reduced from its historical extent, and it is now mostly restricted to the counties west of the Missouri River, where it usually nests in black-tailed prairie dog (*Cynomys ludovicianus*) colonies. Information about the burrowing owl's current range and habitat needs in South Dakota is necessary to maintain the species as a relatively common component of the state's avifauna.

During the summers of 2010 and 2011, I surveyed for burrowing owls in 27 counties in western South Dakota that were known to contain prairie dog colonies. I found burrowing owls in 25 of the surveyed counties, but abundance varied across the study area. I used logistic regression models to examine how percent cover of grassland, cropland, trees, and prairie dog colonies at 4 spatial scales (buffers with radii of 400 m, 800 m, 1,200 m, and 1,600 m) impacted the probability of burrowing owls being detected in a prairie dog colony. Burrowing owls were most likely to occur in prairie dog colonies that had little tree cover within 800 m or 1,200 m, but model performance was relatively poor. Other, unknown landscape variables and/or habitat variables at a more local level are probably utilized by burrowing owls in the selection of a breeding site.

To examine factors driving nest site selection at multiple spatial scales, I searched for owls in 107 prairie dog colonies from May through August 2011. I located nest burrows in owl-occupied colonies, and I randomly selected non-nest burrows in unoccupied colonies for comparison. I collected microhabitat data at each selected burrow, including vegetation composition, visual obstruction, burrow density, and distances to features thought to be potentially utilized or avoided by owls. I also calculated colony-level and landscape-level habitat metrics using a GIS, including colony size and percent cover of trees, grassland, and cropland within 400 m and 800 m of the selected burrow. I used logistic regression to identify variables that impacted nest site selection. Model fit and discrimination was satisfactory for competitive models. The models indicated that burrowing owls in South Dakota selected nest sites in landscapes with little tree cover, perhaps to avoid large avian predators. At the local scale, burrowing owls nested in regions of prairie dog colonies with relatively high percent cover of forbs and bare ground and relatively low visual obstruction readings. These characteristics are associated with prairie dog activity and may increase hunting success for burrowing owls.

Current threats to burrowing owls in South Dakota include conversion of rangeland to cropland, loss of prairie dog colonies to sylvatic plague (*Yersinia pestis*) outbreaks and poisoning campaigns, and shooting by recreational prairie dog hunters. Maintaining active prairie dog colonies in open landscapes across western South Dakota is necessary to ensure preferred breeding habitat remains for burrowing owls.

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CHAPTER 1

BACKGROUND

The western burrowing owl (*Athene cunicularia hypugaea*, hereafter called the burrowing owl) is a small (approximately 19-25 cm in length and 150 g in mass), relatively diurnal owl species native to desert, grassland, and shrub-steppe habitats in western North America and Central America (Haug et al. 1993, Dechant et al. 1999, Johnsgard 2002). The burrowing owl is a migratory species that is present in the northern Great Plains only during its breeding season. Burrowing owls generally arrive in South Dakota in early April and depart by mid-October (Tallman et al. 2002). The birds breed primarily in the western half of the state; however, breeding pairs are reported infrequently in the eastern counties (Peterson 1995; Tallman et al. 2002; South Dakota Ornithologists' Union 2012, unpublished data). Little is known about the wintering locations of burrowing owls that nest in South Dakota, but a few individuals banded in South Dakota and other states in the region have been recaptured during winter in Oklahoma, Texas, and Mexico (Brenckle 1936, Haug et al. 1993, Johnsgard 2002).

Burrowing owls nest underground. Members of the western subspecies rarely, if ever, create their own nest burrows in the northern Great Plains but instead use previously existing burrows, which are usually created by semi-fossorial mammals such as badgers (*Taxidea taxus*), prairie dogs (*Cynomys* spp.), marmots (*Marmota* spp.), and ground squirrels (*Spermophilus* spp.) (Haug et al. 1993, Dechant et al. 1999, Johnsgard 2002). In South Dakota, burrowing owls are closely associated with colonies (often called "towns") of black-tailed prairie dogs (*Cynomys ludovicianus*, hereafter called prairie dogs), although burrows created by other species are occasionally used by burrowing owls where prairie dogs are not present and otherwise suitable habitat is available (Peterson 1995, personal observation). A strong affinity for prairie dog colonies is typical for burrowing owls in regions where colonies 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 in the study areas nested in prairie dog colonies (Butts and Lewis 1982, Thompson 1984, Agnew et al. 1986, Plumpton and Lutz 1993*b*, VerCauteren et al. 2001, Conway and Simon 2003, Winter et al. 2003, Tipton et al. 2008, Conrey 2010, Bayless and Beier 2011). To my knowledge, only 1 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).

Even when other burrow sources are available, burrowing owls seem to prefer nesting in association with colonial mammals such as prairie dogs. Prairie dogs have been called a “keystone species” because of their effects on prairie ecosystems (see Power et al. 1996, Kotliar 2000 for definitions of a keystone species), although these claims have been the subject of some controversy (Miller et al. 1994, Stapp 1998, Kotliar et al. 1999, Miller et al. 2000, Hoogland 2006, Slobodchikoff et al. 2009). Soulé et al. (2003) suggested that prairie dogs could be better described as a “foundation species” because their effects on ecosystems are related to their abundance. Jones et al. (1994) called prairie dogs “ecosystem engineers” because their burrowing and grazing activities alter soils and vegetation. Despite disagreements among researchers about the role of prairie dogs in prairie ecosystems, the literature clearly demonstrates that prairie dogs produce a modified environment that is attractive to burrowing owls. Despite the availability of other sources of burrows in some areas, burrowing owls predominantly nest in prairie dog colonies, suggesting that the habitat conditions produced by prairie dogs may be unique and not duplicated by other mammals. Although multiple species can be considered ecosystem engineers, their effects on the ecosystem are not equal. A study in Argentina compared burrowing owl use of burrows constructed by 2 abundant ecosystem engineers, hairy armadillos (*Chaetophractus villosus*), which are typically solitary and occupy their burrows for short periods of time, and plains vizcachas (*Lagostomus maximus*), which are colonial and use the same burrow system for many years, much like prairie dogs in North America (Machicote et al. 2004). The authors found that even though hairy armadillo burrows were abundant, they were rarely used by burrowing owls, and no burrowing owls nesting in armadillo burrows fledged any young. Burrowing owls frequently nested in plains vizcacha colonies and some were successful. Machicote et al. (2004) concluded that the 2 species were not interchangeable as ecosystem engineers that benefit burrowing owls. In the Great Plains, prairie dog burrows may be superior to those of other species as potential burrowing owl nest sites.

In recent decades, many burrowing owl populations have shown signs of decline. Much of the evidence for declines has come from the United States Geological Survey (USGS) Breeding Bird Survey (BBS). Declines have not been consistent over the species' entire range, but they are especially severe along the northern and eastern edges of the burrowing owl's North American range (Haug et al. 1993, Johnsgard 2002, Davies and Restani 2006). Populations in some northern Great Plains states and provinces have shown some of the strongest decreasing trends (Sauer et al. 2011). Most of South Dakota falls into 2 Bird Conservation Regions (BCRs), the Badlands and Prairies BCR, which is primarily west of the Missouri River, and the Prairie Potholes BCR, which lies to the east of the Missouri River. According to BBS data, burrowing owl populations decreased by 0.6% and 6.8% annually in the Badlands and Prairies BCR and the Prairie Potholes BCR, respectively, over the 1966-2009 survey period (Sauer et al. 2011). The BBS trends should be interpreted with caution, however, as burrowing owls may not be surveyed as effectively as some other species using the BBS methods (Conway and Simon 2003). The National Audubon Society's Christmas Bird Count (CBC) data have also shown declining trends for burrowing owls in some areas (James and Ethier 1989, McIntyre 2004), although these data only reflect populations of wintering birds in southern states. Many of the concerns associated with BBS data also apply to CBC data (McIntyre 2004).

Little is known otherwise about the population status of the burrowing owl in South Dakota. James and Espie (1997) conducted an assessment of the species in North America and asked biologists throughout its range to estimate populations in their respective states or provinces; the estimate provided for South Dakota was 100-1,000 breeding pairs. In South Dakota, burrowing owl surveys and studies have been limited in scale, occurring mostly on publically-owned lands such as the Buffalo Gap National Grasslands (MacCracken et al. 1985*a*, *b*; Agnew et al. 1986; Sidle et al. 2001; Griebel and Savidge 2003, 2007), the Grand River National Grasslands (Knowles 2001, Sidle et al. 2001), the Fort Pierre National Grasslands (Sidle et al. 2001), and Badlands National Park (Martell et al. 1997). Bly (2008) studied burrowing owl nesting ecology on the privately-owned Bad River Ranches in Stanley and Jones counties and Murray (2005) studied the effects of grazing treatments on burrowing owls on the Cheyenne River Sioux Reservation in Dewey and Ziebach counties, but no other studies have assessed the status of burrowing owls on private or tribal lands in South Dakota or across the species' primary range in South Dakota.

Burrowing owls face a variety of threats to their existence, although habitat loss is a likely reason for declines. An increasing amount of rangeland in the Great Plains is being converted to cropland, which decreases the amount of habitat available to the prairie dogs that provide nest burrows (Haug et al. 1993, Hoogland 2006). Even in areas where habitat is not being lost to changes in land use, burrowing owls lose nest sites as prairie dogs and other burrowing mammals are eradicated across much of the western United States (Dechant et al. 1999, Desmond et al. 2000, Holroyd et al. 2001). Desmond et al. (2000) found that declining burrowing owl populations in Nebraska were correlated with declines in the availability of active and inactive prairie dog burrows. Prairie dogs are often treated as pests by ranchers who view them as competitors with livestock for forage (Sharps and Uresk 1990, Knowles et al. 2002, Virchow and Hygnstrom 2002, Hoogland 2006, Slobodchikoff et al. 2009). Prairie dog numbers are usually controlled with poisons (Butts and Lewis 1982, Sharps and Uresk 1990, Hoogland 2006, Slobodchikoff et al. 2009). Shooting prairie dogs is also popular in some areas both as a control method and as a source of recreation, and shooting can be an effective method of controlling some colonies (Vosburgh and Irby 1998, Hoogland 2006, Slobodchikoff et al. 2009). In addition to human control efforts, entire prairie dog colonies can also be eliminated by outbreaks of sylvatic plague, a disease caused by the bacterium *Yersinia pestis* (Desmond et al. 2000, Antolin et al. 2002, Klute et al. 2003, Stapp et al. 2004, Hoogland 2006, Pauli et al. 2006, Slobodchikoff et al. 2009).

However, because not all prairie dog colonies are occupied by burrowing owls, the loss of potential nesting sites cannot completely account for burrowing owl population declines. Burrowing owls apparently respond to other habitat characteristics besides the presence of a prairie dog colony, and some sites must be unsuitable for nesting. Orth and Kennedy (2001) commented that the loss of potential nest sites was probably not a limiting factor for the burrowing owl population in eastern Colorado; many prairie dog colonies were unoccupied by owls, implying that competition was not particularly high for nest sites.

Much research has been conducted on burrowing owl habitat use in different regions. It is known that burrowing owls are generally associated with grassland and desert habitats with relatively sparse vegetation (Haug et al. 1993, Dechant et al. 1999, Johnsgard 2002, Klute et al. 2003). However, most quantitative studies of burrowing owl habitat were conducted at the "local" or "microhabitat" scale, examining habitat characteristics immediately around the nest burrow (e.g., Thompson 1984, MacCracken et al. 1985*b*, Green and Anthony 1989, Plumpton and Lutz 1993*b*, Belthoff and King 2002, Poulin et al. 2005). Several studies have also explored the role of prairie dog colony size in predicting burrowing owl densities and/or nesting success (e.g., Desmond et al. 1995, Desmond and Savidge 1996, Griebel and Savidge 2007, Restani et al. 2008, Bayless and Beier 2011).

Most of these previous studies have found that nest site selection by burrowing owls can be explained in part by local- or colony-level habitat characteristics. However, a body of literature has emerged in recent years suggesting that landscape-level habitat characteristics influence the ultimate nest site selection by grassland birds (e.g., Ribic and Sample 2001; Bakker et al. 2002; Fletcher and Koford 2002; Cunningham and Johnson 2006; Winter et al. 2006*a*, *b*). These studies have generally focused on passerine species, since grassland nesting songbirds are experiencing well-documented population declines of greater magnitude than most other birds in North America (Brennan and Kuvlesky 2005, Sauer et al. 2011). Since burrowing owls are associated with similar habitats, they may also respond to landscape-level features in the nest site selection process.

My study differs from most previous studies by incorporating habitat variables at multiple spatial scales, which is a relatively new approach to burrowing owl habitat studies. My survey area was larger than most previous studies, and my sample size of burrowing owl breeding sites was also larger than that of previous studies. Orth and Kennedy (2001) compared land use in the landscapes surrounding prairie dog colonies occupied by burrowing owls to the landscapes surrounding prairie dog colonies that did not contain owls in northeastern Colorado. The authors did not collect any habitat data near the nest. Gevais et al. (2003) considered several landscape variables in their analysis of home range sizes but did not consider finer-scale variables. Restani et al. (2008) used landscape variables to model burrowing owl density and nest success in western North Dakota, but they also did not include local- or colony-level variables. Tipton et al. (2008) created occupancy models for burrowing owls in eastern Colorado using colony- and landscape-level variables but no local-level variables. A literature search revealed only 2 studies of burrowing owl nest sites 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 Bad River Ranches in central South Dakota (Bly 2008). Both studies found evidence that landscape-level variables do influence burrowing owl nest site selection.

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 2006) and a Level I priority species in the South Dakota All Bird Conservation Plan (Bakker 2005). Maintaining the burrowing owl as a common species in South Dakota is a goal that requires a better understanding of its current range in the state and its specific habitat needs. Information about burrowing owl habitat requirements in South Dakota are critical for management activities because vegetational and structural characteristics associated with burrowing owl nests vary across the species' range (Haug et al. 1993, Klute et al. 2003).

My study aimed to expand on previous studies and to develop models that can be applied to burrowing owls nesting throughout their primary range in South Dakota. The objectives for my study were to document burrowing owl occurrences across the study area, to examine impacts of landscape characteristics on burrowing owl distribution, and to examine habitat characteristics at multiple spatial scales that affect nest site selection by burrowing owls.

CHAPTER 2

STUDY AREA

The study area consisted of most South Dakota counties located west of the Missouri River (Bennett, Butte, Corson, Custer, Dewey, Fall River, Gregory, Haakon, Jackson, Jones, Harding, Lyman, Meade, Mellette, Pennington, Perkins, Shannon, Stanley, Todd, Tripp, and Ziebach; Lawrence County was excluded since it was almost completely forested and did not contain any known prairie dog colonies at the time of the study) and several counties bordering the Missouri River on the east side that were known to contain prairie dog colonies (Buffalo, Brule, Charles Mix, Hughes, Potter, and Sully) (Figure 1). Because burrowing owls are so closely tied to prairie dog colonies in South Dakota, most of my survey efforts were focused on colonies.

Bryce et al. (1998) classified North Dakota and South Dakota into ecoregions based on factors such as geology, soils, topography, vegetation, climate, and land use. The study area lied mostly within the Northwestern Great Plains ecoregion. The counties east of the Missouri River were in the Northwestern Glaciated Plains ecoregion. Parts of Bennett and Todd counties lied in the Nebraska Sandhills ecoregion. The Pine Ridge Escarpment of the Western High Plains ecoregion extended into parts of Bennett, Jackson, and Shannon counties, and some study sites in Custer, Fall River, Meade, and Pennington counties were in the foothills of the Black Hills in the Middle Rockies ecoregion.

Topography was variable throughout the study area, consisting mostly of flat to rolling plains dissected by drainages. However, badlands formations were abundant in parts of southwestern South Dakota, and buttes and rocky outcrops could be found locally across most of the study area.

Regional climate was characterized by cold, dry winters and hot summers, with much of the annual precipitation coming in summer thunderstorms. Precipitation generally decreased from east to west across the state. The High Plains Regional Climate Center (HPRCC; 2011) reported the following mean total annual precipitation figures (1971-2000) from automated weather stations throughout the study area (see Figure 1 for locations): Camp Crook, 35 cm; Faith, 45 cm; Fort Pierre, 43 cm; Gregory, 59 cm; Kadoka, 49 cm; Mobridge, 44 cm; and Oelrichs, 44 cm. The following mean January high temperatures were reported by the HPRCC over the period 1971-2000: Camp Crook, -1°C; Faith, -2°C; Fort Pierre, 0°C; Gregory, 0°C; Kadoka, 0°C; Mobridge, -5°C; and Oelrichs, 1°C. Mean July high temperatures reported by the HPRCC over the same period were as follows: Camp Crook, 30°C; Faith, 30°C; Fort Pierre, 31°C; Gregory, 32°C; Kadoka, 32°C; Mobridge, 29°C; and Oelrichs, 32°C.

Dominant vegetation within prairie dog colonies was variable throughout the study area and was associated with factors such as soil type, precipitation, prairie dog density, and livestock grazing pressure. Western wheatgrass (*Elymus smithii*), blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), red threeawn (*Aristida purpurea*), and sedges (*Carex* spp.) were commonly encountered native graminoid species. The introduced crested wheatgrass (*Agropyron cristatum*) 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 aggressive 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*), fetid marigold (*Dyssodia papposa*), and bracted spiderwort (*Tradescantia bracteata*). Commonly encountered exotic forb species included musk thistle (*Carduus nutans*), field bindweed (*Convolvulus arvensis*), 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 redcedar (*Juniperus virginiana*), and the introduced Russian olive (*Elaeagnus angustifolia*). Eastern redcedar was also a frequent and increasing species in drainages in some areas. At the western edge of the study area, particularly in the Black Hills and the Pine Ridge Escarpment, ponderosa pine (*Pinus ponderosa*) was a locally common tree species.

Most prairie dog colonies were located on pasture land used for grazing of cattle (*Bos taurus*), sheep (*Ovis aries*), horses (*Equus caballus*), and/or bison (*Bison bison*). Wild grazers were locally common throughout the study area, although species varied. Wild ungulates observed on prairie dog colonies included white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), pronghorn (*Antilocapra americana*), elk (*Cervus *elaphus*), and bison. Prairie dog populations were periodically controlled throughout most of the study area, with the exception of the colonies in national parks and some colonies in black-footed ferret (*Mustela nigripes*) reintroduction areas. Many of the colonies surveyed during this project had been poisoned within the previous 1-5 years, and many were also subjected to recreational prairie dog shooting (personal communications with landowners or managers). Some colonies on private or tribal land and many colonies on national grasslands experienced heavy shooting pressure.

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. The most common crops were wheat (*Triticum aestivum*), corn (*Zea mays*), and soybeans (*Glycine max*). Human population was sparse.

Much of the study area was privately owned, but a substantial amount of suitable burrowing owl habitat was located on publically-owned lands, including state-managed Game Production Areas and state parks (e.g., Custer State Park), US Forest Service-managed National Grasslands (Fort Pierre, Buffalo Gap, and Grand River), Bureau of Land Management lands, National Park Service-managed National Parks (Wind Cave and Badlands), and a US Fish and Wildlife Service-managed National Wildlife Refuge (Lacreek). Six Native American reservations (Standing Rock, Cheyenne River, Lower Brule, Crow Creek, Rosebud, and Pine Ridge) were also located in the study area, and some of these lands also contained abundant burrowing owl habitat. Private, state, federal, and tribal lands were all well represented in the study.

Figure 1. Map of South Dakota with study area counties shaded and labeled. The labeled points indicate permanent weather stations from which climate data were acquired. The Fort Pierre weather station was located approximated 27 km west-southwest of the town of Fort Pierre. All other weather stations were located in or near the towns for which they are named.

CHAPTER 3

METHODS

Burrowing Owl Distribution in Western South Dakota

Survey Routes

Burrowing owl distribution data were acquired by conducting road-based point-count surveys throughout the study area. I used a South Dakota Department of Game, Fish, and Parks report on prairie dog distribution (Kempema et al. 2009) and an atlas of South Dakota to establish road surveys. I digitized potential survey routes in a geographic information system (GIS; ArcMap version 9.3, Esri, Inc. 2008). I attempted to create routes that would provide adequate spatial coverage of the survey area and that would minimize backtracking. I allocated routes to each county in proportion to the density of prairie dog colonies.

I conducted the surveys from 2 May to 21 July in 2010 and from 30 April to 9 August in 2011 using a point-count protocol adapted from Conway and Simon (2003). Each point-count was 6 minutes in length, divided into 2 segments of 3 minutes. During the first segment, I searched for owls both visually (using 10x binoculars and a 15-45x spotting scope) and aurally. I divided the landscape surrounding the point into 4 quadrants (I-northeast, II-northwest, III-southwest, and IV-southeast) and recorded the number of owls in each quadrant. I only recorded adult owls for analysis of prairie dog colony use. During the second segment, I played a recording of burrowing owl calls through the sound system of the vehicle. The recording consisted of the following sequence: 30 seconds of the male owl's primary call (or *coo-coo* call), 30 seconds of silence, another 30 seconds of the primary call, another 30 seconds of silence, 30 seconds of alarm calls, and another 30 seconds of silence. Haug and Didiuk (1993), Conway and Simon (2003), and Crowe and Longshore (2010) found that call-broadcasts increased detectability of burrowing owls. I recorded any additional adult owls that I saw or heard during the playback segment using the same methods. I also made notes of owls' behaviors during the survey, particularly in response to the recorded calls. Males often responded to calls by vocalizing, flying in the direction of the vehicle, assuming an aggressive posture with raised feathers, and/or flying to their respective mates. Females would sometimes emerge from burrows in response to the calls but responded with aggression less frequently than males. I used this information to determine the number of pairs present in each colony.

I conducted surveys between 0.5 hr before sunrise and 0.5 hr after sunset. I did not conduct point-counts in the rain as recommended by Conway and Simon (2003), although a slight drizzle began while I was conducting a few point counts. In these situations, I completed the point-count that was already in progress and waited for the precipitation to cease before continuing with the survey. I also stopped surveying when high winds inhibited my ability to hear owls or when heat-caused ground haze noticeably decreased visibility.

While I was able to use the colony maps from the Kempema et al. (2009) report as a guide for potential survey locations, I conducted point-counts anywhere burrows could be viewed from the road. I marked survey points with a handheld global positioning system (GPS) unit (Trimble Juno SB). I could adequately survey many colonies from a single point, but others required multiple points for thorough coverage because of large size and/or variable topography. To ensure the best possible survey effort for each colony, I deviated from the original survey route when necessary to view a colony from additional vantage points. I spaced the points as widely as possible to avoid counting the same owl at multiple points. If an owl flew from the direction where one had been seen at a previous point, I did not count it.

I often needed to modify routes for various reasons. The South Dakota atlas and GIS roads layer that I used to establish the routes included many private access trails or driveways. When I encountered private trails and was not able to get permission for access, I altered the route to contain a nearby public road instead. Less often, I encountered poor road conditions or human activities (e.g., cattle drives and road maintenance) that required the planned route to be changed.

In addition to the road surveys, I also surveyed some prairie dog colonies on public, private, and tribal lands that could not be accessed using public roads. I surveyed most of these colonies using the same methods described previously. However, a few colonies could only be accessed by walking. At those colonies, I did not use call-playback methods but instead used a longer passive survey period (minimum of 20 minutes) at each vantage point.

