INFLUENCE OF LOCAL AND LANDSCAPE CHARACTERISTICS OF PRAIRIE DOG COLONIES ON BURROWING OWL NEST ECOLOGY IN SOUTH DAKOTA

by

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ABSTRACT

In the Great Plains, sylvatic plague (*Yersinia pestis*), poisoning, and habitat conversion continue to reduce and fragment black-tailed prairie dog (*Cynomys ludovicianus*) habitat in which burrowing owls (*Athene cunicularia*) seek shelter and nest sites. Consequently, burrowing owls are experiencing population declines at the periphery of their range. The objective of this research was to evaluate habitat factors affecting a population of burrowing owls at the eastern extent of their range. I modeled hypothesized relationships between nest density (Chapter 2) and colony productivity (Chapter 3) and prairie dog habitat characteristics at two scales on the Bad River Ranches, South Dakota. Colony size, prairie dog and total burrow density, mean nearest neighbor and mean nest-to-colony edge distances, cover of warm-season grasses, and soil texture were variables measured at the colony level. Landscape level variables included the degree of colony isolation and the topographic location of colonies. In Chapter 4, I evaluated the spatial distribution of nests within colonies. Twenty-six prairie dog colonies were surveyed for burrowing owl nests during the 2005 (n =10) and 2006 (n = 16) breeding seasons. I evaluated competing models of nest density using a likelihood cross-validation approach. The model selection results in Chapter 2 suggested the top *a priori* predictor of nest density was colony size. Nest density was greatest on small colonies (<20 ha) and lowest on large colonies (>40 ha); in contrast, owl numbers were higher on large colonies. Exploratory analysis identified the interaction between cover of bare ground and colony habitat as the best approximating model of nest density. In Chapter 3, competing models of colony productivity were assessed. Although an additive model containing the degree of isolation, habitat, and colony size had a positive effect on colony productivity, exploratory analysis suggested colony size and the degree of isolation had the strongest influence. In Chapter 4, results showed that owls displayed a strong preference for nesting near colony perimeters, but this did not translate to higher productivity. The associations I observed lend support for the value of maintaining prairie dog colonies to ensure the persistence of burrowing owl populations in the Great Plains ecosystem.

CHAPTER 1

THESIS OVERVIEW

Conservation efforts for imperiled species may be made more effective by focusing on species interactions (Soulé et al. 2003). The burrowing owl (*Athene cunicularia*) is a good example. Its populations in the Great Plains respond so strongly to the presence and characteristics of black-tailed prairie dog (*Cynomys ludovicianus*; hereafter "prairie dog") colonies (Butts and Lewis 1982, Desmond et al. 2000) that by maintaining populations of prairie dogs, burrowing owls may be restored with less effort.

Prairie dogs and their colonies influence myriad species in the Great Plains ecosystem by altering soil physical and chemical properties; vegetation composition, biomass, and productivity; and availability of prey for carnivores and raptors (Koford 1958, Whicker and Detling 1988a, Jones et al. 1994, Ceballos et al. 1999, Lomolino and Smith 2003). Prairie dogs have been shown to benefit species such as the black-footed ferret (*Mustela nigripes*), swift fox (*Vulpes velox*), and ferruginous hawk (*Buteo regalis*). Thus by most criteria prairie dogs fit definitions of ecological "keystone" (Kotliar et al. 1999, Miller et al. 2000) or "interactive foundation" species (Soulé et al. 2003).

The Endangered Species Act, as historically applied, generally fails to take advantage of inter-species dependencies (i.e., conserving imperiled species by protecting the species that support them). During recent years, however, several state agencies have taken steps toward more integrated ecological approaches. The South Dakota Wildlife Action Plan, for instance, aims to protect species of conservation concern by identifying and protecting the critical habitat types in which species at risk reside (SDGFP 2005). Under this plan, conservation of prairie dogs could subsequently protect local populations of burrowing owls (Klute et al. 2003).

As with many grassland species, burrowing owls primarily seek shelter and nest sites in burrows established by prairie dogs (Haug et al. 1993, Martell et al. 1993, Deschant et al. 2001, McDonald et al. 2004). Due to their close alliance, the status of burrowing owls is subsequently tied to that of prairie dogs (McDonald et al. 2004). Nationally, the U.S. Fish and Wildlife Service list burrowing owls as a Bird of Conservation Concern (USFWS 2002) and in South Dakota they are considered a Species of Concern (McDonald et al. 2004, SDGFP 2005). Prairie dog control efforts, habitat loss, and disease (e.g., sylvatic plague, *Yersinia pestis*) continue to eliminate, fragment, and isolate colonies and this, in part, has led to declines in local populations of burrowing owls (Klute et al. 2003).