Male owls were more visible than females throughout the study period and especially during the incubation and brooding phases of the nesting cycle when females spend more time underground (Coulombe 1971, Butts and Lewis 1982, Johnsgard 2002). Because detectability of female burrowing owls varies throughout the breeding season, comparisons of raw counts of adult owls among colonies surveyed at different stages of the breeding season would not be meaningful. However, occupancy of prairie dog colonies by breeding pairs of burrowing owls can be determined at any point during the breeding season. Upon completion of the surveys, I sorted the colonies into 3 categories: unoccupied, single occupied, or multiple occupied. Unoccupied colonies had no recorded burrowing owls. Single occupied colonies had 1 known pair of owls within the boundaries of the colony. Paired owls could generally be identified by their proximity to each other if both were above ground. In most burrowing owl populations, the proportion of unpaired owls is low (<10%, Conway and Simon 2003; Desmond et al. 2000 and Bayless and Beier 2011 reported no unpaired owls in their study sites), and I assumed that all adult owls had mates. Therefore, if I only recorded 1 adult owl within a prairie dog colony, I classified the colony as single occupied. Multiple occupied colonies had 2 or more pairs of owls within the boundaries of the colony. I classified any colony that contained 3 or more adult owls as a multiple occupied colony. I also classified a colony as multiple occupied if I recorded 2 owls that were both territorial males, as indicated by defensive postures and call responses.

In the 2011 field season, I planned some of my survey routes to include prairie dog colonies that had been surveyed in 2010 to compare the 3 levels of owl occupancy (unoccupied, single occupied, or multiple occupied) between the 2 years. I conducted the counts in the same manner as previously described.

Colony- and Landscape-level Data Collection

The South Dakota Department of Game, Fish, and Parks provided a GIS shapefile of prairie dog colonies that was prepared by digitizing aerial photography and ground-truthing some areas in 2008 (see Kempema et al. 2009 for details). Some colonies were represented by multiple polygons, but I merged polygons into a single colony when they were located close together (<50 m) and difficult to distinguish as separate colonies in the field. A few of the colonies that I surveyed were not included in the GIS layer. I digitized the boundaries of the missing colonies in the GIS using 2010 National Agriculture Imagery Program (NAIP) imagery. Similarly, some large colonies delineated by the Department of Game, Fish, and Parks had been fragmented into smaller colonies since the publishing of the Kempema et al. (2009) report because of plague outbreaks, poisoning, or land conversion, so I digitized the separate colonies using NAIP imagery. Because I did not know the exact location of each owl pair's nest or territory, I used the centroid of each prairie dog colony as the focal point for a landscape analysis. Buffers with radii of 400 m, 800 m, 1,200 m, and 1,600 m around each centroid were generated using the GIS.

Many of the prairie dog colonies were located in close proximity to other colonies and 1 or more buffers overlapped. Overlapping buffers cannot be considered independent of one another (Cunningham and Johnson 2006). If 2 or more centroids had overlapping 1,600 m buffers, then I randomly selected a single centroid from the group and used the data associated with the selected centroid in the analyses. I did not include any colonies that had been surveyed in both 2010 and 2011.

I calculated landscape variables from remotely sensed data. The most accurate remotely sensed tree canopy cover GIS layer available was derived from the 2001 National Land Cover Database (NLCD). Although tree cover had certainly been gained or lost in some areas since 2001, the degree of change was negligible and relatively consistent across the study area. The GIS calculated the percent cover of trees surrounding each centroid at the 4 buffer levels. The GIS also calculated the percent cover of cropland and grassland surrounding each centroid from the 2006 NLCD and the percent cover of prairie dog colonies from the South Dakota Department of Game, Fish, and Parks' 2008 prairie dog layer. I added to the 2008 prairie dog layer colonies that I had surveyed but that were not present in the original layer. These were added to prevent some locations from having a value of 0% prairie dog colony coverage when in fact all locations used in the analysis were found within prairie dog colonies. Otherwise I did not edit the original layer in any way (i.e., I did not alter the shape of colonies that had potentially increased or decreased in extent since 2008).

Burrowing Owl Nest Site Selection in Western South Dakota

Local (Nest Site) Habitat Data Collection

During the summer of 2011, I selected a sample of 107 prairie dog colonies from across the study area to search for nest sites. All 107 selected colonies contained prairie dogs at the time they were surveyed, but densities varied. Some of the colonies were accessible with a 4-wheel drive vehicle, while others were only accessible by walking. I spent a minimum of 20 minutes systematically surveying each colony with binoculars and/or a spotting scope. For some of the larger colonies, I spent several hours surveying them from multiple vantage points to ensure complete coverage. I noted the locations of all owls and observed them until I was relatively certain of the approximate location of each nest burrow. If multiple pairs of owls were nesting within the colony, I assigned a number to each pair and used a random number generator to determine which nest I would use for data collection.

Burrowing owls are generally seen perched or hunting near the nest burrow (Coulombe 1971, Haug and Oliphant 1990, Johnsgard 2002). I was often able to identify a nest site by observing an adult owl perched at the burrow entrance or by watching a male owl deliver prey to the female or nestlings at the burrow. I identified a nest burrow by the presence of at least 2 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, Lutz and Plumpton 1999, Griebel and Savidge 2007, Lantz et al. 2007). Burrowing owls often line the nest burrow entrance with shredded manure, dead vegetation, or other similar material (Butts and Lewis 1982; Martin 1973; Levey et al. 2004; Smith and Conway 2007, 2011), and I used this as the deciding factor for identifying the nest burrow if several burrows in a small area contained owl sign. Often the owls use several burrows surrounding the nest as perch sites and/or satellite burrows, and these may be covered with regurgitated pellets and/or droppings (Griebel and Savidge 2007, Conrey 2010).

Within burrowing owl occupied colonies, I also chose 2 non-nest burrows to use for comparison with the nest burrow. One burrow was considered the adjacent non-nest burrow. I selected this burrow by using a formula in Microsoft Excel to generate a random bearing between 0° and 359°. I then located the first potentially usable burrow (at least 5 cm in diameter and unobstructed for at least 0.5 m; modified from Lantz et al. (2007)) that was at least 20 m, but not more than 40 m, from the nest burrow and fell within 5 m of the randomly selected bearing. If no burrows could be found within these parameters, I used a different random bearing.

I also chose a random burrow that could occur anywhere within the colony boundaries. I used a method described by Restani et al. (2001) where I broke the colony down into progressively smaller quadrants (I, II, III, and IV) selected at random. I continued to select quadrants until a single suitable burrow remained. If the selected burrow was within 20 m of any nest burrow or the adjacent non-nest burrow, I repeated the method to choose a different burrow. In colonies that were not occupied by burrowing owls, I selected a single burrow using this method.

To evaluate the vegetative composition around each selected burrow, I placed marking flags at 2 m and 4 m in each cardinal direction. I centered a 1-m^2 Daubenmire frame (Daubenmire 1959) over each of these flags and recorded the cover class for bare ground, 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%. I 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).

I determined a visual obstruction reading using a modified Robel pole (Robel et al. 1970). I placed the pole in 4 locations around each selected burrow, always 5 m from the burrow in each cardinal direction. After placing the pole, I viewed it from a distance of 4 m and a height of 1 m from each cardinal direction and recorded the lowest mark that was not completely obstructed by vegetation. The pole was marked in increments of 0.5 dm. I calculated the mean value for the 16 visual obstruction readings taken around each burrow.

I measured the distance to the nearest active burrow, or burrow currently being used by prairie dogs, to the nearest 0.1 m. I identified an active burrow by the presence of fresh scat, fresh digging, clipped vegetation, or a prairie dog at the burrow entrance (Desmond et al. 1995, Desmond and Savidge 1996, Lantz et al. 2007). I also measured the distance to the nearest inactive burrow. Inactive burrows 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). I also counted the total number of active and inactive burrows within 10 m of the selected burrow.

I measured the distance to the nearest road surface to the nearest meter. Roads varied from minimum-maintenance trails to paved highways, but I only considered roads with a bare surface (i.e., I did not include infrequently used access trails with vegetated wheel tracks). In rare circumstances, the nearest road surface was actually a private driveway that I could not access, so I measured the distance to the nearest public road. If the distance to the nearest road was ≥600 m, the distance was recorded 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, Gervais et al. 2003).

I measured the distance to the nearest vegetational edge to the nearest 0.1 m. I defined the edge 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 abundant moisture excluded prairie dogs and caused a different plant community to develop.

I also measured the distance to the nearest perch to the nearest 0.1 m. I considered a perch to be any object ≥0.5 m tall that could support a burrowing owl (Lantz et al. 2007). If the perch was a plant, I only measured the distance to it if I was reasonably certain that it was present at the time the owls established the nest. For example, I sometimes observed burrowing owls using thistles as perches in late summer, but during the nest establishment period, the thistles would not have been tall or sturdy enough to support an owl. However, dried, standing plants from the previous year, such as mullein and yucca (*Yucca glauca*) made suitable perches that would have been available in the spring. I 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

Calculations of colony- and landscape-level metrics were performed using a GIS. I had marked the locations of all surveyed colonies with a GPS unit, and I imported these points into the GIS. I then imported 2010 NAIP aerial photographs of the study area into the GIS. Using these photographs and ground truthing, I was able to digitize the boundaries of the prairie dog colonies and use the GIS to calculate the size of each colony in hectares.

I used the GIS to create buffers with radii of 400 m and 800 m around the selected burrow within each colony. If the colony did not contain any owls, the buffers were drawn around the random burrow, and if the colony did contain owls, the buffers were drawn around the selected nest burrow. Within each buffer circle, I used NAIP imagery and ground truthing to digitize trees, grassland, and cropland. I defined crops to include row crops, small grains, and hay. Hay was included in the cropland category because hay fields were usually composed of exotic species that had a different structure from grasslands used for grazing, and hay fields were rarely used for nesting by burrowing owls. I then used the GIS to calculate the percent cover of trees, grassland, and cropland within the buffers around each selected burrow.

Data Analyses

Burrowing Owl Distribution in Western South Dakota

I used logistic regression and the information-theoretic approach (Burnham and Anderson 2002) to evaluate the influence of landscape factors on burrowing owl presence. I checked for correlations between pairs of variables before developing models. I did not include 2 variables in the same model if they had a Spearman rank correlation ≥0.5. For a list of all variables, see Table 1. I created 8 a priori models using combinations of uncorrelated variables based on existing literature and observations in the field (Table 2). To evaluate the most important landscape scale for burrowing owl occurrence, I followed an approach similar to that of Cunningham and Johnson (2006).

Each a priori model was run at all 4 buffer levels (400 m, 800 m, 1,200 m, and 1,600 m) for a total of 32 models. The dependent variable for binary logistic regression was "occupied" (coded as a "1") or "unoccupied" (coded as a "0").

All modeling and statistical analyses were conducted using the program SYSTAT (version 12, SYSTAT Software, Inc. 2007). I used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to rank the models according to the level of support. I calculated the AIC difference (ΔAIC) between the model with the lowest AIC value and each other model in the set, and I considered all models with $\Delta AIC < 4$ to have adequate support for making inferences (Burnham and Anderson 2002). I also calculated Akaike model weights. Model weights indicate the strength of evidence that a particular model is the best model in the set, and they can also be used to evaluate which variables have the most importance relative to other variables (Burham and Anderson 2002). AIC values only indicate the relative strength of models in a set (Burnham and Anderson 2002, Cunningham and Johnson 2006), so I also considered McFadden's ρ^2 and area under receiver operating characteristic (ROC) curve as metrics of goodness of fit when selecting competitive top models.

Table 1. Habitat variables collected for use in burrowing owl occurrence/distribution models for western South Dakota, 2010-2011.

Variable	Description
GRASS_400	% cover of grassland within 400 m
GRASS_800	% cover of grassland within 800 m
GRASS_1200	% cover of grassland within 1,200 m
GRASS_1600	% cover of grassland within 1,600 m
CROP_400	% cover of cropland and hayland within 400 m
CROP_800	% cover of cropland and hayland within 800 m
CROP_1200	% cover of cropland and hayland within 1,200 m
CROP_1600	% cover of cropland and hayland within 1,600 m
TREE_400	% cover of trees within 400 m
TREE_800	% cover of trees within 800 m
TREE_1200	% cover of trees within 1,200 m
TREE_1600	% cover of trees within 1,600 m
PDOG_400	% cover of prairie dog colonies within 400 m
PDOG_800	% cover of prairie dog colonies within 800 m
PDOG_1200	% cover of prairie dog colonies within 1,200 m
PDOG_1600	% cover of prairie dog colonies within 1,600 m

Table 2. A priori burrowing owl occurrence/distribution models for western South Dakota, 2010-2011. Each of these models was run at 4 different buffer sizes—400 m, 800 m, 1,200 m, and 1,600 m.

PDOG
PDOG + TREE
PDOG + CROP
PDOG + TREE+ GRASS
PDOG + TREE + CROP
TREE
TREE + GRASS
TREE + CROP

Nest Site Selection

I used logistic regression and the information-theoretic approach to evaluate the influence of local, colony, and landscape variables on nest site selection by burrowing owls. I checked for correlations between pairs of variables before developing models. I did not include 2 variables in the same model if they had a Spearman rank correlation ≥0.5. For a list of all variables, see Table 3. I created 48 a priori models using combinations of local, colony, and landscape variables (Table 4). When models included landscape variables, I 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, I 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" (coded as a "1") or "non-nest" (coded as a "0"). Because I used variables collected at multiple spatial scales to build the models, I did not include any of the randomly selected non-nest burrows within occupied colonies in the analysis.

All modeling and statistical analyses were conducted using the program SYSTAT. I used AIC to rank the models according to the level of support. Because the ratio of samples (n) to parameters (K) was small ($n/K < 40$) for some models, I used the correction for small sample sizes, AIC_C, suggested by Burnham and Anderson (2002). I calculated the AIC_C difference (ΔAIC_C) between the model with the lowest AIC_C value and all other models in the set, and I considered all models with $\Delta AIC_C < 4$ to have adequate support for making inferences. For each model, I also calculated the Akaike weight, McFadden's ρ^2, and area under receiver operating characteristic (ROC) curve to further evaluate the support for the model.

I also used a hypothesis testing approach to compare local habitat characteristics of nest burrows, adjacent non-nest burrows, random non-nest burrows in occupied colonies, and random burrows in unoccupied colonies. I compared each variable among groups using the Kruskal-Wallis test, since many of the variables were non-normally distributed (Zar 1999). If the Kruskal-Wallis statistic was significant ($p < 0.05$), indicating that at least 1 group differed from the others, I conducted post-hoc comparisons using the method described in Zar (1999) for nonparametric multiple comparisons with unequal sample sizes and tied ranks. Preliminary analyses showed no differences between single occupied and multiple occupied colonies for any of the local habitat variables. Therefore, data were combined for both classes of colony occupancy to increase sample size and power.

Table 3. Habitat variables collected in 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies in western South Dakota for use in nest site selection models and Kruskal-Wallis comparison tests. Variables marked with an asterisk (*) were not used in any a priori models because of correlations with other variables assumed to be more important based on the available literature.

Variable	Description
ACTIVE	The number of active prairie dog burrows within 10 m
INACTIVE*	The number of inactive prairie dog burrows within 10 m
TOTAL_BURROWS	The total number of prairie dog burrows within 10 m
NEAR_ACTIVE	Distance in m to the nearest active prairie dog burrow
NEAR_INACTIVE*	Distance in m to the nearest inactive prairie dog burrow
GRASS*	Estimated % cover for grass using Daubenmire method
FORB	Estimated % cover for forbs using Daubenmire method
BARE	Estimated % cover for bare ground using Daubenmire method
ROBEL	Average visual obstruction reading in dm
ROAD	Distance in m to the nearest road surface
EDGE	Distance in m to the nearest vegetational edge
PERCH	Distance in m to the nearest potential elevated perch site
COL_AREA	Area of the prairie dog colony in ha
GRASS_400	% cover of grassland within 400 m
GRASS_800	% cover of grassland within 800 m
CROP_400	% cover of cropland and hayland within 400 m
CROP_800	% cover of cropland and hayland within 800 m
TREE_400	% cover of trees within 400 m
TREE_800	% cover of trees within 800 m

Table 4. A priori nest site selection models for burrowing owls in western South Dakota, 2011. (Continued on next page.)

TOTAL_BURROWS + NEAR_ACTIVE + FORB + BARE + ROBEL + PERCH + ROAD + EDGE + COL_AREA + TREE_400 + CROP_400
TOTAL_BURROWS + NEAR_ACTIVE + FORB + BARE + ROBEL + PERCH + ROAD + EDGE + COL_AREA + TREE_800 + CROP_800
TOTAL_BURROWS + NEAR_ACTIVE + FORB + BARE + ROBEL + PERCH + ROAD + EDGE + COL_AREA + TREE_400 + GRASS_400
TOTAL_BURROWS + NEAR_ACTIVE + FORB + BARE + ROBEL + PERCH + ROAD + EDGE + COL_AREA + TREE_800 + GRASS_800
TREE_400
TREE_800
TREE_400 + CROP_400
TREE_800 + CROP_800
TREE_400 + GRASS_400
TREE_800 + GRASS_800
COL_AREA + TREES_400
COL_AREA + TREES_800
ROBEL + TREE_400
ROBEL + TREE_800
ROBEL + TREE_400 + CROP_400
ROBEL + TREE_800 + CROP_800
TOTAL_BURROWS + ROBEL + TREE_400 + CROP_400
TOTAL_BURROWS + ROBEL + TREE_800 + CROP_800
FORB + BARE + ROBEL
FORB + BARE + ROBEL + TREE_400
FORB + BARE + ROBEL + TREE_800
FORB + ROBEL + TREE_400
FORB + ROBEL + TREE_800
FORB + ROBEL + COL_AREA
ACTIVE + ROBEL

Table 4 (Continued).

ACTIVE + COL_AREA + TREE_400
ACTIVE+ COL_AREA + TREE_800
TOTAL_BURROWS + ROBEL
TOTAL_BURROWS + ROBEL + TREE_400
TOTAL_BURROWS + ROBEL + TREE_800
TOTAL_BURROWS + ROBEL + TREE_400 + GRASS_400
TOTAL_BURROWS + ROBEL + TREE_800 + GRASS_800
TOTAL_BURROWS + EDGE
ROBEL + COL_AREA + TREE_400
ROBEL + COL_AREA + TREE_800
FORB + ROBEL + COL_AREA
NEAR_ACTIVE + COL_AREA
FORB + ROAD + COL_AREA
FORB + ROBEL + ROAD + TREE_400
FORB + ROBEL + ROAD + TREE_800
ROAD + COL_AREA + TREES_400
ROAD + COL_AREA + TREES_800
NEAR_ACTIVE + FORB + EDGE
ROBEL + COL_AREA
ROBEL + PERCH + COL_AREA
FORB + PERCH + COL_AREA
ROBEL + TREE_400 + GRASS_400
ROBEL + TREE_400 + GRASS_800

CHAPTER 4

RESULTS

Burrowing Owl Distribution in Western South Dakota

In 2010, I surveyed 776 prairie dog colonies and recorded 1,189 adult burrowing owls (all counts of burrowing owls reported in this section are raw counts). Of the surveyed colonies, 405 (52.2%) were unoccupied, 193 (24.9%) were single occupied, and 179 (22.9%) were multiple occupied (Figure 2).

In 2011, I surveyed 460 colonies that had not been surveyed in 2010. I recorded 784 adult burrowing owls in these colonies—187 (40.7%) of the colonies were unoccupied, 144 (31.3%) were single occupied, and 129 (28.0%) were multiple occupied (Figure 3).

Also in 2011, I resurveyed 231 of the prairie dog colonies that I had surveyed in 2010 (Figure 4) and recorded 462 burrowing owls in these colonies. I also revisited a few other previously surveyed colonies but did not include them in the dataset as they had been converted to agriculture by the 2011 field season and no longer had available burrows. The majority of the colonies (55.8%) remained in the same occupancy category in 2011 (Table 5). Colonies that were occupied (either single or multiple) in 2010 tended to be occupied again in 2011, with only 9.5% becoming unoccupied. Colonies that were unoccupied in 2010 likewise tended to remain unoccupied in 2011, with only 13.4% becoming occupied, usually by a single pair.

I located burrowing owls in every county where I conducted surveys with the exception of Buffalo and Charles Mix counties. Estimation of population densities was not an objective of my study, but some regions of the study area had noticeably higher concentrations of burrowing owls than others. The proportion of surveyed colonies occupied by burrowing owls was also inconsistent across the study area (Figures 2-4).

I modeled burrowing owl occurrence using 613 surveyed prairie dog colonies after eliminating colonies with overlapping buffers (Figure 5). Means, standard deviations, and ranges for all variables are presented in Table 6. Eleven a priori models were considered competitive by having ΔAIC < 4 (Table 7). Akaike model weights were similar among the competitive models, suggesting that none of the models had a particularly strong probability of being the best model in the set (Burnham and Anderson 2002). All competitive models were at the 800 m or 1,200 m buffer level. The only variables with significant coefficients in any models were tree cover variables (TREE_800 and TREE_1200, Tables 8-14). Tree cover had a negative relationship with the probability of burrowing owl occurrence (Figures 6-7). Other variables occurred in competitive models, but the coefficients of these variables were not significant and odds ratios did not differ from 1 (Tables 9, 11-14).

Model fit and performance were unsatisfactory for the competitive models. McFadden's ρ^2 is a metric related to goodness-of-fit for logistic regression (Tabachnick and Fidell 2007), and values were low (0.047-0.051) for competitive models in the set. Area under ROC curve values were also low (0.646-0.672) for competitive models, indicating poor discrimination between unoccupied and unoccupied colonies (Hosmer and Lemeshow 2000).

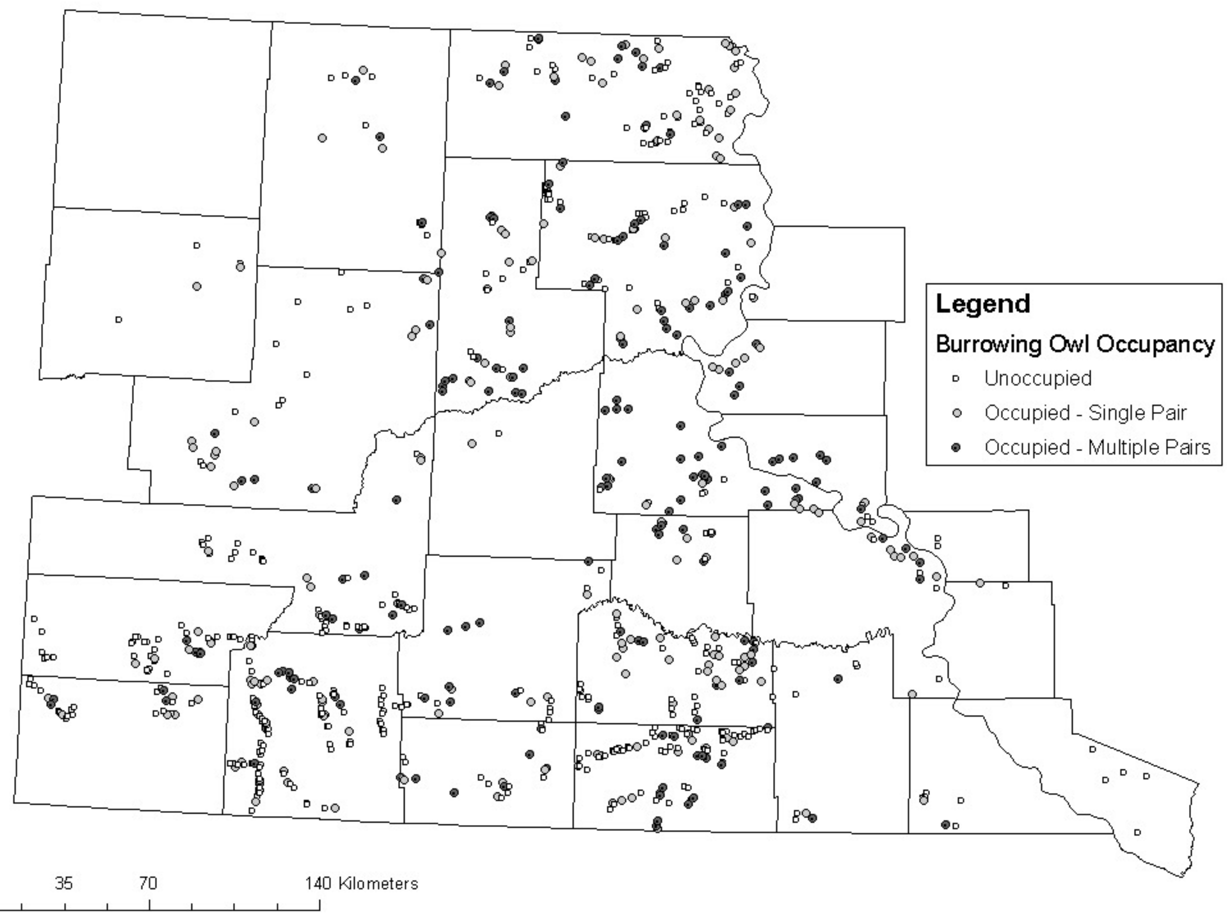

Figure 2. Locations of western South Dakota prairie dog colonies (n = 776) surveyed for burrowing owls in 2010. Circles represent the centroids of surveyed colonies.

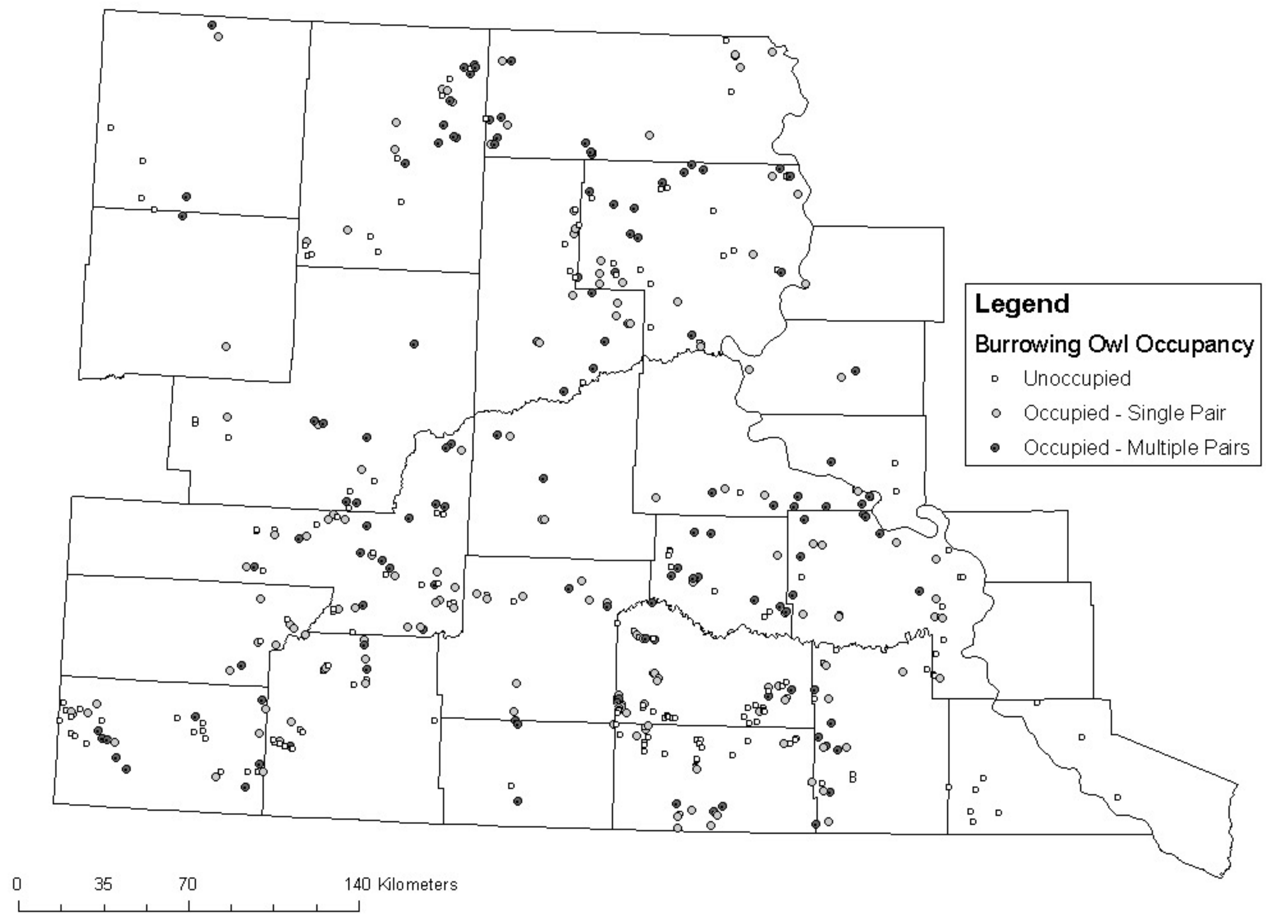

Figure 3. Locations of western South Dakota prairie dog colonies (n = 460) surveyed for burrowing owls in 2011 which had not been surveyed in 2010. Circles represent the centroids of surveyed colonies.

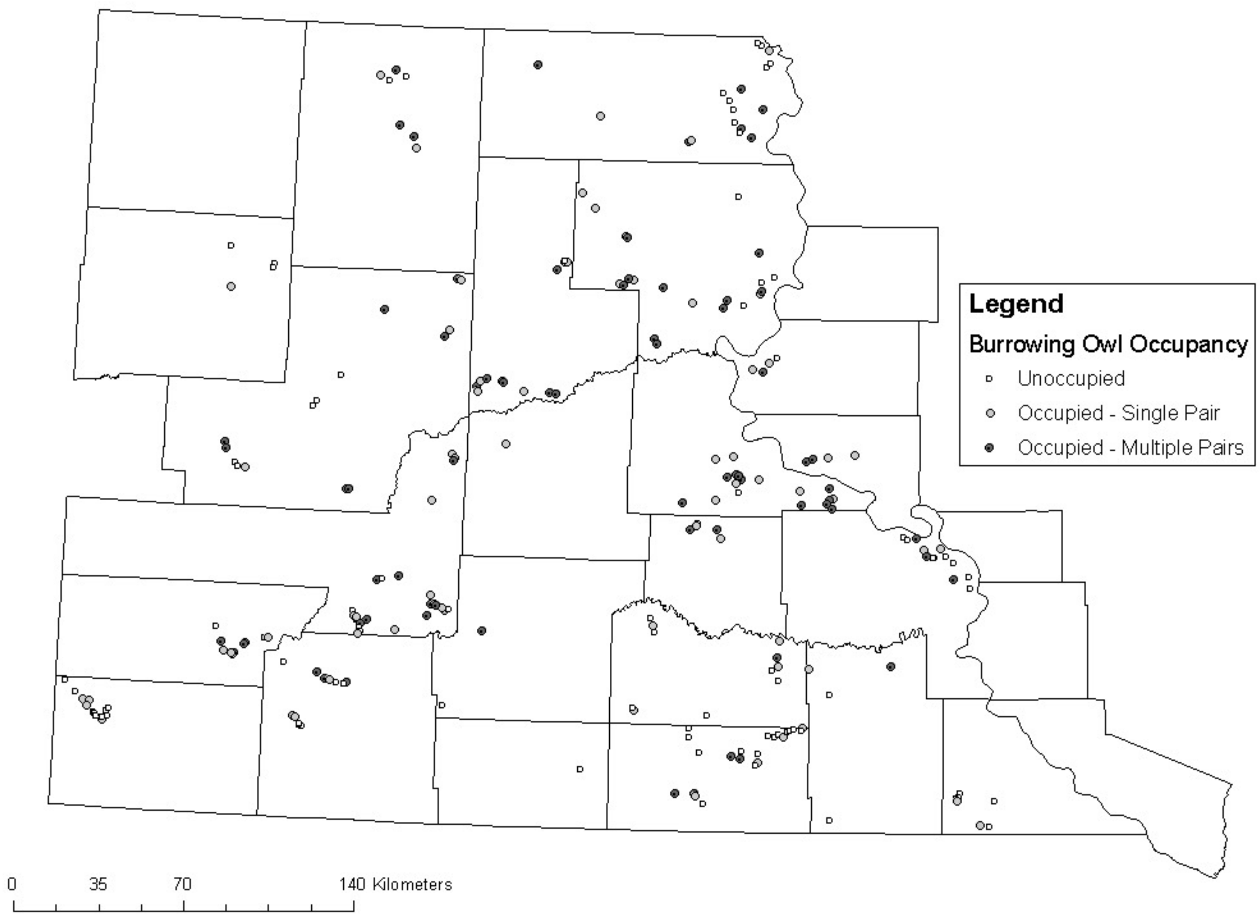

Figure 4. Locations of western South Dakota prairie dog colonies (n = 231) surveyed for burrowing owls in 2011 that had also been surveyed in 2010. Circles represent the centroids of surveyed colonies. The 2011 burrowing owl occupancy is shown.

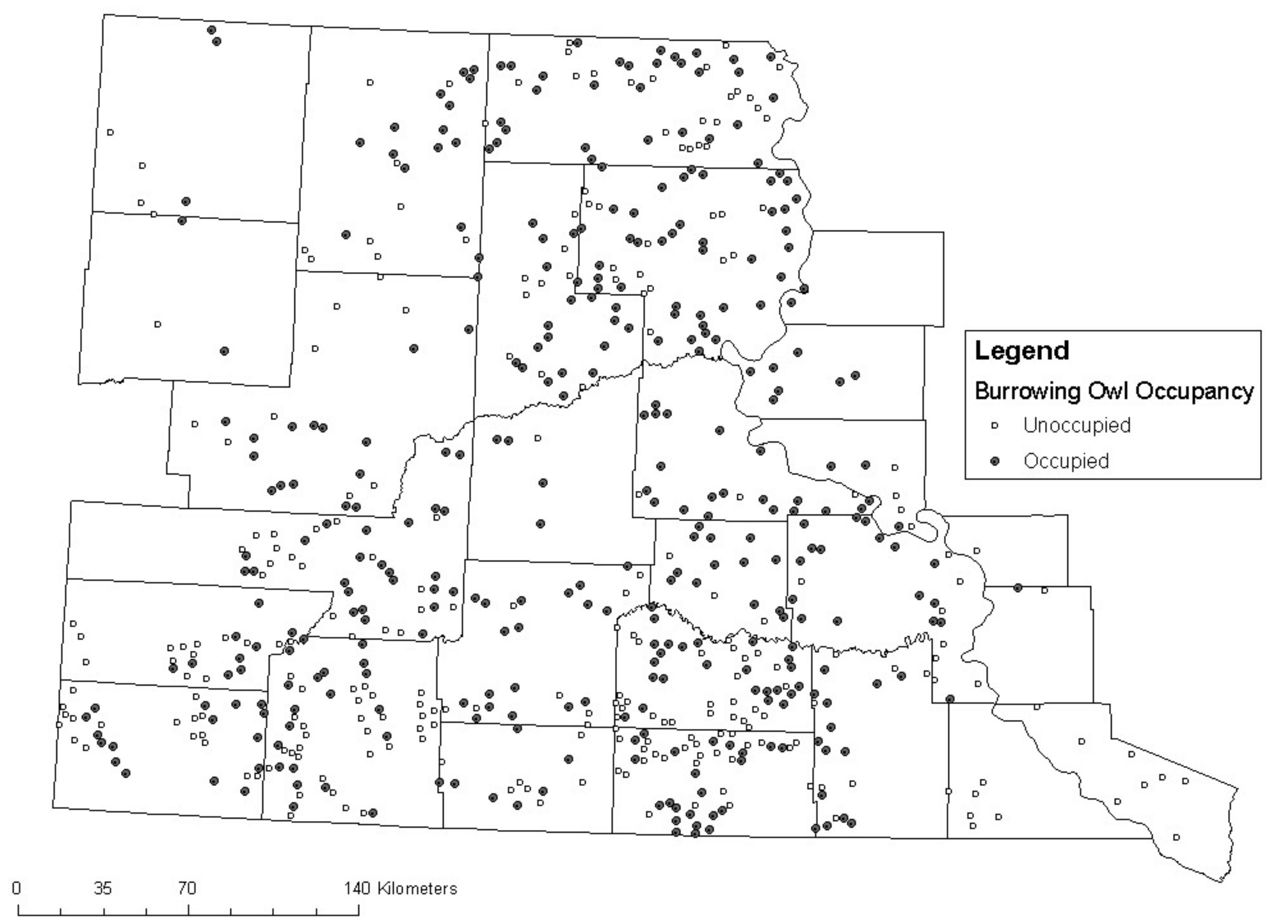

Figure 5. Locations of western South Dakota prairie dog colonies (n = 613) surveyed for burrowing owls in 2010 or 2011 and used to develop occurrence/distribution models. Circles represent the centroids of surveyed colonies. Colony centroids were at least 3,200 m apart for all colonies used for modeling.

Table 5. Changes in burrowing owl occupancy of 231 western South Dakota prairie dog colonies surveyed in 2010 and 2011.

Status Change (2010 to 2011)	Number of Colonies
Unoccupied to Unoccupied	66
Unoccupied to Single Occupied	23
Unoccupied to Multiple Occupied	8
Single Occupied to Unoccupied	14
Single Occupied to Single Occupied	22
Single Occupied to Multiple Occupied	23
Multiple Occupied to Unoccupied	8
Multiple Occupied to Single Occupied	26
Multiple Occupied to Multiple Occupied	41

Table 6. Means, standard deviations, and ranges for all variables calculated for western South Dakota prairie dog colonies (n = 613) surveyed for burrowing owls in 2010 or 2011 and used to develop occurrence/distribution models. See Table 1 for variable descriptions. Units are percent cover for all variables.

Variable	Mean	Standard Deviation	Range
GRASS_400	86.595	16.840	0.000 - 99.968
GRASS_800	80.758	18.519	0.000 - 99.984
GRASS_1200	77.696	19.026	0.650 - 99.990
GRASS_1600	76.258	18.885	1.311 - 99.566
CROP_400	7.184	14.978	0.000 - 98.324
CROP_800	11.490	17.093	0.000 - 95.151
CROP_1200	13.683	17.965	0.000 - 95.075
CROP_1600	14.533	17.866	0.000 - 90.379
TREE_400	1.226	3.203	0.000 - 26.822
TREE_800	2.518	5.081	0.000 - 55.727
TREE_1200	3.197	5.704	0.000 - 63.335
TREE_1600	3.358	5.555	0.000 - 62.513
PDOG_400	42.138	29.830	0.126 - 99.968
PDOG_800	18.696	18.840	0.032 - 97.718
PDOG_1200	11.296	12.646	0.014 - 86.054
PDOG_1600	8.450	10.074	0.008 - 84.372

Table 7. Competitive burrowing owl occurrence/distribution models (ΔAIC < 4). Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) throughout western South Dakota. W_i is the Akaike weight, ρ^2 is the McFadden's rho-squared value, and ROC is the area under the receiver operating characteristics curve.

Model	ΔAIC	W_i	ρ^2	ROC
TREE_1200	0	0.168	0.048	0.656
TREE_1200 + GRASS_1200	0.158	0.155	0.050	0.657
TREE_800	0.645	0.121	0.047	0.672
TREE_800 + GRASS_800	1.038	0.100	0.049	0.659
PDOG_1200 + TREE_1200 + GRASS_1200	1.466	0.081	0.051	0.646
PDOG_1200 + TREE_1200	1.726	0.071	0.048	0.656
TREE_1200 + CROP_1200	1.733	0.070	0.048	0.652
TREE_800 + CROP_800	2.311	0.053	0.047	0.659
PDOG_800 + TREE_800	2.584	0.046	0.047	0.664
PDOG_800 + TREE_800 + GRASS_800	3.034	0.037	0.049	0.657
PDOG_1200 + TREE_1200 + CROP_1200	3.289	0.032	0.048	0.652

Table 8. Parameter estimates and odds ratios for the burrowing owl occurrence/distribution model TREE_1200. Values in parentheses are 95% confidence intervals. Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) in western South Dakota.

Parameter	Coefficient	p-value	Odds Ratio
Constant	0.614 (0.418, 0.809)	0.000	
TREE_1200	-0.107 (-0.145, -0.070)	0.000	0.898 (0.865, 0.933)

Table 9. Parameter estimates and odds ratios for the burrowing owl occurrence/distribution model TREE_1200 + GRASS_1200. Values in parentheses are 95% confidence intervals. Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) throughout western South Dakota.

Parameter	Coefficient	p-value	Odds Ratio
Constant	0.148 (-0.549, 0.845)	0.677	
TREE_1200	-0.107 (-0.145, -0.069)	0.000	0.899 (0.865, 0.933)
GRASS_1200	0.006 (-0.003, 0.015)	0.174	1.006 (0.997, 1.015)

Table 10. Parameter estimates and odds ratios for the burrowing owl occurrence/distribution model TREE_800. Values in parentheses are 95% confidence intervals. Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) throughout western South Dakota.

Parameter	Coefficient	p-value	Odds Ratio
Constant	0.580 (0.390, 0.770)	0.000	
TREE_800	-0.125 (-0.170, -0.080)	0.000	0.883 (0.843, 0.9240

Table 11. Parameter estimates and odds ratios for the burrowing owl occurrence/distribution model TREE_800 + GRASS_800. Values in parentheses are 95% confidence intervals. Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) throughout western South Dakota.

Parameter	Coefficient	p-value	Odds Ratio
Constant	0.115 (-0.627, 0.856)	0.762	
TREE_800	-0.124 (-0.169, -0.078)	0.000	0.884 (0.845, 0.925)
GRASS_800	0.006 (-0.003, 0.015)	0.204	1.006 (0.997, 1.015)

Table 12. Parameter estimates and odds ratios for the burrowing owl occurrence/distribution model PDOG_1200 + TREE_1200 + GRASS_1200. Values in parentheses are 95% confidence intervals. Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) throughout western South Dakota.

Parameter	Coefficient	p-value	Odds Ratio
Constant	0.148 (-0.549, 0.846)	0.677	
PDOG_1200	-0.006 (-0.019, 0.008)	0.404	0.994 (0.981, 1.008)
TREE_1200	-0.107 (-0.144, -0.069)	0.000	0.899 (0.866, 0.934)
GRASS_1200	0.007 (-0.002, 0.016)	0.132	1.007 (0.998, 1.016)

Table 13. Parameter estimates and odds ratios for the burrowing owl occurrence/distribution model PDOG_1200 + TREE_1200. Values in parentheses are 95% confidence intervals. Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) throughout western South Dakota.

Parameter	Coefficient	p-value	Odds Ratio
Constant	0.652 (0.409, 0.895)	0.000	
PDOG_1200	-0.003 (-0.016, 0.009)	0.600	0.997 (0.984, 1.010)
TREE_1200	-0.107 (-0.145, -0.069)	0.000	0.899 (0.865, 0.933)

Table 14. Parameter estimates and odds ratios for the burrowing owl occurrence/distribution model TREE_1200 + CROP_1200. Values in parentheses are 95% confidence intervals. Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) throughout western South Dakota.

Parameter	Coefficient	p-value	Odds Ratio
Constant	0.652 (0.408, 0.897)	0.000	
TREE_1200	-0.109 (-0.147, -0.071)	0.000	0.897 (0.863, 0.932)
CROP_1200	-0.002 (-0.012, 0.007)	0.605	0.998 (0.988, 1.007)

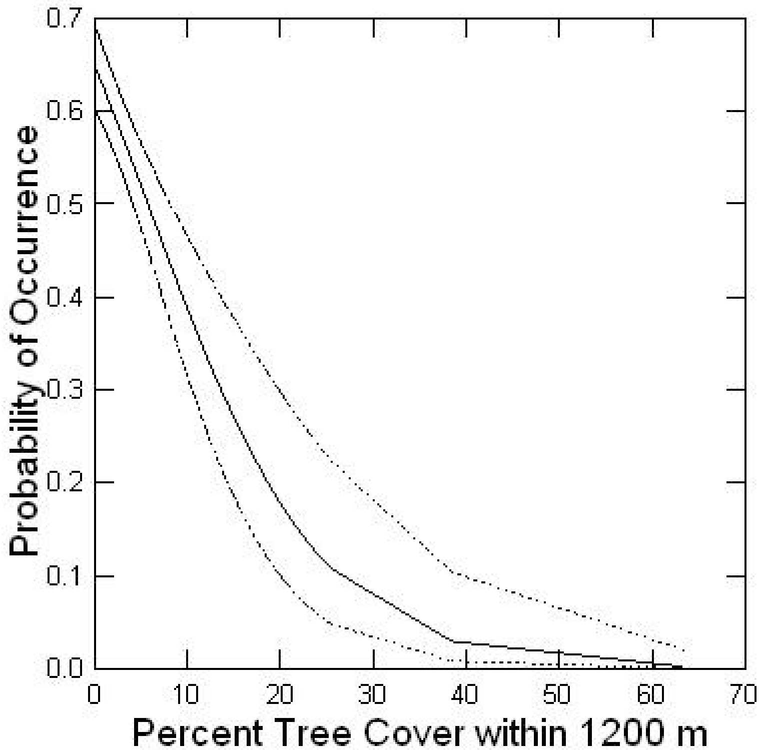

Figure 6. Probability of burrowing owl occurrence in relation to percent tree cover within 1,200 m of the prairie dog colony centroid. The dotted lines represent the upper and lower 95% confidence limits. Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) throughout western South Dakota.

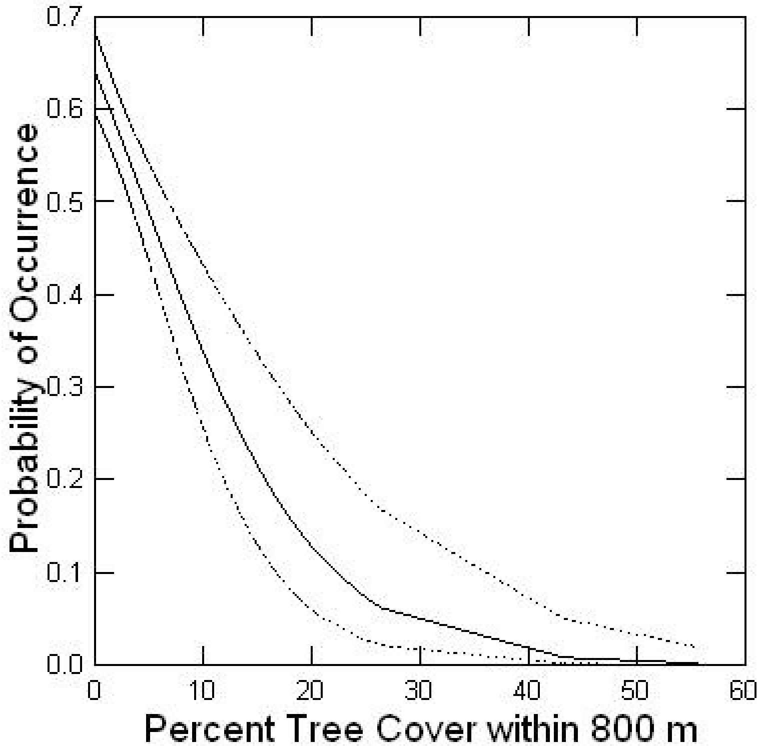

Figure 7. Probability of burrowing owl occurrence in relation to percent tree cover within 800 m of the prairie dog colony centroid. The dotted lines represent the upper and lower 95% confidence limits. Data were collected during the summers of 2010 and 2011 at prairie dog colonies (n = 613) throughout western South Dakota.

Burrowing Owl Nest Site Selection in Western South Dakota

I searched for burrowing owl nests in 107 prairie dog colonies in 2011 (Figure 8). Data collected at nest burrows and randomly selected non-nest burrows were used to develop nest site selection models. Means, standard deviations, and ranges for all variables are presented in Table 15. Five of the a priori models were considered competitive by having $\Delta AIC_C < 4$ (Table 16). The top model in the set carried 33.6% of the Akaike model weight, and the top 5 models in the set carried 76.5%. All competitive models contained local- and landscape-level variables. Models containing variables at only 1 scale or combinations of local- and colony-level variables were not competitive.

All competitive models contained the variable for percent tree cover within 800 m of the burrow (TREE_800). Increasing tree cover within the landscape surrounding a potential nest site led to a reduced probability of that site being chosen for nesting (Figure 9). In all competitive models, the coefficient of the variable was significant and the 95% confidence interval (CI) on the odds ratio for the variable did not include 1 (Tables 17-21). Odds ratios <1 indicate that the outcome of interest (in this instance, colony occupancy) is less likely to result as the independent variable increases in value, while odds ratios >1 indicate an increasing likelihood that the outcome will result as the independent variable increases in value (Hosmer and Lemeshow 2000).

The variable for average visual obstruction reading (ROBEL) also occurred in all competitive models. Increasing visual obstruction readings led to reduced probabilities of burrows being chosen as nest sites (Figure 10). This variable also had a significant coefficient and an odds ratio different from 1 in all competitive models (Tables 17-21).

The variable for average forb cover class (FORB) appeared in 3 of the top models in the set. As percent forb cover increased, so did the probability of the burrow being used for nesting (Figure 11). The coefficient of the variable approached significance in all the competitive models where it appeared, and the confidence interval for the odds ratio of the variable in these models slightly overlapped 1 (Tables 17-19).

One competitive model in the set also contained the variable for average bare ground cover class (BARE). The weight of support for BARE was low relative to the variables TREE_800, ROBEL, and FORB. The effect of bare ground was similar to the effect of forb cover on the probability of nesting. As percent bare ground increased, so did the probability of a burrow being a nest burrow (Figure 12). However, the coefficient of the variable was not significant, and the 95% confidence interval for the odds ratio included 1 (Table 17).

One competitive model contained the variable for distance to the nearest road (ROAD). The coefficient was not significantly different from 0, and the 95% confidence interval for the odds ratio included 1 (Table 19). The distance to a road did not have a detectable effect on the likelihood of a burrow being used as a nest.

Another competitive model contained the variable for colony size (COL_AREA). This variable had a coefficient value that did not differ from 0, and the odds ratio did not differ from 1 (Table 21). The area of the colony also did not have a detectable effect on the likelihood of a burrow in that colony being used as a nest.

All competitive models fit the data well. McFadden's ρ^2 values ranged from 0.237 to 0.297 for the competitive models. Values in the 0.2 to 0.4 range are considered highly satisfactory (Tabachnick and Fidell 2007). The top models also performed well in discriminating nest burrows from non-nest burrows. Area under receiver operating characteristic (ROC) curves ranged from 0.793 to 0.823 for competitive models. 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.” Three of the competitive models had area under ROC curve values in the latter category.

Some local habitat characteristics differed among the 4 burrow types according to the Kruskal-Wallis test (Table 22). Visual obstruction readings were significantly lower for nest burrows than for random non-nest burrows in both occupied and unoccupied colonies, but they did not differ from adjacent non-nest burrows (Figure 13). Nest burrows had lower average percent grass cover than random burrows in unoccupied colonies but did not differ from the other burrow types within occupied colonies (Figure 14). Percent cover of forbs and bare ground did not differ among burrow types (Figures 15 and 16, respectively). Total burrow density was lowest for random sites in occupied colonies, differing significantly from nest sites and random sites in unoccupied colonies (Figure 17). Active burrow density was also lowest for random sites in occupied colonies, differing significantly from nest sites and adjacent non-nest sites (Figure 18). No differences were detected among burrow types for inactive burrow density when multiple comparisons were made (Figure 19). The distance to an active burrow was significantly lower for nest burrows and adjacent non-nest burrows than for random burrows in occupied colonies, but the distance did not differ from random burrows in unoccupied colonies (Figure 20). The distance to an inactive burrow was lowest for nest burrows; this distance differed significantly from adjacent burrows and random non-nest burrows in occupied colonies but did not differ from random burrows in unoccupied colonies (Figure 21). The distance to the nearest vegetational edge was greatest for nest burrows, but the difference was only significantly different between nest burrows and random burrows in occupied colonies (Figure 22). Distances to the nearest road and the nearest perch did not differ among burrow types (Figures 23 and 24, respectively).

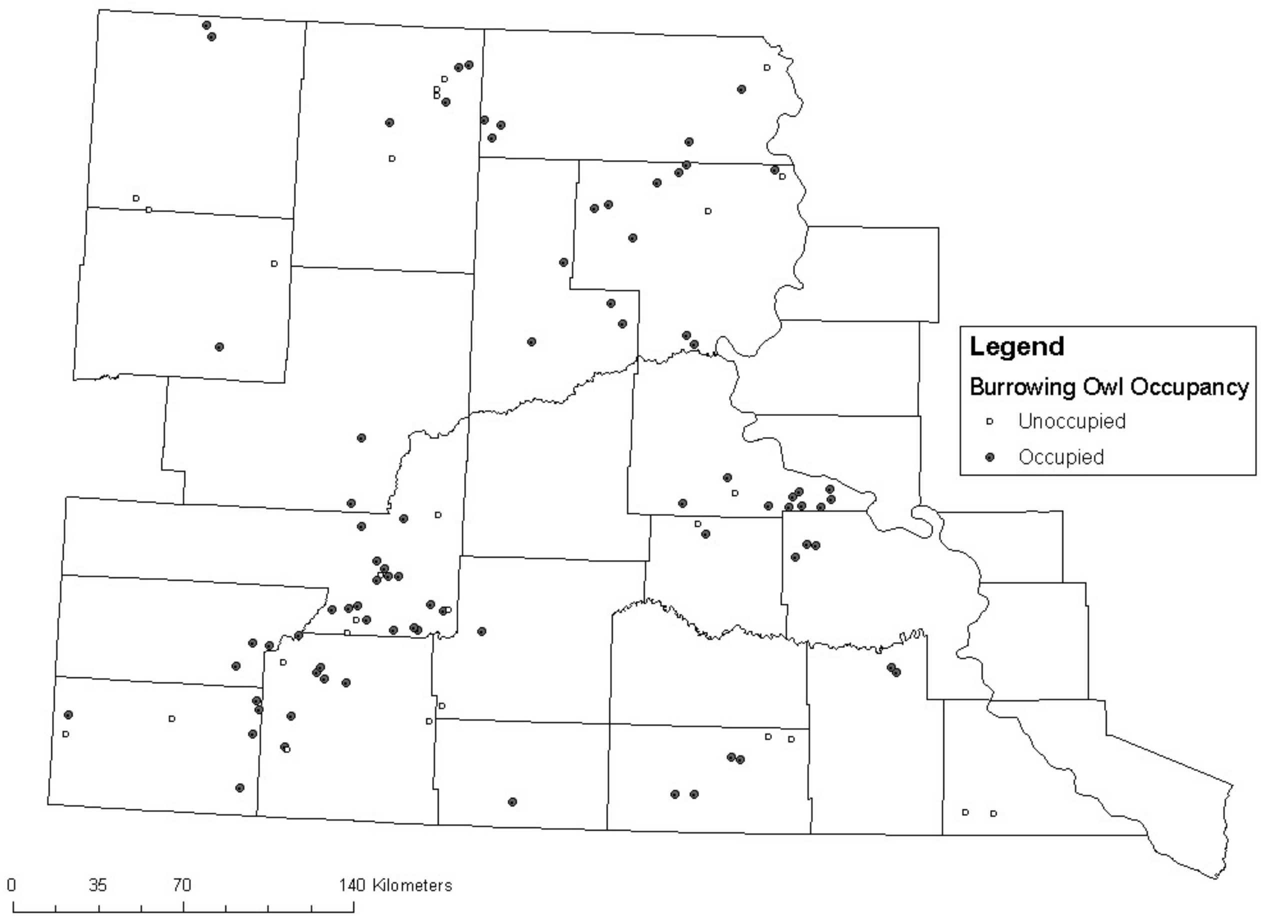

Figure 8. Locations of western South Dakota prairie dog colonies (n = 107) surveyed for burrowing owls in 2011 and used to develop nest site selection models. Circles represent the burrows within colonies where data were collected. In occupied colonies, this was a burrowing owl nest burrow, and in unoccupied colonies, this was a randomly selected burrow.

Table 15. Means, standard deviations, and ranges for all nest site selection model variables calculated for burrowing owl nest burrows and randomly selected non-nest burrows located in western South Dakota prairie dog colonies (n = 107) in 2011. See Table 2 for variable descriptions and units.

Variable	Mean	Standard Deviation	Range
ACTIVE	2.551	2.220	0 - 9
INACTIVE	2.963	2.757	0 - 13
TOTAL_BURROWS	5.514	3.541	0 - 19
NEAR_ACTIVE	11.093	17.073	1.2 - 100.0
NEAR_INACTIVE	6.897	4.461	1.2 - 30.1
GRASS	59.229	18.747	8.750 - 91.250
FORB	31.352	22.694	2.500 - 85.313
BARE	13.817	13.447	2.500 - 67.813
ROBEL	0.756	0.379	0.500 - 2.469
ROAD	342.112	198.961	2 - 600
EDGE	33.223	33.048	0.1 - 181.4
PERCH	125.779	117.151	0.1 - 600.0
COL_AREA	37.154	65.00	0.484 - 426.689
GRASS_400	89.250	13.519	44.222 - 100.000
GRASS_800	81.416	18.606	30.753 - 99.848
CROP_400	5.277	11.457	0.000 - 48.297
CROP_800	10.390	15.995	0.000 - 55.120
TREE_400	0.619	1.794	0.000 - 10.751
TREE_800	5.277	11.457	0.000 - 48.297

Table 16. Competitive burrowing owl nest site selection models ($\Delta AIC_C < 4$). Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota. W_i is the Akaike weight, ρ^2 is the McFadden's rho-squared value, and ROC is the area under the receiver operating characteristics curve.

Model	ΔAIC_C	W_i	ρ^2	ROC
FORB + BARE + ROBEL + TREE_800	0	0.336	0.297	0.822
FORB + ROBEL + TREE_800	1.137	0.190	0.269	0.812
FORB + ROBEL + ROAD + TREE_800	2.211	0.111	0.278	0.823
ROBEL + TREE_800	2.862	0.080	0.237	0.793
ROBEL + COL_AREA + TREE_800	3.898	0.048	0.246	0.794

Table 17. Parameter estimates and odds ratios for the burrowing owl nest site selection model FORB + BARE + ROBEL + TREE_800. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota. Values in parentheses are 95% confidence intervals.

Parameter	Coefficient	p-value	Odds Ratio
Constant	1.824 (0.028, 3.619)	0.047	
FORB	0.027 (0.000, 0.053)	0.051	1.027 (1.000, 1.055)
BARE	0.049 (-0.009, 0.106)	0.098	1.050 (0.991, 1.112)
ROBEL	-1.836 (-3.432, -0.240)	0.024	0.159 (0.032, 0.787)
TREE_800	-0.573 (-0.907, -0.239)	0.001	0.564 (0.404, 0.787)

Table 18. Parameter estimates and odds ratios for the burrowing owl nest site selection model FORB + ROBEL + TREE_800. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota. Values in parentheses are 95% confidence intervals.

Parameter	Coefficient	p-value	Odds Ratio
Constant	2.646 (1.065, 4.227)	0.001	
FORB	0.025 (-0.001, 0.051)	0.063	1.025 (0.999, 1.052)
ROBEL	-2.158 (-3.713, -0.603)	0.007	0.116 (0.024, 0.547)
TREE_800	-0.525 (-0.847, -0.203)	0.001	0.591 (0.429, 0.816)

Table 19. Parameter estimates and odds ratios for the burrowing owl nest site selection model FORB + ROBEL + ROAD + TREE_800. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota. Values in parentheses are 95% confidence intervals.

Parameter	Coefficient	p-value	Odds Ratio
Constant	2.005 (0.073, 3.937)	0.042	
FORB	0.026 (-0.001, 0.052)	0.056	1.026 (0.999, 1.053)
ROBEL	-1.977 (-3.555, -0.398)	0.014	0.139 (0.029, 0.671)
ROAD	0.001 (-0.001, 0.004)	0.291	1.001 (0.999, 1.004)
TREE_800	-0.514 (-0.839, -0.190)	0.002	0.598 (0.432, 0.827)

Table 20. Parameter estimates and odds ratios for the burrowing owl nest site selection model ROBEL + TREE_800. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota. Values in parentheses are 95% confidence intervals.

Parameter	Coefficient	p-value	Odds Ratio
Constant	3.473 (2.093, 4.852)	0.000	
ROBEL	-2.357 (-3.850, -0.864)	0.002	0.095 (0.021, 0.421)
TREE_800	-0.471 (-0.774, -0.169)	0.002	0.624 (0.461, 0.844)

Table 21. Parameter estimates and odds ratios for the model ROBEL + COL_AREA + TREE_800. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota. Values in parentheses are 95% confidence intervals.

Parameter	Coefficient	p-value	Odds Ratio
Constant	3.254 (1.812, 4.696)	0.000	
ROBEL	-2.317 (-3.817, -0.818)	0.002	0.099 (0.022, 0.441)
COL_AREA	0.006 (-0.007, 0.018)	0.390	1.006 (0.993, 1.018)
TREE_800	-0.458 (-0.762, -0.154)	0.003	0.633 (0.467, 0.857)

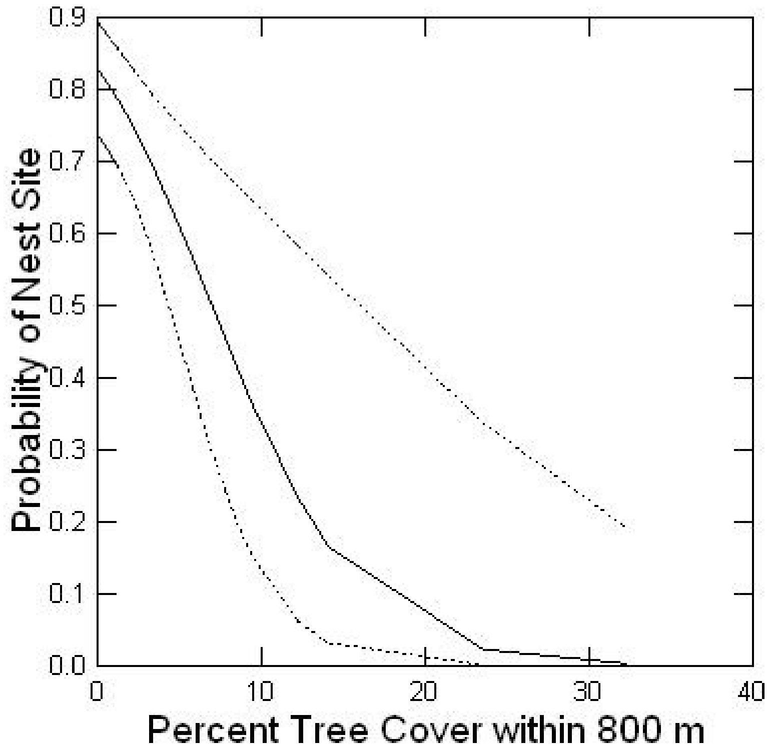

Figure 9. Probability of a prairie dog burrow being selected as a nest burrow in relation to percent tree cover within 800 m of the burrow. The dotted lines represent the upper and lower 95% confidence limits. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

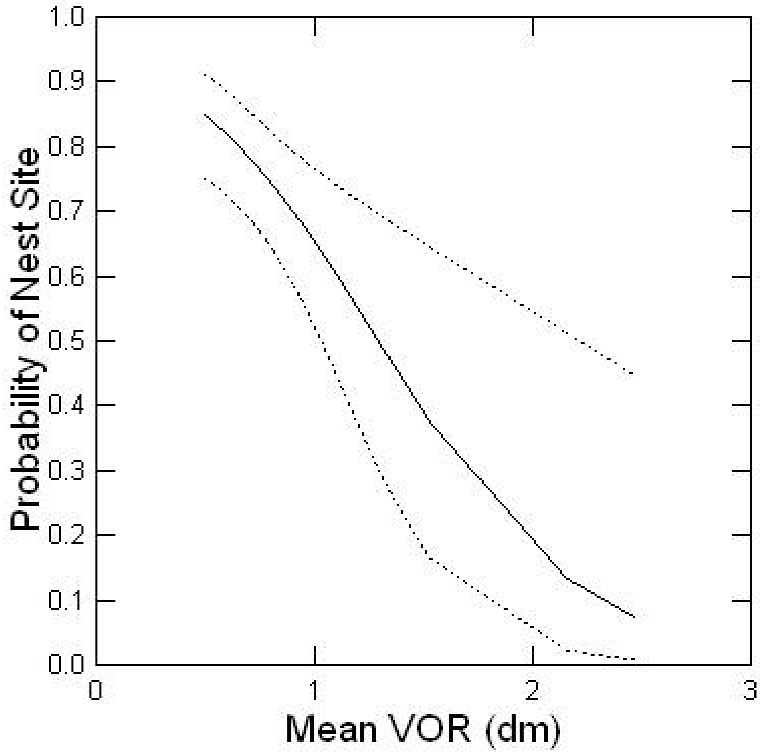

Figure 10. Probability of a prairie dog burrow being selected as a nest burrow in relation to the mean visual obstruction reading (VOR) near the burrow. The dotted lines represent the upper and lower 95% confidence limits. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

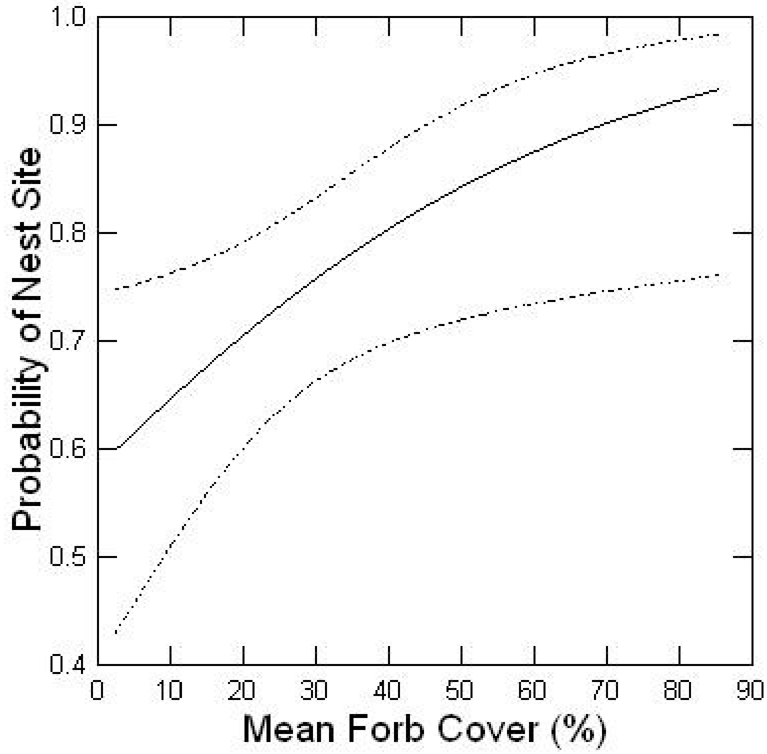

Figure 11. Probability of a prairie dog burrow being selected as a nest burrow in relation to the mean percent cover of forbs near the burrow. The dotted lines represent the upper and lower 95% confidence limits. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

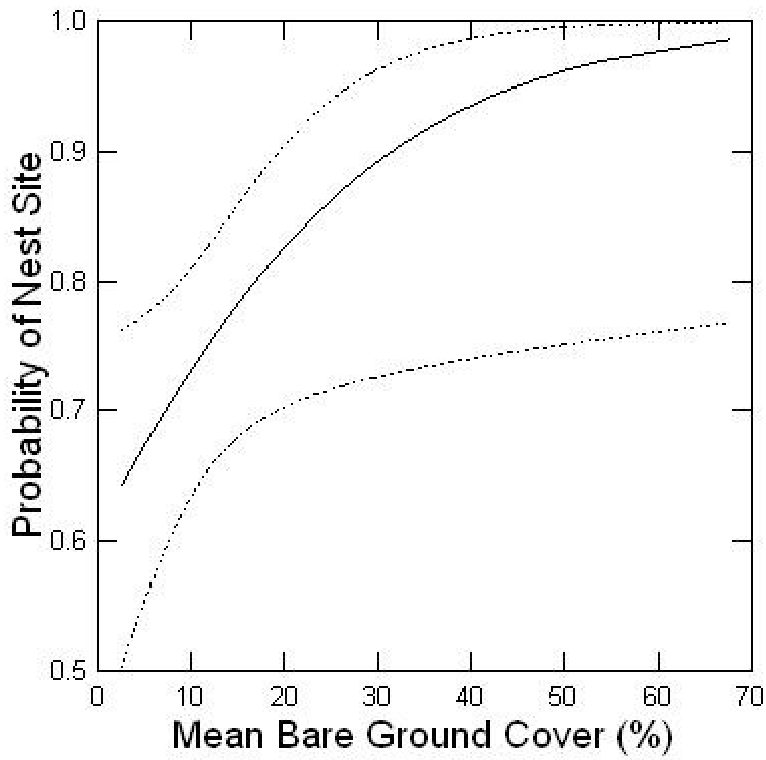

Figure 12. Probability of a prairie dog burrow being selected as a nest burrow in relation to the mean percent cover of bare ground near the burrow. The dotted lines represent the upper and lower 95% confidence limits. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

Table 22. Kruskal-Wallis test results for local-level habitat variables. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota. Four burrow types were compared—nest, adjacent non-nest, random non-nest in an owl-occupied colony, and random non-nest in an unoccupied colony. The test was considered significant if $p < 0.05$. See Table 4 for descriptions of the variables.
***INACTIVE produced a significant K-W test statistic, but none of the groups significantly differed from the others when pairwise comparisons were made.**

Variable	K-W Test Statistic	p-value
ACTIVE	15.342	0.002
INACTIVE*	8.431	0.038
TOTAL_BURROWS	19.297	0.000
NEAR_ACTIVE	10.145	0.017
NEAR_INACTIVE	11.565	0.009
GRASS	9.999	0.019
FORB	4.362	0.225
BARE	2.889	0.409
ROBEL	12.467	0.006
ROAD	3.050	0.384
EDGE	8.852	0.031
PERCH	6.720	0.081

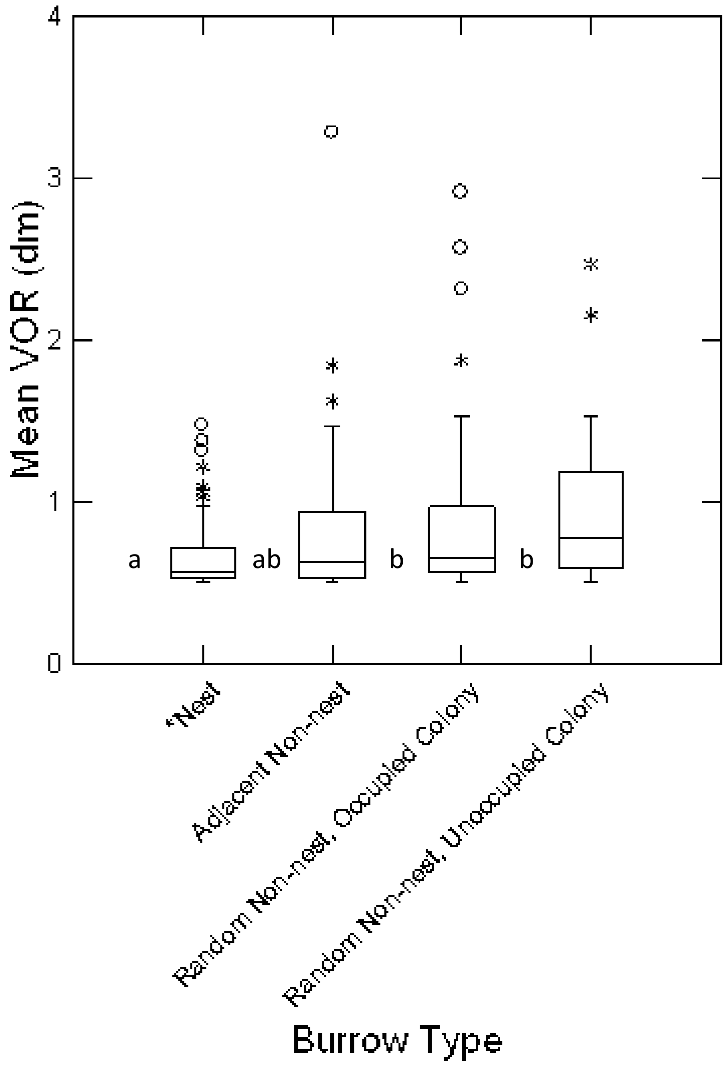

Figure 13. Boxplots of the mean visual obstruction reading (VOR) for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Open circles (°) indicate values >3× the interquartile range. Burrow types labeled with different letters have significantly different distributions ($p < 0.05$) according to the nonparametric multiple comparison method in Zar (1999). Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies ($n = 107$) located throughout western South Dakota.

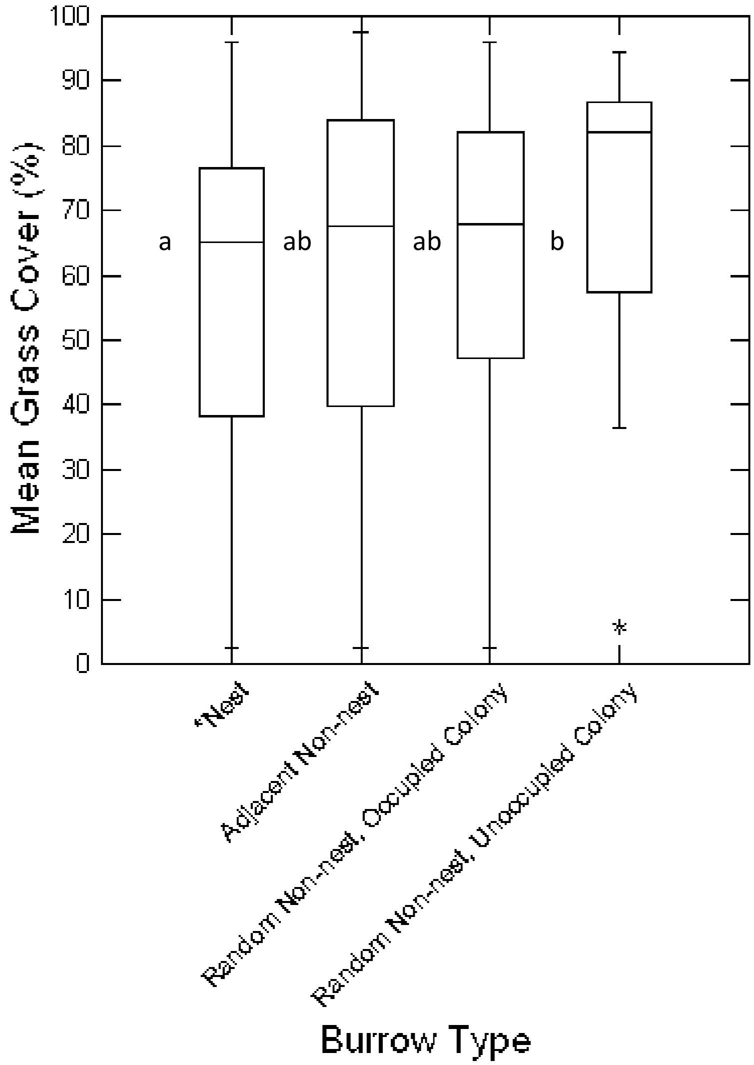

Figure 14. Boxplots of the mean percent cover of grass for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Burrow types labeled with different letters have significantly different distributions ($p < 0.05$) according to the nonparametric multiple comparison method in Zar (1999). Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

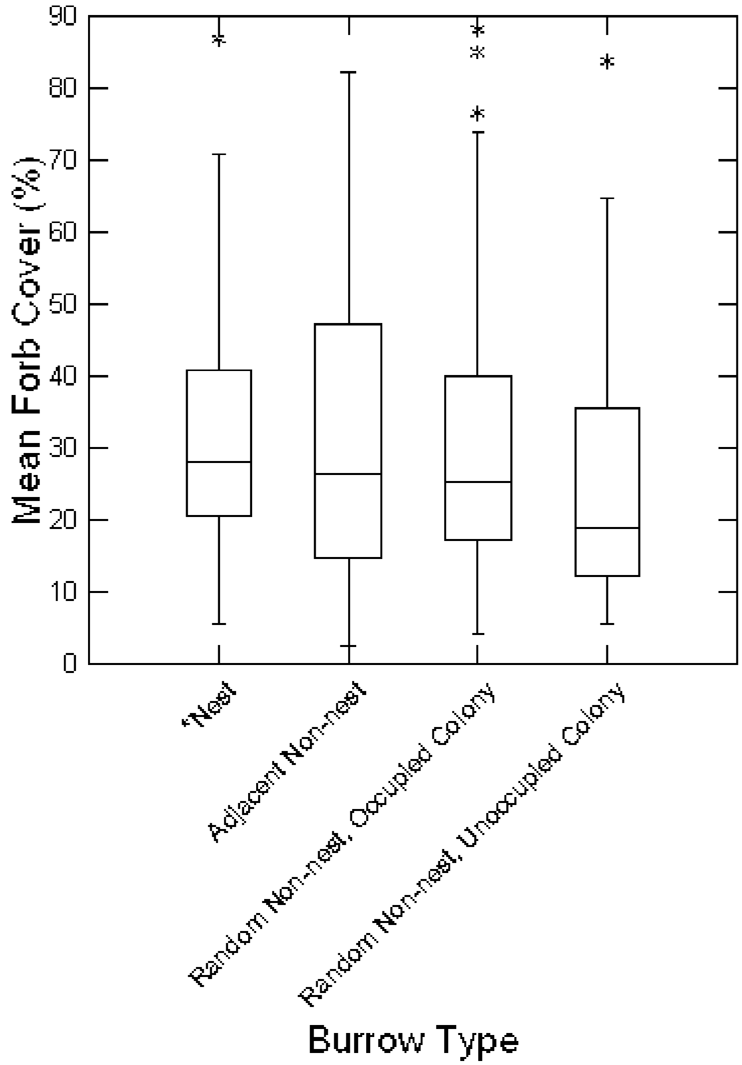

Figure 15. Boxplots of the mean percent cover of forbs for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. No significant differences were detected among the burrow types. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

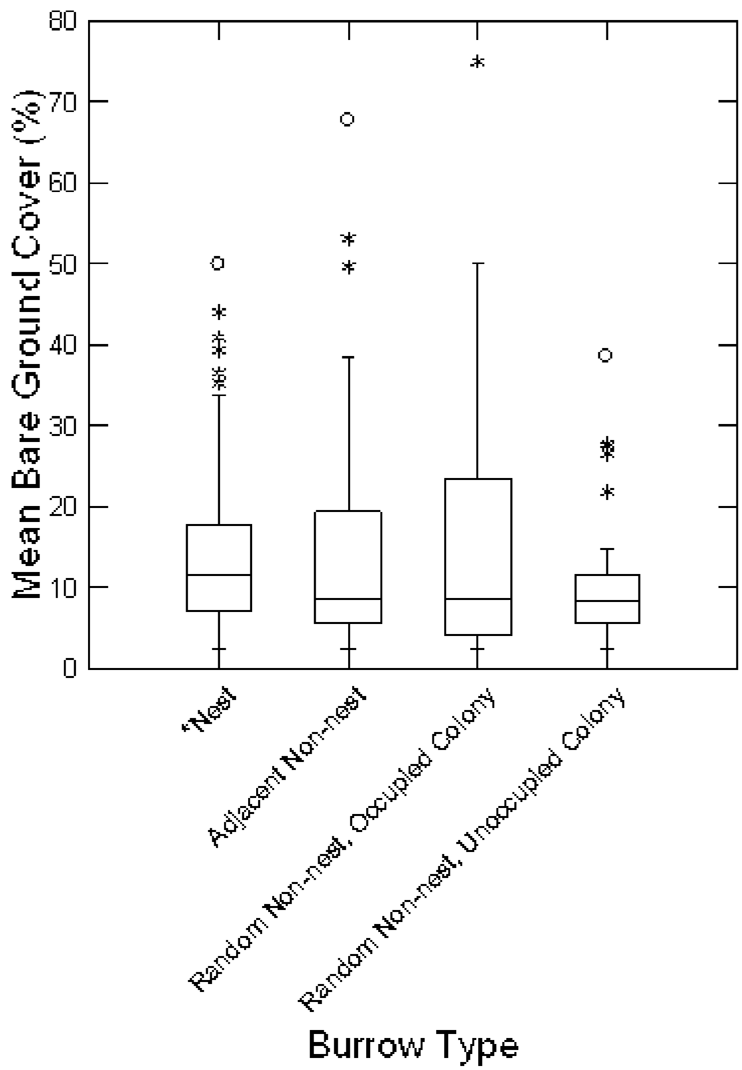

Figure 16. Boxplots of the mean percent cover of bare ground for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Open circles (°) indicate values >3× the interquartile range. No significant differences were detected among the burrow types. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

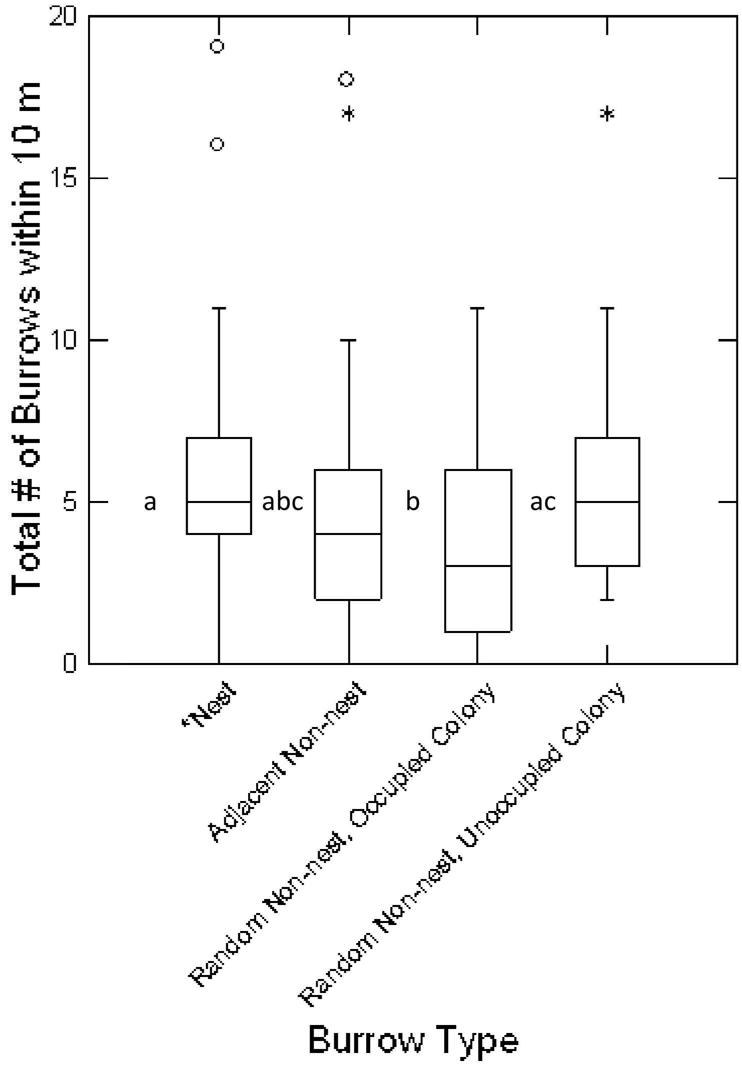

Figure 17. Boxplots of the total number of burrows within 10 m for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Open circles (°) indicate values >3× the interquartile range. Burrow types labeled with different letters have significantly different distributions ($p < 0.05$) according to the nonparametric multiple comparison method in Zar (1999). Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies ($n = 107$) located throughout western South Dakota.

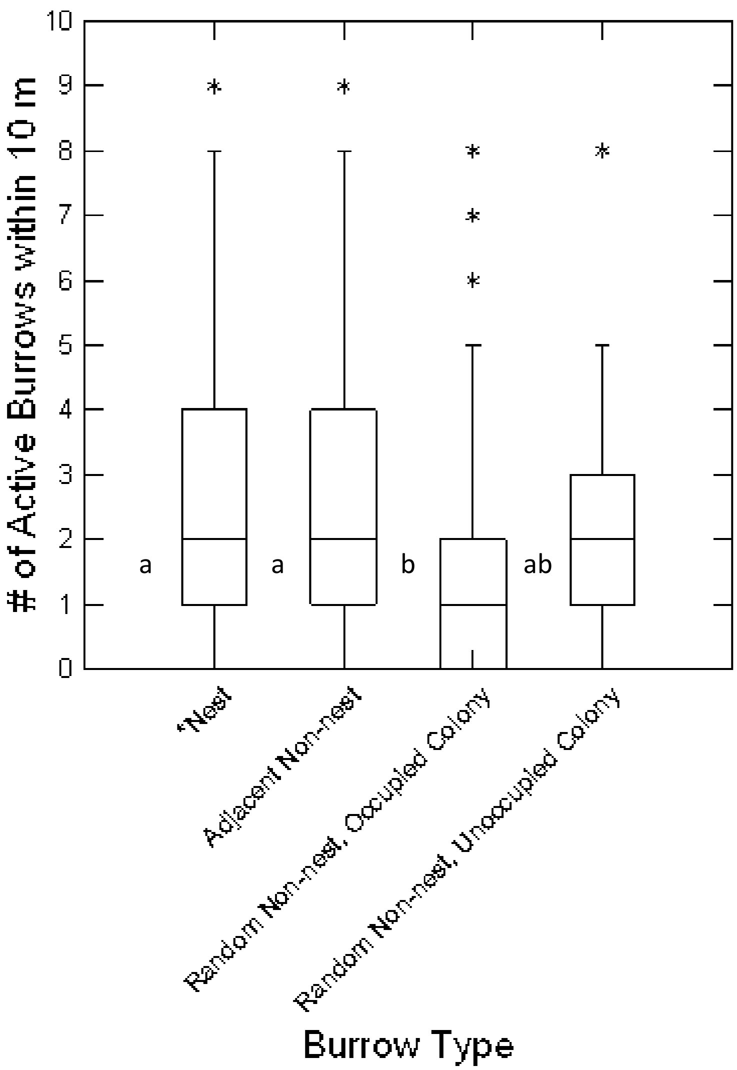

Figure 18. Boxplots of the number of active burrows within 10 m for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Burrow types labeled with different letters have significantly different distributions ($p < 0.05$) according to the nonparametric multiple comparison method in Zar (1999). Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies ($n = 107$) located throughout western South Dakota.

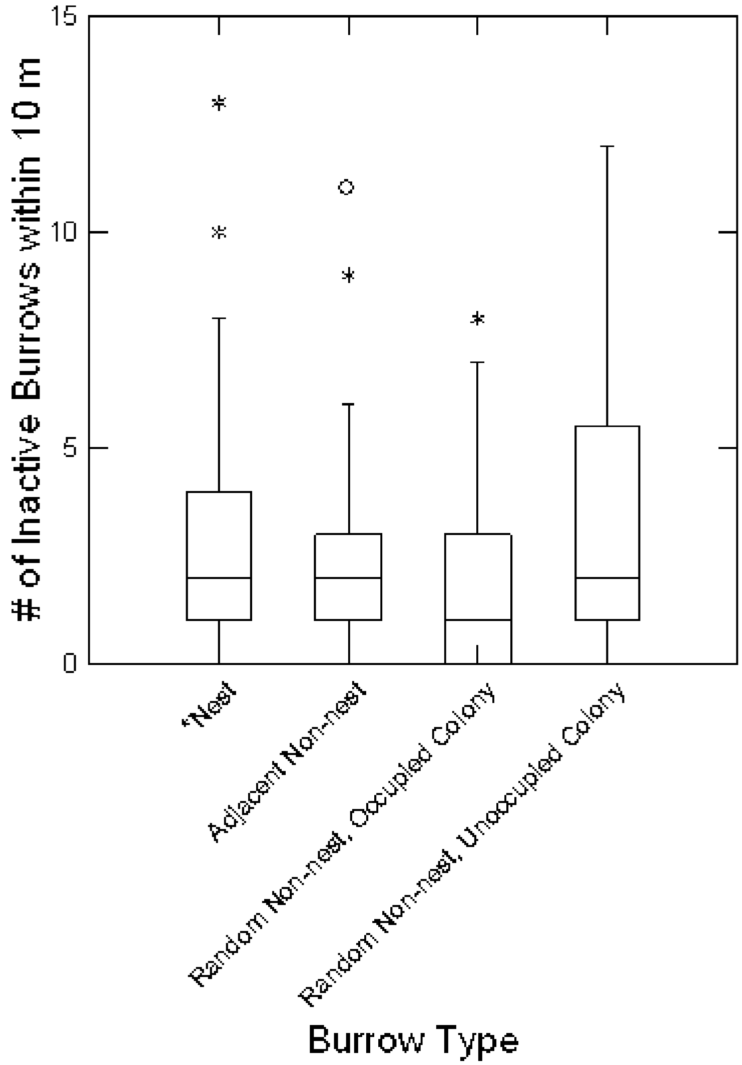

Figure 19. Boxplots of the number of inactive burrows within 10 m for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Open circles (°) indicate values >3× the interquartile range. No significant differences were detected among burrow types. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

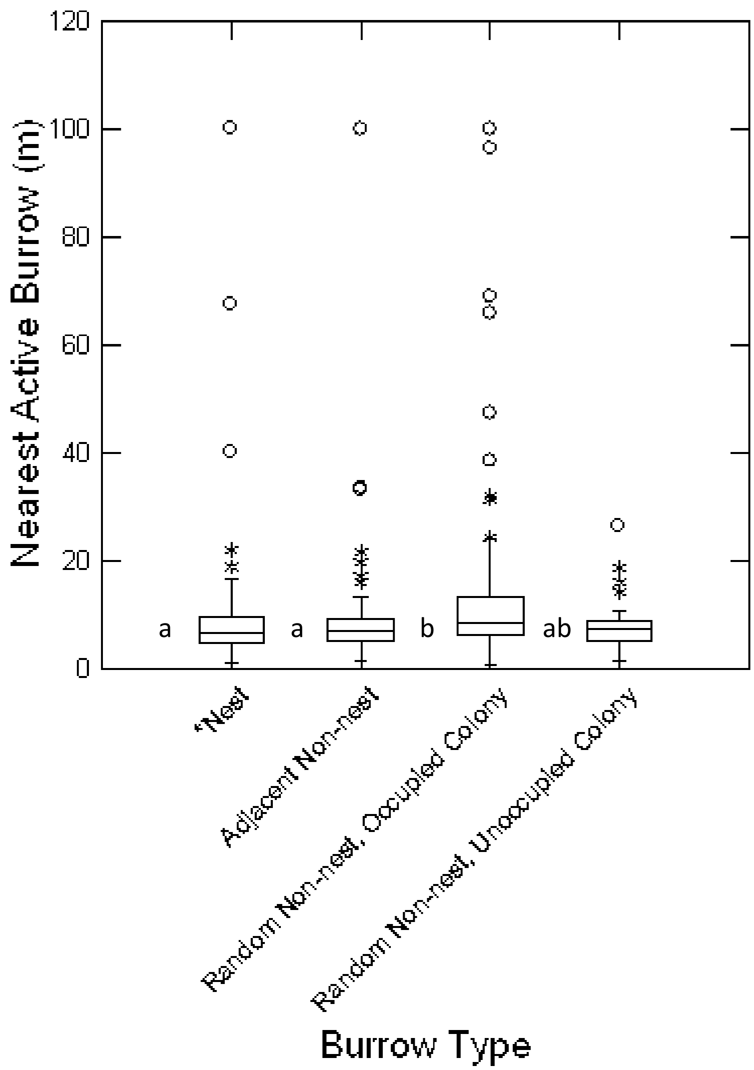

Figure 20. Boxplots of the distance to the nearest active burrow for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Open circles (°) indicate values >3× the interquartile range. Burrow types labeled with different letters have significantly different distributions ($p < 0.05$) according to the nonparametric multiple comparison method in Zar (1999). Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

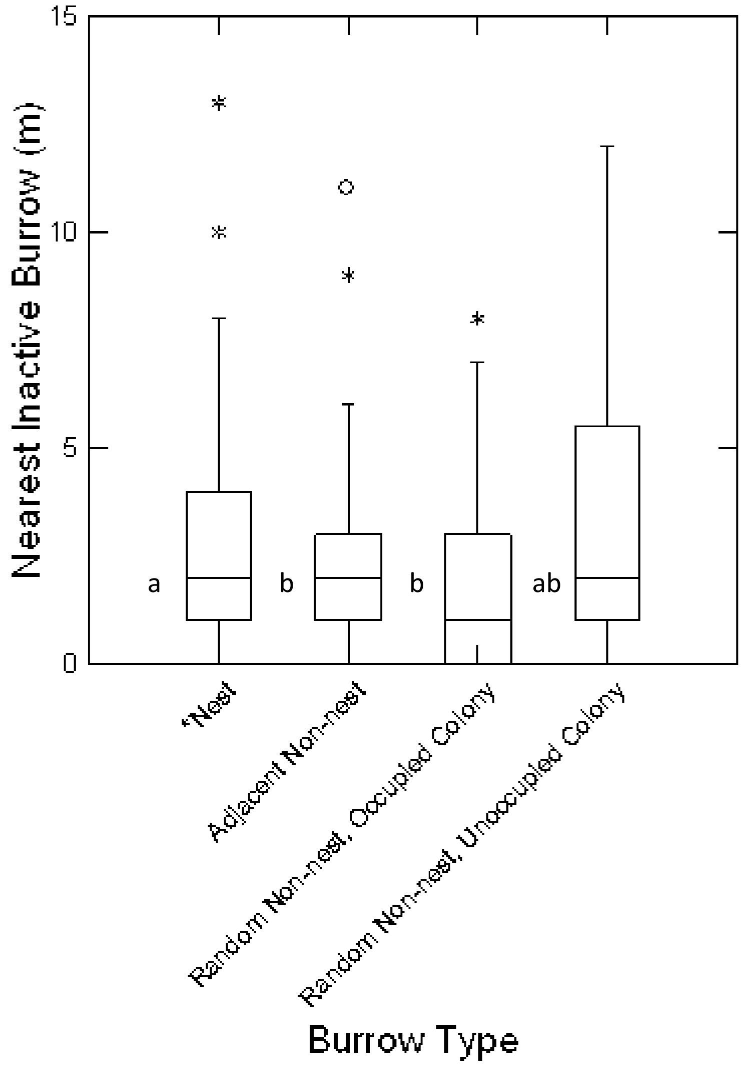

Figure 21. Boxplots of the distance to the nearest inactive burrow for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Open circles (°) indicate values >3× the interquartile range. Burrow types labeled with different letters have significantly different distributions (p < 0.05) according to the nonparametric multiple comparison method in Zar (1999). Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

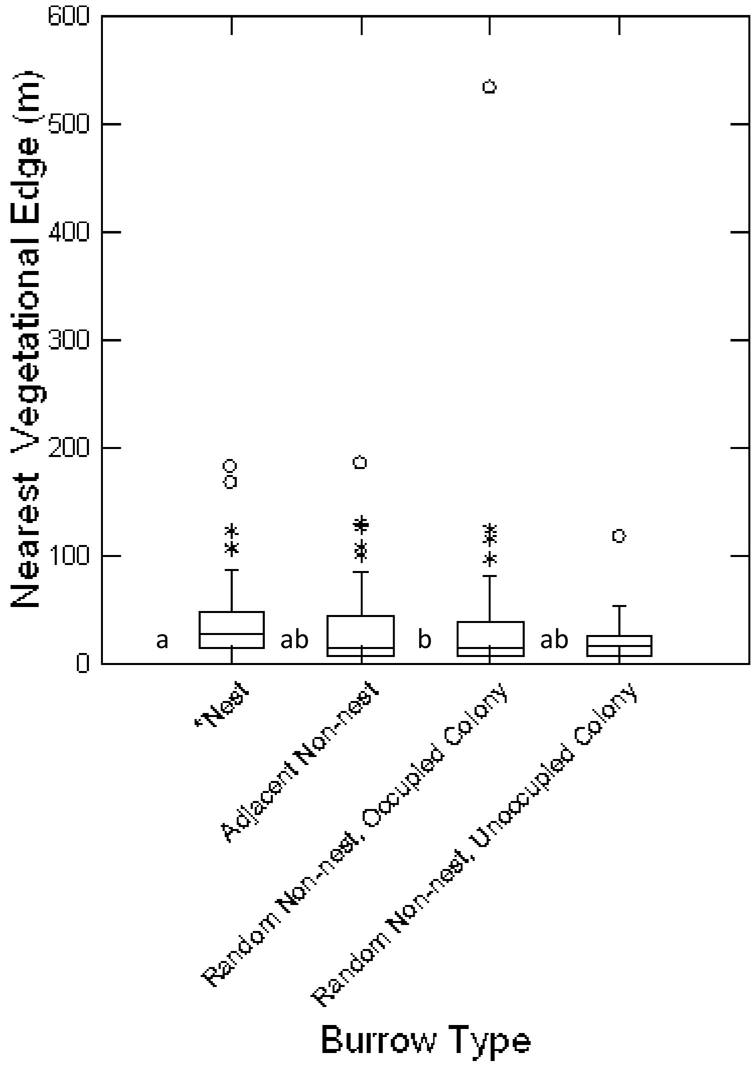

Figure 22. Boxplots of the distance to the nearest vegetational edge for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Open circles (°) indicate values >3× the interquartile range. Burrow types labeled with different letters have significantly different distributions ($p < 0.05$) according to the nonparametric multiple comparison method in Zar (1999). Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

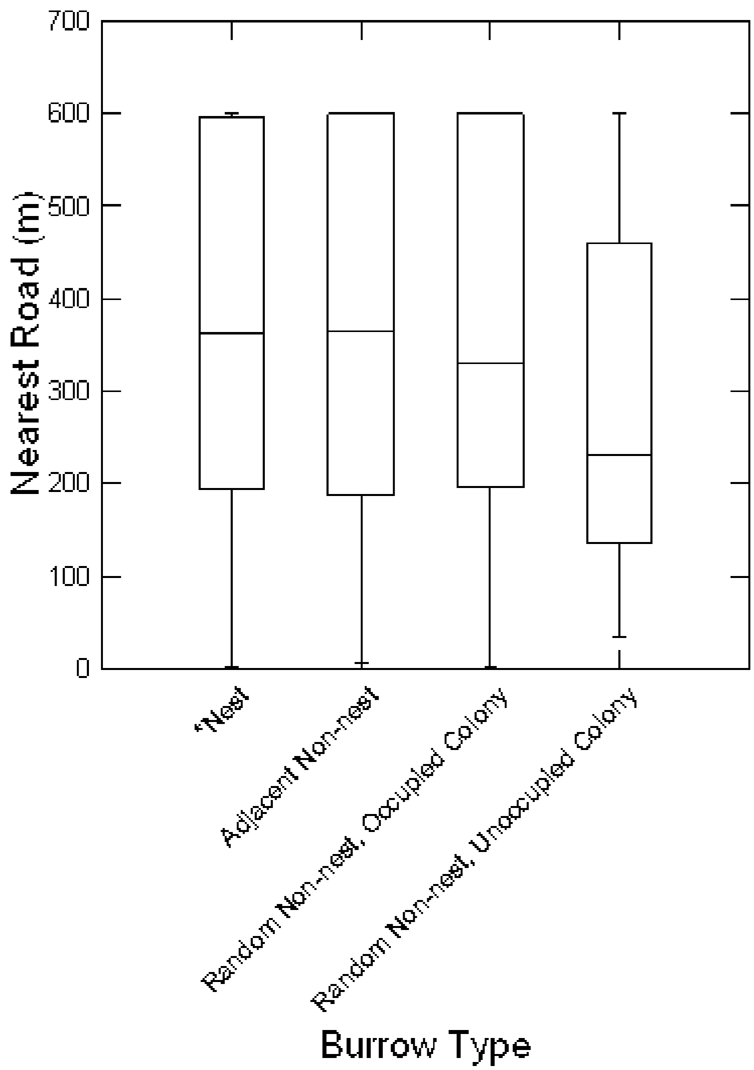

Figure 23. Boxplots of the distance to the nearest road for the 4 burrow types. No significant differences were detected among burrow types. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

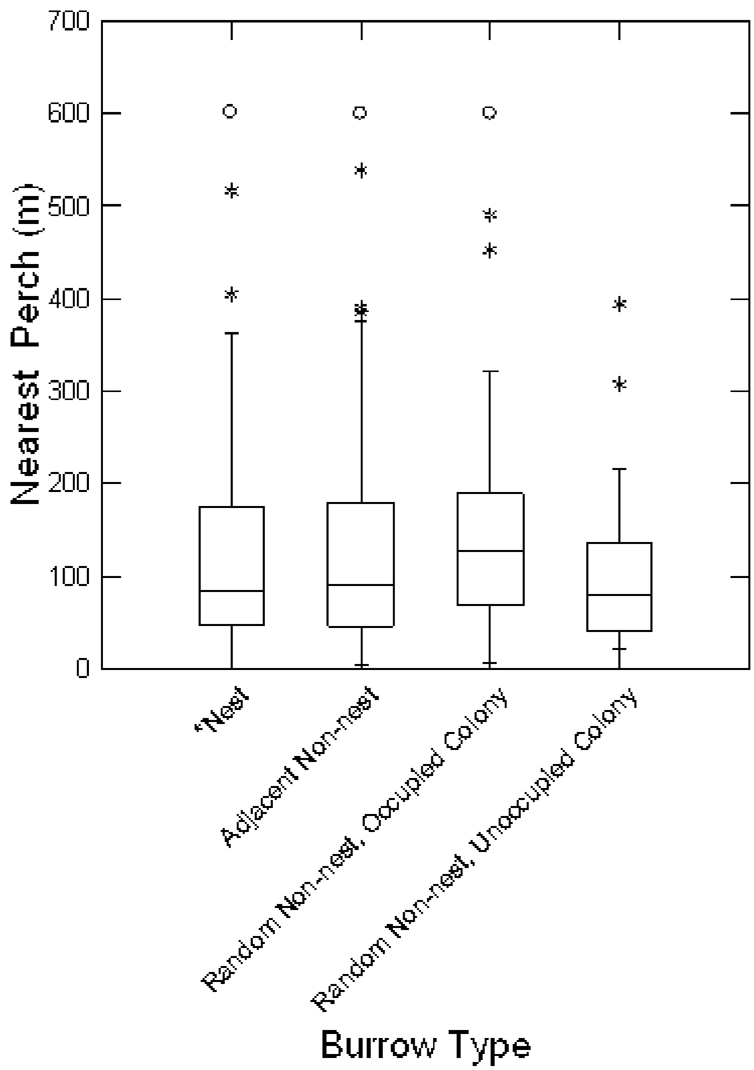

Figure 24. Boxplots of the distance to the nearest perch for the 4 burrow types. Asterisks (*) indicate values 1.5-3× the interquartile range. Open circles (°) indicate values >3× the interquartile range. No significant differences were detected among burrow types. Data were collected during the summer of 2011 at burrowing owl nest burrows and random non-nest burrows in prairie dog colonies (n = 107) located throughout western South Dakota.

CHAPTER 5

DISCUSSION

Burrowing Owl Distribution in Western South Dakota

Results of my study demonstrated that burrowing owls are widespread across western South Dakota. I confirmed the presence of breeding burrowing owls in nearly every county in the study area. The only counties where I did not locate burrowing owls were located on the east side of the Missouri River. Despite widespread occurrence, burrowing owl detection frequency was inconsistent across the study area. Most of my surveys were conducted around prairie dog colonies, and differences were evident in the proportion of colonies occupied by owls in different regions of the study area.

The survey method was effective at detecting burrowing owls in most instances. However, some colonies could not be completely surveyed because of colony size, local topography, and/or lack of public roads near the colony. The largest colonies were particularly difficult to survey with the same level of completeness as smaller colonies. Sometimes substantial portions of very large prairie dog colonies could not be seen from roads, and it is possible that burrowing owls were present but out of sight. Therefore, a few surveyed colonies that were recorded as unoccupied might have actually been occupied. For most colonies, I am confident that owls were detected if they were present. Male owls spent much of their time above ground throughout the breeding season and responded aggressively to call playbacks until chicks began to fledge.

The rates of prairie dog colony occupancy by burrowing owls that I found in western South Dakota fell within the range of rates found in the literature. However, rates of colony occupancy noted by other researchers are highly variable. Only 16% of colonies surveyed in southeastern Montana contained burrowing owls (Restani et al. 2001). Toombs (1997) found burrowing owls in 76% of the colonies that he surveyed in southeastern Colorado. Murphy et al. (2001) found that burrowing owl occupancy varied across regions in North Dakota, but many historical locations were no longer occupied. Bayless and Beier (2011) studied burrowing owls nesting in Gunnison's prairie dog (*Cynomys gunnisoni*) colonies in northeastern Arizona and recorded owls in 36% of the surveyed colonies. Several local studies in South Dakota have demonstrated the variability in colony occupancy as well. Berdan and Linder (1973) documented burrowing owls in 36% of the prairie dog colonies that they surveyed in Mellette County. Knowles (2001) reported burrowing owls in 55% of the prairie dog colonies that he surveyed in the Grand River National Grasslands in northwestern South Dakota. Bly (2008) located owls on 90% of surveyed colonies in 2005 and 88% of surveyed colonies in 2006 on the Bad River Ranches in Stanley and Jones counties. Inconsistency in colony occupancy among different regions of the state was consistent with my observations.

A general pattern that emerged across the study area was a greater proportion of owl-occupied colonies in regions with relatively few colonies compared to regions with many colonies. A possible explanation for this pattern is that burrowing owls can be more selective about which colonies they choose to occupy when many prairie dog colonies are available. A different, although not mutually exclusive, explanation is that some of the regions of South Dakota that contain the greatest numbers of prairie dog colonies have also experienced sylvatic plague outbreaks in recent years, virtually eliminating prairie dogs from some colonies and perhaps causing differences in habitat between colonies with prairie dogs and colonies without prairie dogs (see “Burrowing Owl Nest Site Selection in Western South Dakota” in this chapter for further discussion of the effects of prairie dogs on habitat). I did not quantify prairie dogs in this study, but burrowing owls did seem more likely to occur in colonies that had prairie dogs than in colonies where prairie dogs were no longer present.

I found that nearly half of all occupied colonies in my study contained 2 or more pairs of owls. Burrowing owls can be considered a semicolonial species, as they are often found nesting in small groups (Thomsen 1971, Butts and Lewis 1982, Desmond et al. 1995, Desmond and Savidge 1996, Restani et al. 2008). A study conducted in western North Dakota found that 60% of owl-occupied prairie dog colonies contained multiple pairs of owls in 2003 and 55% of owl-occupied colonies contained multiple pairs in 2004 (Davies and Restani 2006). Although the presence of more pairs may not necessarily indicate better habitat quality (Van Horne 1983), burrowing owls may perhaps benefit from the availability of colonies that allow them to nest colonially (Desmond et al. 1995, Welty 2010).

Burrowing owls in western South Dakota were more likely to be found in prairie dog colonies embedded in landscapes with little tree cover. Of the landscape variables examined in this study, only percent tree cover had a detectable effect on the probability of a prairie dog colony being occupied by burrowing owls. Tree cover seems to have an influence on the distribution of burrowing owls in western South Dakota. However, the models did not adequately discriminate between occupied and unoccupied colonies.

Poor model performance may be explained in part by the landscapes sampled in the study area. Most of the prairie dog colonies in western South Dakota are found in grassland-dominated, relatively unfragmented landscapes. Although relatively small increases in the amount of tree cover in the surrounding landscape decreased the probability of a colony being occupied by burrowing owls, most western South Dakota landscapes have very little tree cover. Current levels of tree cover in most areas of western South Dakota may not completely exclude burrowing owls from selecting prairie dog colonies. Winter et al. (2006*a*) studied the effects of landscape composition on the density of a variety of grassland bird species and detected an apparent threshold level of tree or shrub cover in the landscape above which relatively large-bodied, nonpasserine bird species would not occur. If tree cover increases in the future, this variable could become more effective in predicting occupancy of prairie dog colonies by burrowing owls. Similarly, most western South Dakota landscapes have relatively little cropland. If cropland in the landscape is avoided or favored by burrowing owls, the effect is probably not yet realized at current levels of crop cover (see "Burrowing Owl Nest Site Selection in Western South Dakota" in this chapter for further discussion of the effects of trees and cropland on burrowing owl habitat selection). Burrowing owls might also be responding to additional landscape-level variables that I did not include in these models. The remotely sensed variables that I used for the models were relatively simple to calculate and interpret, but alone they could not produce a satisfactory occurrence model.

The scales of the most competitive models in the set were in the middle of the range I examined (i.e., 800 m and 1,200 m but not 400 m or 1,600 m), and these distances roughly approximate the maximum distances that burrowing owls will travel in search of prey (Butts 1973, Green and Anthony 1989, Haug and Oliphant 1990, Gervais et al. 2003). Burrowing owls may prefer to breed in landscapes where they have very few trees within their home ranges. Migrating owls probably seek out the most favorable landscapes and then begin searching for an appropriate nest site at a more local scale. Models using data collected at nest burrows and random non-nest burrows support this hypothesis (see “Burrowing Owl Nest Site Selection in Western South Dakota” in this chapter).

My results suggest that colonies which contain burrowing owls in a particular year are likely to contain them in subsequent years. Colonies that were occupied in 2010 were generally reoccupied in 2011. I had no way of knowing if the same owls had returned in 2011 or if they had been replaced by other owls. Nevertheless, prairie dog colonies that are used by burrowing owls in consecutive years may represent the best available habitat (Plumpton and Lutz 1993*b*). Year-to-year reuse of prairie dog colonies, and even specific burrows within colonies, has been noted in other studies. All burrowing owl nest burrows studied by MacCracken et al. (1985*b*) in prairie dog colonies in the Conata Basin of southwestern South Dakota had been used in previous years. In north-central Colorado, Plumpton and Lutz (1993*b*) found that 90% of prairie dog colonies occupied by burrowing owls in 1990 were reoccupied in 1991, and some nest burrows were also reused. In northeast Colorado, Woodard (2002) found 91% of colonies occupied by burrowing owls in 1999 to be reoccupied in 2000. Desmond et al. (1995) noted burrowing owls reoccupying the same prairie dog colonies from year to year in western Nebraska and commented that the owls seemed to return to certain areas of colonies.

Evidence from other studies suggests that burrowing owls returning to the same locations experience increased breeding success. In Colorado, Lutz and Plumpton (1999) did not find differences in productivity between adults that returned to the same nesting area and adults that were new to the area, but they found that brood sizes were significantly larger for returning females. Burrowing owls nesting in previously used burrows in South Dakota fledged more young than those nesting in previously unused burrows (Griebel and Savidge 2007). Similarly, burrowing owl nests in Wyoming were more likely to be successful if they were used the previous year (Lantz and Conway 2009).

Many bird species are known to commonly disperse to new nest sites following nest or brood failures, either in the same breeding season if the birds renest, or during the following breeding season (Greenwood and Harvey 1982, Lima 2009). Catlin and Rosenberg (2008) removed eggs from burrowing owl nests in southeastern California to simulate predation and found that the owls whose nests were experimentally predated were more likely to disperse to a new nesting site than control owls. The owls dispersed relatively long distances (mean = 2,802 ± 2,553 m) following experimental nest predation (Catlin and Rosenberg 2008). In the same region, burrowing owls whose nests were lost to natural causes were more likely to disperse to a new nest site the following year than those whose nests were successful, and failed nesters dispersed farther than successful nesters (Catlin et al. 2005). Dispersal distances varied from <100 m to >3,200 m for failed nesters in the Catlin et al. (2005) study. In South Dakota, it is possible that burrowing owls that fail to nest successfully in a particular prairie dog colony would be likely to seek a different colony during the following breeding season. Colonies that consistently contain burrowing owls could reflect successful breeding at these sites. However, some occupied sites may actually be sink habitats, depending on immigration of burrowing owls from other sites to remain occupied (Conway et al. 2006).

Burrowing Owl Nest Site Selection in Western South Dakota

My results suggest that burrowing owls use habitat characteristics at multiple spatial scales when selecting nest sites within prairie dog colonies in western South Dakota. This is consistent with habitat selection theory for birds. Habitat selection is a hierarchical process; birds consider conditions at large scales before selecting for habitat features at smaller scales (Johnson 1980). Landscape-level characteristics seemed to be strong predictors of nest sites, as models that did not contain landscape variables were not competitive. However, models containing only landscape variables were not competitive either. Cunningham and Johnson (2006) observed similar patterns for some grassland passerines. Their models containing only landscape-level variables were relatively poor, but landscape variables contributed to good models when combined with smaller-scale variables.

At the landscape scale, burrowing owls in western South Dakota avoided trees when selecting nest sites in prairie dog colonies. Tree cover at the 800 m buffer radius emerged as the most important landscape-level variable, appearing in all competitive models. The models containing percent tree cover at the smaller scale (400 m buffer radius) were not competitive with the models containing percent tree cover at the larger scale (800 m buffer radius). This trend may be an artifact of the locations of the prairie dog colonies themselves. Prairie dogs typically establish colonies in upland areas that are relatively free of trees (Hygnstrom and Virchow 1994), so tree cover is generally sparse near colonies. Many trees that occurred within 400 m of prairie dog colonies were in shelter belts that might have been planted after the colonies were established. Trees were usually more prevalent away from colonies, and burrowing owls seemed to avoid selecting nest sites where trees would be abundant within their home ranges.

Many grassland bird species are known to respond negatively to the presence of trees. Bakker (2003) reviewed multiple studies demonstrating lower densities and/or lower reproductive success of grassland birds as tree cover increased. Even small increases in tree cover can have disproportionately negative effects on grassland bird occurrence (Grant et al. 2004; Cunningham and Johnson 2006; Winter et al. 2006*a*, *b*). Quamen (2007) experimentally demonstrated avoidance of woodland edges (mostly shelter belts and other anthropogenic woodlands) by grassland songbirds in eastern North Dakota and South Dakota. The available habitat seemed otherwise suitable, and grassland birds occupied the sites after the trees were removed (Quamen 2007). The mechanisms behind the negative effects of trees vary by bird species (Coppedge et al. 2001, Grant et al. 2004) and are not necessarily directly applicable to burrowing owls because of differences in life histories among species, but any bird that is adapted to the openness of a grassland ecosystem is likely to be negatively impacted when that ecosystem changes. Although other authors have mentioned that burrowing owls seem to prefer landscapes with few or no trees (e.g., Wedgewood 1976, Haug et al. 1993, Clayton and Schmutz 1999), no previous studies have quantified tree cover as a factor in occurrence or nest site selection.

The presence of trees in the landscape may have deleterious effects on burrowing owls that have led to owls avoiding landscapes with a high proportion of tree cover. Perhaps burrowing owls avoid trees because they provide perch sites and nesting sites for larger species of raptors. Aerial predators can be significant causes of burrowing owl mortality, with merlins (*Falco columbarius*), prairie falcons (*F. mexicanus*), peregrine falcons (*F. peregrinus*), golden eagles (*Aquila chrysaetos*), red-tailed hawks (*Buteo jamaicensis*), Swainson's hawks (*B. swainsonii*), ferruginous hawks (*B. regalis*), northern harriers (*Circus cyaneus*), Cooper's hawks (*Accipiter cooperii*), and great horned owls (*Bubo virginianus*) being known or suspected predators of burrowing owls (Martin 1973, Konrad and Gilmer 1984, Haug et al. 1993, Belthoff et al. 1995, Clayton and Schmutz 1999, Leupin and Low 2001, Davies and Restani 2006). All of these species occur in western South Dakota as residents or migrants, and all of the breeding species except for prairie falcons, peregrine falcons, and northern harriers will use trees as nest sites (Johnsgard 1990, Tallman et al. 2002).

The most likely avian predators of burrowing owls in my study area were the *Buteo* hawks and great horned owls. I observed hawks and great horned owls hunting near prairie dog colonies on multiple occasions. Habitat for these raptors includes wooded draws or other patches of trees surrounded by upland prairie (Faanes 1983; Johnsgard 1990, 2002). Some studies have also found associations between several of the large raptors and prairie dog colonies. Red-tailed hawks were associated with black-tailed prairie dog colonies during summer in Oklahoma (Smith and Lomolino 2004). Sharps and Uresk (1990) found that ferruginous hawks, red-tailed hawks, Swainson's hawks, and great horned owls frequently used prairie dog colonies during the spring and summer in western South Dakota. *Buteo* hawks and great horned owls usually take mammalian prey (Johnsgard 1990, 2002). However, large raptors hunting around prairie dog colonies would be expected to opportunistically capture burrowing owls, especially chicks.

I did not witness any predation events of burrowing owl chicks during my study, but I found predated chicks near multiple nest sites. These chicks did not show evidence of predation by badgers (*Taxidea taxus*), which some authors have identified as major predators of burrowing owls (Green and Anthony 1989, Haug et al. 1993, Holmes et al. 2003, Desmond et al. 2000). My observations were consistent with those of Restani et al. (2001) and Griebel and Savidge (2007), who reported low rates of predation by badgers in southeastern Montana and southwestern South Dakota, respectively. Because badgers hunting in active prairie dog colonies have abundant sources of prey and many burrows to search, burrowing owls are probably less likely to be predated by badgers in active prairie dog colonies with relatively high burrow densities (Desmond et al. 2000, Restani et al. 2001, Davies and Restani 2006, Griebel and Savidge 2007).

The presence of trees that are used by large raptors may lead to increased burrowing owl mortality. In a study in Saskatchewan, avian predators accounted for 47% of all mortalities of radio-tagged burrowing owls in 1998 (Todd 2001). Todd speculated that an increase in the amount of tree cover on the Canadian prairies in combination with smaller and more discontinuous patches of nesting habitat was leading to elevated levels of avian predation. Clayton and Schmutz (1999) noted that the burrowing owl population in their southeastern Alberta study area had declined as populations of *Buteo* hawks increased, perhaps in response to increasing availability of trees and shrubs for nesting sites.

Based on a large body of evidence, predation risk is believed to influence many behavioral and reproductive decisions for birds (Lima 2009). Even if predation of burrowing owls by larger raptors is relatively rare, the mere threat of predation may be enough to cause burrowing owls to avoid nesting in some areas. Perceived risk of predation impacts habitat selection by many bird species in a variety of habitats. Fontaine and Martin (2006) removed nest predators from plots of coniferous forest in central Arizona before the arrival of migrant passerine birds and found that breeding bird densities were higher in the removal areas than in adjacent plots where predators were not removed. Lima and Valone (1991) modified the density of woody cover in plots on southeastern Arizona grasslands and found that the species composition of small passerines changed to reflect the species' preferred modes of escape from predators. Species that tend to fly to cover (e.g., shrubs or small trees) when threatened increased in numbers after artificial mesquite trees were added to plots, while numbers of open-country species that usually employ aerial escape methods generally decreased, despite no observable change in the predator community.

The phenomenon of predator avoidance has also been studied in raptors. Black kites (*Milvus migrans*) in the Italian Alps often clustered their territories in "spatial refugia" outside of the territories of eagle owls (*Bubo bubo*), which sometimes preyed on kites (Sergio et al. 2003). The kites were more likely to abandon their territories as predation risk increased, and often they would avoid otherwise suitable habitat when eagle owls were present. Similarly, rough-legged hawks (*Buteo lagopus*) avoided territories of larger snowy owls (*Nyctea scandiaca*) in Siberia (Potapov 1997). In Finland, Tengmalm's owls (*Aegolius funereus*) used available nest sites (i.e., nest boxes and natural tree cavities) more frequently when a potential predator, the Ural owl (*Strix uralensis*) was absent than when it was present (Hakkarainen and Korpimäki 1996). In Germany, Krüger (2002) found that common buzzards (*Buteo buteo*) experienced decreased reproductive success when presented with a dummy of a northern goshawk (*Accipiter gentilis*). Some of the buzzards presented with the goshawk dummy abandoned their nest sites and occupied new sites the following year. Similar relationships may occur between burrowing owls and larger raptors in South Dakota. Birds should be expected to select breeding sites that minimize predation risk for themselves and their offspring (Lima and Dill 1990, Lima 2009).

Ultimately, burrowing owls were probably avoiding prairie dog colonies located in landscapes with relatively high percent tree cover because they gain a fitness advantage by selecting open habitats. A bird's habitat preferences may be innate and/or learned (Klopfer and Hailman 1965, Morse 1980, Bairlein 1983, Hutto 1985). In either instance, habitat use by burrowing owls is influenced by the decisions of previous generations. Burrowing owls may be genetically programmed to seek open habitats because of relatively high reproductive success in these habitats over time. Predation is a strong selection pressure that could have produced an aversion to trees by burrowing owls. Adding to an innate preference for open habitats, burrowing owls may rely in part on their own experiences to select quality habitats. An animal's experiences on its natal area may impact its habitat preferences; when it disperses to a new territory, it is likely to select habitat characteristics that are similar to those of its natal habitat (Stamps and Davis 2006, Stamps and Swaisgood 2007). Breeding experiences can also impact nest site selection, and birds may disperse to new sites after a nest failure in either the same breeding season or the following breeding season (Greenwood and Harvey 1982, Lima 2009). Burrowing owls have been recorded dispersing to new nest sites following the failure of a nest (Catlin et al. 2005, Catlin and Rosenberg 2008). I found no direct evidence of nest predation during this study, but I did find chicks that were predated after leaving the nest. A variety of bird species are known to change breeding sites after unsuccessful attempts in the previous year (Greenwood and Harvey 1982). If burrowing owls lose their broods to avian predators associated with trees, they might avoid nesting near trees the following year.

Vegetative structure near the selected burrow was also important for burrowing owl nest site selection in western South Dakota. Low visual obstruction readings were associated with a greater likelihood of a burrow being chosen as a nest site. Visual obstruction readings varied within and among colonies, but the readings for nest burrows were consistently low and showed less variation than all other burrow types. An association with short vegetation is similar to results of previous studies. For example, Butts and Lewis (1982) found that nest burrows in Oklahoma were located where vegetation was shorter than approximately 10 cm. Green and Anthony (1989) reported that nest sites in north-central Oregon were located in areas with good horizontal visibility and that nests were not found in areas of tall, dense vegetation. Clayton and Schmutz (1999) also noted selection of nest sites with low visual obstruction in Alberta and Saskatchewan.

Though my results showed that burrowing owls selected for areas of short vegetation within prairie dog colonies, because I only located nests in 2011, I cannot conclude that this pattern occurs in most years. Some studies did not find a difference in vegetation height between nest sites and random sites (MacCracken et al. 1985*b*, Belthoff and King 2002). Precipitation may influence the heterogeneity of vegetation within the boundaries of colonies. Plumpton and Lutz (1993*b*) did not find differences in vertical density of vegetation between nest sites and random sites, but they found that average grass and forb heights were lower at nest sites during the second year of their study, which was much wetter than the first. In wet years, vegetation will grow faster and taller, causing more dramatic differences between clipped and unclipped vegetation (Plumpton and Lutz 1993*b*, Lomolino and Smith 2003, Tipton et al. 2008). The summer of 2011 was unusually wet in western South Dakota, and prairie dogs were often unable to maintain vegetation at a short height throughout colonies. In wet years, the presence of prairie dogs may be especially important for burrowing owls to locate suitable nesting habitat.

Several factors may explain why burrowing owls tend to nest in areas with short vegetation (i.e., 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 chasing prey on the ground, flying from a perch, and hovering (Coulombe 1971, Thomsen 1971, Butts 1973, Thompson and Anderson 1988, Haug et al. 1993, Clayton and Schmutz 1999, Johnsgard 2002). These hunting methods are more likely to be successful when vegetation is short and relatively sparse. Thompson and Anderson (1988) noted that burrowing owls in east-central Wyoming were not observed "ground foraging" where vegetation height exceeded 20 cm or where vegetation was very thick. Burrowing owls may not be capable of 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 (personal observation). Short vegetation may also be important for predator detection (Green and Anthony 1989).

The nest site selection models also suggested that burrowing owl nest sites in western South Dakota are associated with a relatively high abundance of forbs and, to a lesser extent, bare ground. The effects of these variables were not as strong as those of percent tree cover or visual obstruction, but their presence in competitive models may indicate biological significance. Several other studies also compared vegetation composition near nest sites and random sites in prairie dog colonies, but the results were inconsistent among study areas. Thompson (1984) found forb cover to be greater around nest burrows than around non-nest burrows in central Wyoming, but he found no significant differences in bare ground. MacCracken et al. (1985*b*) found that nest sites had greater forb cover than random sites in the Conata Basin of southwestern South Dakota. Plumpton and Lutz (1993*b*) found no differences in forb cover between nest burrows and random burrows in north-central Colorado, but bare ground was greater around nest burrows in 1 year of their study. However, no vegetative characteristics were significantly related to burrowing owl nests in northern Texas (Teaschner 2005).

The local habitat characteristics of nest sites chosen by burrowing owls provide evidence that the owls benefit from nesting in active prairie dog colonies. Prairie dogs most obviously benefit burrowing owls by creating burrows, but they also modify the habitat in other ways that may improve its suitability for owls. The digging, scratching, grazing, and clipping behaviors of prairie dogs cause changes in the vegetation community by reducing the abundance of some perennial grasses in favor of shorter, more grazing-tolerant grasses, such as buffalograss, and more annual forbs than would typically occur in uncolonized areas (Agnew et al. 1986, Archer et al. 1987, Whicker and Detling 1988, Winter et al. 2002). The structure associated with areas of prairie dog activity (i.e., short vegetation, especially forbs, interspersed with bare ground) was found to be used by nesting burrowing owls in western South Dakota. Like short vegetation, patches of bare ground probably benefit burrowing owls by allowing for easier detection of prey. Burrowing owls often hunt in areas with patches of bare ground (Thompson and Anderson 1988, Chipman et al. 2008). The dominance of annual forbs around nest burrows may be an artifact of the owls choosing relatively bare sites within prairie dog colonies, since most forbs germinate after nesting is established (MacCracken et al. 1985*b*). My results provided some evidence that burrowing owls may just be selecting nest sites that lack dense grass cover. I did not include grass cover in any of my a priori models because it was correlated with forb cover, and previous studies have found relationships between forbs and burrowing owl nest sites. However, the relationship with percent grass cover may warrant further investigation. Regardless of why burrowing owls select for a particular ground cover type, my results suggest that differences in vegetative composition among colonies may be a strong factor in selecting a colony for nesting. Vegetative differences can be attributed to any combination of soil type, local climate conditions, grazing management history, and prairie dog density.

Availability of some prey items may actually be higher within active prairie dog colonies than in the surrounding habitat. Many other species respond to the changes in vegetation structure and composition produced by prairie dog activity. Studies in western South Dakota (Agnew et al. 1986, 1988) and northern Mexico (Ceballos et al. 1999) found that small mammals were more abundant in prairie dog colonies than in the surrounding habitat. Similarly, Shipley and Reading (2006) captured more small mammals in prairie dog colonies than in off-colony sites, but capture rates were not significantly different. O'Meilia et al. (1982) released prairie dogs into experimental pastures in western Oklahoma over a 3-year period and noted greater small mammal biomass in the experimental pastures compared with control pastures without prairie dogs 4 and 5 years after the initial release. Russell and Detling (2003) concluded that some grasshopper species (family Acrididae) preferred prairie dog colonies as ovipositing sites because of the abundance of patches of bare ground. O'Meilia et al. (1982) found that insect biomass (mostly grasshoppers) was lower in pastures with prairie dogs than in those without. However, insects are probably easier for burrowing owls to capture within the boundaries of a prairie dog colony because of the shorter vegetation. Several researchers who studied burrowing owl diets found that they shifted their diets in the summer (i.e., during the nestling period) to be more reliant on insects (MacCracken et al. 1985*a*, Green and Anthony 1989, Haug and Oliphant 1990, Woodard 2002, Poulin and Todd 2006). Haug and Oliphant (1990) studied home ranges of burrowing owls in Saskatchewan and found that average home range size decreased when grasshopper consumption increased in mid-July. Burrowing owls likely gain a fitness advantage by placing their nests in areas with high insect abundance, as these are important food resources for chicks. Some species of small mammals, such as grasshopper mice (*Onychomys* spp.) may also respond positively to the increase in insects, providing another food source (Agnew et al. 1988). Adult owls spend less energy while hunting for their chicks if prey is available near the nest site. Burrowing owl chicks will also capture grasshoppers and other insects for themselves even before fledging (personal observation), so chicks that can easily supplement prey provided by the adults with prey they catch themselves might be more likely to survive to independence. Since burrowing owls, particularly juveniles, spend little time away from their selected prairie dog colonies (Butts and Lewis 1982, Teaschner 2005, Davies and Restani 2006, Chipman et al. 2008), the possibility of abundant prey and high visibility on active prairie colonies seems particularly important.

Several variables that have been noted as important by other researchers did not emerge as strong predictors of burrowing owl nest occurrence in my study. At the landscape scale, I found no effect of crop fields in determining nest sites. Previous studies have found mixed effects of cropland in the landscape. Butts (1973) found that regions of high burrowing owl nest density in the Oklahoma panhandle had significantly more cropland in the landscape than regions of low nest density. Rangeland and cropland (mostly small grains) were approximately equal in proportion in his study areas. In western North Dakota, cropland was positively associated with the number of burrowing owl pairs and reproductive success, although cropland was scarce in the study area (Restani et al. 2008). Gleason and Johnson (1985) found no difference in brood size between burrowing owls nesting in rangeland and those nesting near alfalfa fields in southeastern Idaho, but the landscape composition was not clear from the paper. Burrowing owls rarely nest in crop fields (Butts 1973, Clayton and Schmutz 1999, Gervais et al. 2003, DeJong et al. 2004, Poulin et al. 2005, this study), but crop fields are sometimes used as hunting areas (Butts 1973, Gervais et al. 2003, Restani et al. 2008). Moulton et al. (2006) found that burrowing owls in southwestern Idaho actually consumed more prey in agricultural habitats than in nonagricultural habitats. I use caution in applying the results of the Moulton et al. (2006) study to western South Dakota, however, as their study area was in a sage-steppe plant community, most agricultural fields were irrigated (dryland farming is predominant in western South Dakota), and the major crops were different from the typical crops in western South Dakota. In contrast, studies in the mixed-grass region of Saskatchewan found that burrowing owls generally avoided cereal crop fields relative to their availability (Haug and Oliphant 1990, Sissons et al. 2001). I classified hay fields as crop fields because most hay fields were planted to alfalfa or other introduced species whose vegetative structure was dissimilar to typical rangeland and because I observed few burrowing owls nesting in hay fields. I did observe some burrowing owls hunting in hay fields. Haug and Oliphant (1990) and Sissons et al. (2001) mentioned that burrowing owls used hay fields as habitat, but they did not specify if the owls were actually nesting in them.

Grassland cover was highly correlated with cropland cover at both the 400 m and the 800 m buffer levels. Grassland and cropland are closely related to each other because virtually the only type of land conversion that occurs in western South Dakota is from grassland to cropland (or, less often, from cropland to grassland). When either of these cover types increases, it is nearly always at the expense of the other. The percent cover of grassland was not a variable in any of the competitive models.

In part, the lack of an effect of grassland or cropland in the landscape may be a result of land use in western South Dakota. Although row crop and small grain agriculture have increased in western South Dakota, approximately 70% of the study area was grassland (calculated from the 2006 NLCD) and most areas were relatively unfragmented. In addition, regions of intensive agriculture rarely contained prairie dog colonies, so highly altered landscapes were not well represented in the sample. In northeastern Colorado, burrowing owls were more likely to nest in fragmented landscapes, but the study area was predominantly shortgrass prairie with relatively little cultivated land (Orth and Kennedy 2001). Habitat fragmentation is a concern for declining grassland bird species, but some species, including the burrowing owl, will use small patches of grassland found in large, fragmented grassland complexes (Ribic et al. 2009). I observed many burrowing owls in western South Dakota that had successfully raised broods in small prairie dog colonies located in pastures adjacent to crop fields.

Any negative effects of habitat fragmentation are probably less than the effects of habitat loss (Fahrig 2003, Ribic et al. 2009). As grasslands are converted to crop fields, fragmenting the remaining grasslands and the associated prairie dog colonies, burrowing owls will often still use the remaining habitat. While the results of my study suggest that a small amount of cropland may not have a strong impact on burrowing owls, no one has determined a threshold level of cropland on the landscape at which burrowing owls are negatively affected (Restani et al. 2008). Although burrowing owls occasionally incorporated crop fields or hay fields into their home ranges, they seldom nested in these habitats in western South Dakota. Burrows are usually unavailable in crop or hay fields because prairie dogs will rarely occupy areas with tall, dense vegetation (Hygnstrom and Virchow 1994), and any prairie dogs that do colonize these fields are usually poisoned to avoid crop and/or farm equipment damage. Conversion of rangeland to row crops, small grains, or hay essentially causes potential burrowing owl nesting habitat to be lost.

My results suggest that habitat structure at both the local and landscape level is more important to burrowing owls than prairie dog colony size when selecting a nest site in western South Dakota, as colony size did not have a positive or negative effect on the likelihood of burrowing owls choosing a particular site for nesting. Results of previous studies have found mixed effects of colony size on burrowing owl use. Prairie dog colonies occupied by burrowing owls in southeastern Colorado were significantly larger than unoccupied colonies (Toombs 1997). Griebel and Savidge (2007) found that large prairie dog colonies were usually occupied by burrowing owls in the Buffalo Gap National Grasslands of South Dakota while 85% of unoccupied colonies were less than

10 ha in size. Other researchers have found no significant differences in size between occupied and unoccupied colonies, including studies conducted in north-central Colorado (Plumpton and Lutz 1993*b*), northeastern Colorado (Orth and Kennedy 2001), and southeastern Montana (Restani et al. 2001). Likewise, Bayless and Beier (2011) found no size differences between occupied and unoccupied Gunnison's prairie dog colonies in northeastern Arizona. Large colonies may sometimes contain more pairs of burrowing owls, probably because of more available space to establish territories, but small colonies often have higher densities of owls (Desmond et al. 1995, Desmond and Savidge 1996, Woodard 2002, Griebel and Savidge 2007, Bly 2008). In contrast, Restani et al. (2008) found colony size to be a poor predictor of burrowing owl density in western North Dakota. In some regions, burrowing owls seem to prefer to nest in larger prairie dog colonies, perhaps because they can nest in clusters within large colonies (Desmond et al. 1995, Desmond and Savidge 1996, Griebel and Savidge 2007). The strategy of nesting in high-density clusters, even when other habitat is available, could have advantages for survival, such as better detection of predators and mutual defense of nesting sites (Desmond et al. 1995, Welty 2010). In South Dakota, burrowing owls have been found to have higher nesting and/or fledging success in large colonies than in small colonies (Griebel and Savidge 2007, Bly 2008), but the reasons for the higher survival rates are not known. The effect of colony size is probably regional, however, as results of a study in Colorado showed higher fledging rates per breeding attempt for burrowing owls in smaller colonies (Woodard 2002). I did not collect data on reproductive success, so I can

only comment on factors that impacted burrowing owl nest presence or absence in my study area.

I did not find any meaningful relationship between nest sites and burrow density or distance to available burrows. Burrow density has been mentioned as an important factor in nest site selection and/or reproductive success by other researchers. Plumpton and Lutz (1993*b*) noted that in 1 of the 2 years of their study in north-central Colorado, burrowing owls nested in colonies of greater burrow density. In southeastern Colorado, Toombs (1997) found burrowing owls nested in colonies with higher burrow densities and also selected areas within the colonies that had higher burrow densities. Lantz et al. (2007) also found a positive relationship between burrow density and nest sites in northeastern Wyoming. In Gunnison's prairie dog colonies in northern Arizona, burrow density within 50 m of burrowing owl nest burrows was greater than that of random burrows (Bayless and Beier 2011).

Some evidence from other studies has suggested that burrowing owls may select for a high density of active prairie dog burrows. Several authors have noted that burrowing owls prefer active prairie dog colonies with relatively high prairie dog densities rather than inactive colonies (Butts and Lewis 1982, Toombs 1997, Desmond et al. 2000, Sidle et al. 2001). Selection may also occur at a more local scale. Restani et al. (2001) found that nest burrows were closer to active prairie dog burrows than random burrows in southeastern Montana. Bayless and Beier (2011) counted more active burrows within 50 m of nest burrows than they counted within 50 m of random burrows. Nesting near active prairie dog burrows may also increase survival of burrowing owl nests.

Successful nests in western Nebraska were found in areas with more active prairie dog burrows than unsuccessful nests (Desmond and Savidge 1999). Davies and Restani (2006) did not find a difference in brood survival based on burrow density but commented that active burrow densities on their study sites in western North Dakota were more than double those reported by Desmond and Savidge (1999).

The relationship between burrowing owl nest sites and a relatively high density of available burrows is logical. Burrowing owls frequently use a system of burrows including the nest burrow and several satellite burrows when rearing young (Martin 1973, Butts and Lewis 1982, Konrad and Gilmer 1984, Thompson and Anderson 1988, Plumpton and Lutz 1993*b*, Desmond and Savidge 1999, King and Belthoff 2001). Broods are often spread among several burrows once chicks become mobile, perhaps to reduce competition for food and space and/or to minimize parasite loads (Butts and Lewis 1982). Spreading a brood among multiple burrows also reduces the likelihood that the entire brood will be predated (Desmond and Savidge 1999). A high density of burrows provides escape cover as well, since burrowing owl chicks usually retreat into burrows when predators are present (Coulombe 1971, Butts 1973, Martin 1973, Plumpton and Lutz 1993*b*, personal observation). Once young burrowing owls become independent in the late summer, an even larger system of burrows may be needed, as the owls may disperse over 300 m from the nest site (King and Belthoff 2001).

Burrow availability is clearly important for nesting burrowing owls, but none of the burrow density variables were strong predictors of nest sites in my study. Studies in western Nebraska (Desmond et al. 1995) and northern Texas (Teaschner 2005) have also found no differences in burrow density between nest sites and random sites in prairie dog colonies. In central Wyoming, Thompson (1984) actually found slightly higher burrow densities around random burrows than around nest burrows in prairie dog colonies. Generally, potential nest and satellite burrows are not limited in prairie dog colonies (Desmond et al. 1995). Randomly selected sites in unoccupied colonies in my sample actually had burrow densities that were very similar to nest sites in occupied colonies. In regions where prairie dog colonies are absent and burrowing owls use burrows constructed by badgers or other mammals, burrow density is probably a stronger factor in nest site selection (Desmond and Savidge 1996, Poulin et al. 2005). Because the nest site data were collected within active prairie dog colonies, the density of available burrows was probably almost always adequate for burrowing owls and therefore did not differ substantially between nest sites and random sites in unoccupied colonies. At a more local level, my results showed that nest sites were located closer to available burrows and had higher burrow densities than random sites in occupied colonies. Although most prairie dog colonies probably have a suitable burrow density, burrowing owls might seek out areas of high density within the selected colony. I suspect that burrow density may also be an important factor in determining whether burrowing owls nest in prairie dog colonies that have been lost or reduced because of human control efforts or plague outbreaks.

My models also showed no evidence that roads affect the selection of nest sites by burrowing owls. Direct and indirect effects of roads have been implicated in the declines of some bird populations (Kociolek et al. 2011), but the effects of roads on burrowing owls remains unclear. In some areas, burrowing owls often nest close to roads (Haug and Oliphant 1990; Plumpton and Lutz 1993*a*, *b*; Belthoff et al. 1995). Previous studies have found no significant differences between nest burrows and random burrows in the mean distance to a road (Plumpton and Lutz 1993*b*, Restani et al. 2001, Bayless and Beier 2011). Ultimately, any selection for or avoidance of roads by burrowing owls probably depends on the road type. Many of the roads in my study area were dirt or gravel roads with little vehicle traffic. McCarthy et al. (2011) studied 15 bird species associated with different habitats in western Montana and northern Idaho and found that only 2 species were more likely to occur near roads and no species were more likely to occur away from roads. Most roads in the McCarthy et al. study were low-maintenance dirt or gravel roads. In some situations, roads such as these may actually serve as unique resources within a burrowing owl's home range. I commonly observed burrowing owls hunting (primarily for grasshoppers) on or near gravel roads. Other researchers have noted similar behavior (Butts 1973, Wedgewood 1976, Gervais et al. 2003, Bayless and Beier 2011).

Burrowing owls seem relatively tolerant of vehicle traffic. Plumpton and Lutz (1993*a*) found that many burrowing owl nests in their study area (Rocky Mountain Arsenal in Colorado) were located near roads, and traffic had little effect on behavior and no effect on productivity. However, nesting near roads does increase the likelihood of collisions with vehicles. I did not observe any road-killed burrowing owls in western South Dakota, but vehicle collisions have been documented as sources of mortality in many studies (Brenckle 1936, McClure 1951, Wedgewood 1976, Konrad and Gilmer

1984, Gleason and Johnson 1985, Haug et al. 1993, Belthoff et al. 1995, Clayton and Schmutz 1999, Davies and Restani 2006, Conrey 2010).

A potential effect of roads not frequently discussed in the literature is access to prairie dog colonies by recreational prairie dog hunters. Prairie dog hunting is a popular activity in South Dakota, especially for nonresident hunters. Surveys of resident and nonresident hunters produced estimates of 1.19 million and 1.52 million prairie dogs killed by hunters in 2000 and 2001, respectively (Gigliotti 2002). Hunting pressure is highest on colonies that are easily accessed by a vehicle, especially on public land (personal observation). Burrowing owls are sometimes killed accidentally or intentionally by shooters. I located dead burrowing owls that had obviously been shot on several prairie dog colonies. Shooting has also been noted as a source of mortality in Oklahoma (Butts 1973), Idaho (Belthoff et al. 1995), and Colorado (Woodard 2002, Conrey 2010). It is unclear how often events like this occur, but even if prairie dog hunters rarely shoot burrowing owls, the noise and disturbance caused by frequent shooting could interfere with important burrowing owl activities such as feeding chicks. I was not able to quantify shooting pressure to determine if it had any impact on nest site selection.

I found no effect of the distance to a perch on the probability of a nest site being selected. Elevated perches have been mentioned by multiple authors as being used by burrowing owls for hunting, watching for predators, and thermoregulation (Coulombe 1971, Thomsen 1971, Butts 1973, Thompson and Anderson 1998, Johnsgard 2002). However, my study and some previous studies have found little to no difference in the distance to a perch between nest burrows and random burrows (Belthoff and King 2002, Plumpton and Lutz 1993*b*, Lantz et al. 2007). Perches were usually widely available in my study area. Many of the prairie dog colonies were located near fences, and fence posts were often used as perches. When fence posts or other perch structures are not available, the soil mounds created by prairie dogs may be adequate perch sites so long as the vegetation is short. In south-central Saskatchewan, burrowing owls nested in burrows with taller soil mounds than unused burrows, perhaps because few other perches were available (Poulin et al. 2005). In north-central Oregon, perch height was important in nest site discrimination only in habitats with relatively tall vegetation; burrowing owls might not have needed elevated perches where the vegetation was very short (Green and Anthony 1989). Plumpton and Lutz (1993*b*) said that burrowing owls used perches in north-central Colorado, but they were probably not necessary since the vegetation in the prairie dog colonies was short. Elevated perches may be important for meeting certain life history requirements, but burrowing owls nesting in prairie dog colonies in South Dakota were seemingly not lacking in perch sites.

The models provided no evidence that the distance to a vegetational edge had an effect on the probability a burrow being selected for nesting. Other researchers have commented that burrowing owls often seem to nest near the perimeter of prairie dog colonies (Butts and Lewis 1982, Desmond et al. 1995, Toombs 1997, Orth and Kennedy 2001, Teaschner 2005, Conrey 2010). My observations of burrowing owls in South Dakota also suggested that they often nested along the edges of prairie dog colonies. Few previous studies have quantified the distance to an edge. Toombs (1997) found that nest burrows were closer than random burrows to colony edges in southeastern Colorado.

Teaschner (2005) found that nest burrows were significantly closer to colony edges than to colony centers. Restani et al. (2001) found no difference in the distance to colony edge between nest burrows and random burrows in southeastern Montana. In previous studies, the authors considered an edge to be the perimeter of a colony. Burrowing owls might nest near edges to have access to different types of prey (Griebel and Savidge 2003, Conrey 2010), so I also considered all edges, including the outer edge (i.e., perimeter) of a colony and any vegetational edges that occurred inside the colony boundaries. Nest burrows in occupied colonies were significantly farther from edges than random burrows in the same colonies. Therefore, edge avoidance might occur at a small scale once burrowing owls have selected a prairie dog colony for nesting, but the overall influence of edge on site selection is probably weak. Most nest and random burrows in this study were relatively close to a vegetational edge. Unusually wet conditions during the early summer in 2011 probably contributed to an abundance of edges because often the prairie dogs could not keep all vegetation clipped within the boundaries of a colony. Patches of tall vegetation and their associated edge were abundant within many colonies, so most potential nest locations were close to an edge. An effect of edges may vary among years as weather and other factors cause changes in vegetation structure and associated prey communities.

Summary

Burrowing owls were detected in all surveyed counties west of the Missouri River and in several counties bordering the east side of the Missouri River. Approximately half of all surveyed prairie dog colonies were occupied by burrowing owls, but owls were detected more frequently in some areas than in others.

Two separate analyses provided strong evidence that trees affect the distribution and nest site selection of breeding burrowing owls in western South Dakota. A given prairie dog colony was less likely to be occupied by burrowing owls when tree cover in the surrounding landscape was relatively high. Trees provide perch and nest sites for large raptors which may prey on burrowing owls. Other large-scale variables, such as grassland, cropland, and prairie dog colony coverage in the landscape and prairie dog colony area did not improve model fit and performance. Models containing combinations of colony and/or landscape variables could not adequately discriminate between prairie dog colonies that were occupied by burrowing owls and those that were not occupied by owls. Western South Dakota is dominated by grasslands. Most landscapes that contain prairie dog colonies probably contain enough grassland to meet the needs of burrowing owls, and most landscapes have relatively little tree cover that may not completely exclude burrowing owls from nesting.

Model performance was satisfactory for nest site selection models incorporating both landscape and local variables. Some local habitat variables were important predictors of nest burrows. Burrowing owls in western South Dakota selected nest sites with low visual obstruction (i.e., short, sparse vegetation). Within prairie dog colonies, burrowing owls also tended to select areas where the vegetation was composed of relatively high proportions of forbs and bare ground. Burrowing owls probably select this type of habitat to maximize hunting success near the nest burrow. Burrowing owls seem to select nesting areas that are actively modified by prairie dogs. Although burrowing owls do occasionally use inactive prairie dog colonies or burrows created by other semi-fossorial mammals, active prairie dog colonies in western South Dakota generally provide the habitat characteristics necessary to meet the life history requirements of burrowing owls. Within active colonies, nest and satellite burrows, perches, and diverse prey are usually available to meet the life history requirements of burrowing owls.

CHAPTER 5

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Burrowing owls were common in most areas of western South Dakota where suitable habitat existed. In some locations, they were actually quite abundant. James and Espie (1997) obtained estimates of the burrowing owl's population status in different states and provinces, and the population estimate provided for South Dakota was between 100 and 1,000 breeding pairs. Since prairie dog activity varies from year to year in South Dakota because of factors such as weather, poisoning, and plague outbreaks, I cannot be certain how many colonies were not surveyed during each year of this study. However, based on the most recent prairie dog acreage report (Kempema et al. 2009) and my observed rates of colony occupancy by burrowing owls in western South Dakota, I suspect that the population estimate in James and Espie (1997) may be somewhat conservative. I detected over 600 pairs (or assumed pairs) of burrowing owls in each year of this study, and in every county there were known prairie dog colonies that I was unable to survey. Under the assumption that approximately 50% of the remaining colonies contained burrowing owls, and taking into account occasional burrowing owls breeding outside of prairie dog colonies, I believe that South Dakota probably supports at least 1,000 breeding pairs of burrowing owls.

However, the long-term outlook for burrowing owls in the state is not necessarily as positive as the results might indicate. Most burrowing owls in South Dakota nest in prairie dog colonies, and maintaining the burrowing owl as a relatively common component of the state's avifauna almost certainly depends in part on the management of prairie dogs.

I believe that an important need for further monitoring and study is the interaction of burrowing owl populations with sylvatic plague outbreaks among prairie dogs. Although I did not directly study the effects of sylvatic plague on burrowing owls, it does seem to be a potential threat to the South Dakota population. Plague was first documented in South Dakota in Custer County in 2004 and has since spread into other counties (Kempema et al. 2009). Loss of prairie dogs to plague may be detrimental to burrowing owls for several reasons. Although burrow availability for owls will initially increase following a plague outbreak because the burrows will no longer be occupied by prairie dogs, within a few years, the burrows will begin to collapse without maintenance by prairie dogs (Butts and Lewis 1982, Desmond and Savidge 1999, Restani et al. 2001, Sidle et al. 2001).The longevity of burrows is influenced by several factors, including soil type and the abundance of large grazing mammals, which can trample burrows and cause them to collapse (Holmes et al. 2003). Since burrowing owls do not construct their own burrows, they will eventually lose potential nest sites unless prairie dogs recolonize the plague-affected area. Owls may also avoid plague-affected colonies because the colonies may no longer retain the altered vegetational structure produced by the grazing and clipping activities of prairie dogs.

Both anecdotal (personal observations and communications with biologists in western South Dakota) and published evidence (e.g., Restani et al. 2001, Sidle et al. 2001, Antolin et al. 2002) suggest that burrowing owls usually decline in plague-affected areas within a few years unless prairie dogs recolonize the areas. Augustine et al. (2008) studied the relationship between plague outbreaks and populations of mountain plovers (*Charadrius montanus*), another grassland bird species closely associated with prairie dog colonies. The authors found that the number of mountain plover nests in prairie dog colonies affected by plague declined at a significantly higher rate than the number of nests in colonies without plague, presumably because the vegetation rapidly recovered to a later seral stage. However, Augustine et al. (2008) also found that mountain plovers would nest in very recently established prairie dog colonies. I was not able to determine the age of most prairie dog colonies that I surveyed. However, I documented burrowing owls nesting in areas that had only been colonized within the previous 1-2 years according to aerial imagery and conversations with landowners. Allowing sufficient "source" populations of prairie dogs to persist across the landscape that can replenish plagued colonies and/or establish small new colonies should be an important management objective for burrowing owls. My observations suggest that migrating burrowing owls can locate potential nest sites as they become available.

The conserved prairie dog colonies may not necessarily need to be very large to benefit burrowing owls, as my results indicated that colony size is not useful as a predictor of nesting. The state of South Dakota has a plan in place to maintain at least a minimum acreage of prairie dog colonies, including several large colonies and complexes (Cooper and Gabriel 2005). The South Dakota plan was developed as part of a larger cooperative agreement with other states to prevent the need to list the black-tailed prairie dog as a threatened species under the Endangered Species Act (see Luce 2003 for details). The plan also considered maintenance of adequate prairie dog colony acreage for conservation of the endangered black-footed ferret. While ferrets are known to require large complexes of prairie dogs to maintain viable populations (Miller et al. 1996), this does not seem to be true for burrowing owls. I suggest that more attention should be given to conserving small prairie dog colonies, even those that are quite isolated from others. Burrowing owls in South Dakota often nest in small- to medium-sized colonies, and I have observed high reproductive success in many of these smaller colonies. Bly (2008) suggested that maintaining many small- and medium-sized colonies on the landscape might be the best strategy to maximize burrowing owl populations since population densities are high in these colonies.

Prairie dogs are typically controlled on rangeland, and increasing the number or size of prairie dog colonies is very unlikely because of concerns of landowners and fragmentation of federal lands, where prairie dogs have at least some degree of protection (Sidle et al. 2001, Restani et al. 2008). However, even small colonies provide important habitat for many rare and imperiled vertebrates in the Great Plains (Lomolino and Smith 2003). Much success can probably be achieved in conserving burrowing owls by finding ways to maintain the many small prairie dog colonies distributed across western South Dakota.

Conserving small prairie dog colonies offers several potential benefits from the standpoint of maintaining the burrowing owl as a common bird that does not require state or federal listing as a threatened or endangered species. First of all, maintaining small prairie dog colonies across the landscape should be easier to promote to private landowners, since the economic losses associated with small colonies are minimal (Derner et al. 2006), particularly when these colonies are embedded in large areas of grass (Vermeire et al. 2004). Although prairie dogs can reduce livestock carrying capacity and livestock do sometimes experience lower weight gain in pastures occupied by prairie dogs (O'Meilia et al. 1982, Vermeire et al. 2004, Derner et al. 2006), in some situations, the costs of prairie dog control may not be offset by the amount of forage gained (Collins et al. 1984, Uresk 1985). The economic effects of prairie dogs on ranching operations are site-dependent, and control may be necessary in some situations to prevent colonies from increasing in size or density to unsustainable levels (Hygnstrom and Virchow 1994, Vermeire et al. 2004). However, improving range management practices (e.g., adjusting stocking rates to prevent overgrazing and preventing soil disturbance by livestock and human activities) could help to prevent prairie dog colonies from expanding or becoming established in areas where they might cause unacceptable economic harm (Snell and Hlavachick 1980, Knowles 1986*b*, Hygnstrom and Virchow 1994, Truett 2003). These strategies may be particularly effective in the mixed-grass prairie region (eastern part of my study area), as evidence from multiple studies has demonstrated that the taller, faster-growing vegetation of this region generally prevents rapid expansion of prairie dogs and allows size to be controlled through grazing management (Truett 2003).

Small prairie dog colonies offer another hypothetical benefit to burrowing owls. Small colonies tend to receive less pressure than large colonies from recreational prairie dog hunters (Murphy et al. 2001, personal observation). My conversations with prairie dog hunters revealed that many prefer to hunt large complexes simply because they present more shot opportunities, especially at long ranges. Prairie dog shooting is probably at best neutral to burrowing owls, and at its worst it causes direct mortality, so colonies that do not experience heavy shooting pressure could be important refuges for burrowing owls.

Many of the small prairie dog colonies that I surveyed, especially near the eastern edge of the study area, tended to be relatively isolated from others. Colony isolation has implications for the persistence of prairie dogs and therefore also for the suitability of burrowing owl habitat. Isolated colonies are less likely to receive dispersing prairie dogs or other carriers of fleas such as coyotes (*Canis latrans*), which may impact plague dynamics. Wide-traveling mammals could potentially transmit infected fleas to plague-free colonies and cause new outbreaks (Gage et al. 1994, Antolin et al. 2002, Salkeld and Stapp 2006, Slobodchikoff et al. 2009). However, dispersing prairie dogs may also be important for recolonizing areas where prairie dog populations have been reduced or extirpated by plague. Prairie dogs are known to disperse from the colonies where they were born (Knowles 1985, Garrett and Franklin 1988, Hoogland 2006, Sflobodchikoff et al. 2009). Dispersing prairie dogs in Wind Cave National Park traveled a mean straight-line distance of 2.4±1.7 km; actual dispersal distances were longer (Garrett and Franklin 1988). Knowles (1985) recorded dispersal distances of up to approximately 10 km in Montana. If a colony is lost to sylvatic plague, it can be recolonized if unaffected colonies are located nearby. Prairie dog populations do recover from die-offs; for example, Knowles (1986*a*) found that prairie dog colonies that were poisoned with zinc phosphide could recover to pretreatment densities in as little as a year (but usually 3-5 years) of treatment because of immigration and possible changes in demographic rates. While some prairie dogs in a colony might survive a plague outbreak and contribute to repopulation (Pauli et al. 2006), immigration from other colonies is probably an important mechanism in recovery (Antolin et al. 2002).

Lomolino et al. (2003) studied the persistence of prairie dog colonies in Oklahoma and found evidence that isolated colonies may be more likely to persist when sylvatic plague outbreaks begin to occur. Likewise, Collinge et al. (2005) found that plague-negative colonies in north-central Colorado and northeastern Montana were more isolated than plague-positive colonies. Stapp et al. (2004) found no relationship between isolation and colony persistence in northeastern Colorado, but colonies in their study area were generally well within the dispersal distances of prairie dogs. If isolated colonies are in fact more likely to persist, many of the relatively small and isolated colonies, which are often found on private property, may serve as important refuges of suitable burrowing owl habitat as plague continues to spread across South Dakota. Plague outbreaks are usually spatially and temporally cyclical (Cully and Williams 2001, Antolin et al. 2002, Stapp et al. 2004, Hoogland 2006, Pauli et al. 2006), so conserving prairie dog colonies in locations across South Dakota could prove to be important for burrowing owls.

Plague might also interact with anthropogenic factors to cause loss of prairie dog colonies. Areas impacted by plague are more susceptible to local extirpations of prairie dogs through poisoning programs. As a case in point, in 2011, I spoke with several ranchers and prairie dog hunters who said that some landowners were poisoning prairie dogs as they recolonized areas affected by plague. Before sylvatic plague had spread to these areas, landowners probably did not find complete control of prairie dogs to be economically feasible, so some colonies were allowed to persist. Following plague outbreaks that killed most of the prairie dogs, complete control was more easily achieved. I do not know if the practice of preventing the reestablishment of prairie dogs following plague outbreaks was restricted to a few areas or widespread, but it would certainly contribute to more rapid deterioration of burrowing owl habitat.

My results also suggest that management that favors burrowing owls is likely to have lasting effects. If landowners or agencies determine that controlling some prairie dogs is necessary, I suggest considering the use of colonies by burrowing owls when deciding which areas to poison. If burrowing owls are seen using a particular prairie dog colony, the likelihood that they will continue to use it is probably fairly high, while unused colonies are not likely to be used in the following year. Assuming that limited funds are available for prairie dog control, poisoning colonies that do not have a history of nesting burrowing owls should minimize the impact on the owl population. Plumpton and Lutz (1993*b*) suggested protecting prairie dog colonies traditionally used by burrowing owls at the Rocky Mountain Arsenal in Colorado, as repeated use of these sites suggested that they represented the best habitat in the area.

Maintaining ranching as the primary land use in western South Dakota is also an important objective for conservation of burrowing owls and other grassland birds. Grasslands provide most nest sites for burrowing owls, while croplands provide essentially no potential for nesting. Prairie dogs and other burrowing mammals are rare in regions of intensive cultivation, but they tend to persist in regions dominated by rangeland, even when efforts are made to control them.

The results of my study provide evidence that burrowing owls may not necessarily be limited by the lack of prairie dog colonies per se, but instead by a lack of prairie dog colonies embedded in suitable landscapes. A very important factor was the amount of tree cover. Burrowing owls are likely to benefit from strategies to manage the invasion of trees into existing grasslands. Planting trees in open grasslands should be discouraged, and efforts to remove trees encroaching on rangeland when practicable could benefit burrowing owls. The open, grass-dominated landscapes also need to be protected from conversion to cropland. Unfortunately, the presence of trees in western South Dakota landscapes could be closely linked to the likelihood of grasslands being converted to crop fields. In western South Dakota, trees are most commonly found in areas of rugged topography that are unsuitable for farming. The most rugged regions of western South Dakota (e.g., the foothills of the Black Hills) will probably remain as rangeland for the foreseeable future, but the presence of forested areas makes these regions less attractive to burrowing owls, even when prairie dog colonies are present. Much of the prime burrowing owl habitat is located in regions that are at high risk for land conversion. For example, in some of the central counties (e.g., Dewey, Jones, Stanley), a high proportion of the remaining prairie dog colonies contain burrowing owls, but grasslands are being lost to cultivation at a relatively rapid rate. Protecting the remaining open grasslands through public purchase, perpetual easements, or other programs should be a high priority for burrowing owl conservation.

Information acquired about the burrowing owl's current range and the habitat features it requires can aid burrowing owl conservation efforts in South Dakota. However, some questions do remain unanswered that may be needed to prevent further declines in the species' populations in South Dakota and elsewhere throughout its range. First of all, I was not able to examine factors that impact reproductive success for burrowing owls in South Dakota. A more detailed burrowing owl nesting study could provide much valuable information to aid conservation. Habitat quality cannot be fully evaluated based on presence or population density but should also include metrics of survival and reproduction (Van Horne 1983). My observations during the 2010 and 2011 breeding seasons suggested that burrowing owls in South Dakota were fledging young at rates comparable with those found in the literature, but the literature is lacking in studies of factors that limit reproductive success for burrowing owls. Also, very few studies have quantified sources of mortality for burrowing owl chicks. Better information about the causes of burrowing owl mortality can aid in the identification of possible population sinks.

I believe that prairie dog hunters are stakeholders in conservation of both prairie dogs and burrowing owls. Hunters want prairie dog colonies to persist, and sometimes they are willing to pay for the opportunity to hunt; therefore, hunters can provide incentives for landowners to tolerate the presence of some prairie dogs (Hoogland 2006). However, whenever hunters are present at a prairie dog colony, burrowing owls could be negatively affected. Legislation in 2011 removed the former 1 March – 15 June closed season on prairie dogs on public lands (Mercer 2011). Because some public lands contain relatively high populations of burrowing owls, there could be impacts on owls during the early breeding season. Further studies would help to determine if shooting pressure affects colony use and/or reproductive success. Any potential negative impacts could be minimized by educating hunters on burrowing owl identification and possibly increasing enforcement of the laws that protect burrowing owls (e.g., Migratory Bird Treaty Act).

A final aspect of burrowing owl conservation that is in great need of study is the wintering ecology of the species. Few papers have been published about where burrowing owls that breed in the northern Great Plains spend the winter and what affects their survival during the migration and wintering periods. Banding efforts have turned up little information, possibly because some North American burrowing owls may winter in Central America, where band recoveries are unlikely to be reported (James and Ethier 1989). Attaching radios, GPS units, or light-level geolocators to burrowing owls nesting in South Dakota and/or nearby states could help identify conservation issues that had not been previously considered. A secondary benefit would be information about the fidelity of individual burrowing owls to specific prairie dog colonies.

Western South Dakota currently supports a seemingly healthy burrowing owl population, but the population is not completely secure due to changing conditions across the landscape that can negatively impact the habitat available to owls. Many of these changes are directly related to human activities (e.g., conversion of grassland to cropland, prairie dog poisoning) while others are only indirectly related to human activities (e.g sylvatic plague outbreaks), but most can possibly be managed to minimize the negative impacts on burrowing owls.

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