Numerous investigations of burrowing owl ecology have evaluated hypothesized mechanisms driving nest density and productivity within prairie dog colonies (Desmond 1991, Desmond and Savidge 1996, Ekstein 1999, Griebel 2000, Restani et al. 2001, Berardelli 2003, Lantz 2005). Yet due to design constraints, differences in variables measured, and heterogeneity among study colonies, few conclusive mechanisms have been supported. As burrowing owl habitat continues to diminish in the Great Plains ecosystem, it is increasingly important to understand the factors contributing to burrowing owl nest placement, density, and reproductive survival. To gain insights into burrowing owl ecology, I identified and measured potentially important environmental variables influencing populations of burrowing owls at the eastern extent of their range in South Dakota.

In chapter two my primary goal was to evaluate hypothesized associations between burrowing owl nest density and multi-scale (i.e., colony and landscape) habitat characteristics within and among prairie dog colonies. The focus of chapter three was to investigate hypothesized associations between burrowing owl colony productivity within and among prairie dog colonies at the colony and landscape level scales. Chapter four was a preliminary evaluation of the spatial organization of burrowing owls and their nests within colonies.

Given the sensitive status of burrowing owls in North America, additional study regarding the mechanisms driving burrowing owl nest density on prairie dog colonies is warranted. Habitat loss, eradication campaigns, and sylvatic plague (*Yersinia pestis*) continue to fragment and isolate prairie dog colonies, which can have detrimental impacts on burrowing owl populations. A better understanding of the ecological dynamics of prairie dog colonies of varying size on burrowing owls may assist grassland managers to effectively manage and mitigate further losses of the species. Such research may also contribute to a better understanding of burrowing owl nesting ecology and aid in the development and implementation of comprehensive management and recovery plans.

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CHAPTER 2

INFLUENCE OF LOCAL AND LANDSCAPE HABITAT CHARACTERISTICS OF BLACK-TAILED PRAIRIE DOG COLONIES ON BURROWING OWL NEST DENSITY IN SOUTH DAKOTA

Introduction

Accompanying the significant range-wide decline in abundance of black-tailed prairie dogs (*Cynomys ludovicianus*; hereafter "prairie dogs") and the average size of their colonies (Miller et al. 1994, Lomolino and Smith 2003) are population declines in associated vertebrate species (Oldemeyer et al. 1993, Soulé et al. 2003), including the western burrowing owl (*Athene cunicularia hypugaea*, hereafter "burrowing owl"). Regarded as a grassland specialist, the burrowing owl is sympatric with prairie dog colonies throughout the Great Plains ecosystem (Butts 1973, Ross 1974). Prairie dog colonies provide habitat for burrowing owl nests, roosts, and belowground refuge from predators and inclement weather (O'Meila et al. 1982, Desmond 1991, Desmond and Savidge 1996, Desmond et al. 2000).

Encompassing a majority of the prairie dog's range from southern Canada to Mexico, burrowing owls were once distributed across much of western North America (Johnsgard 1988, Sibley 2000; Figure 2.1). Habitat fragmentation, environmental contaminants, and loss of prairie dog colonies due to eradication campaigns and sylvatic plague (*Yersinia pestis*) are contributing to local burrowing owl population declines and range contractions at the perimeter of the species' distribution (Klute et al. 2003). As a result, the U.S. Fish and Wildlife Service (USFWS) listed burrowing owls as a "National

Bird of Conservation Concern" (Sheffield 1997, USFWS 2002, Klute et al. 2003) and in South Dakota they are considered a Species of Concern (McDonald et al. 2004, SDGFP 2005).

Figure 2.1. Current and historical ranges of the western burrowing owl in North America. Reprinted from Wellicome and Holroyd (2001).

Maintaining large, well-connected prairie dog colonies may be important to the long-term persistence of burrowing owls (McDonald et al. 2004). Relative to the historic distribution and size of prairie dog colonies, however, contemporary colonies are mostly isolated remnants of small size (≤40 ha; Fagerstone 1981, Daley 1992, Lomolino and

Smith 2003). Because restoration of prairie dog colonies to original distributions and extents is unlikely, there is a need to better understand the impacts of smaller colonies on breeding burrowing owls. Individually or combined, ecological characteristics of prairie dog colonies strongly influence burrowing owl distribution, nest density, and productivity (Butts 1973, Ross 1974, Desmond and Savidge 1996, Desmond et al. 2000, Griebel 2000). Given the sensitive status of burrowing owls in North America, research evaluating burrowing owl nesting ecology is warranted and may aid in the development and implementation of comprehensive management plans.

The goal of my research was to evaluate associations between burrowing owl nest density (nests/hectare) and prairie dog habitat characteristics at the colony and landscape scales in South Dakota. I hypothesized that five within-colony habitat factors would influence burrowing owl nest density, including: (1) prairie dog colony size (hectares), (2) prairie dog density (individuals/hectare), (3) total (active and inactive) burrow density, (4) cover of warm-season grasses (percent), and (5) soil texture. At the landscape scale, the degree of colony isolation and the topographic location of colonies may be important to breeding burrowing owls.

Colony Scale Habitat Characteristics

Studies in Colorado, Nebraska, and South Dakota demonstrated that burrowing owl density was inversely related to prairie dog colony size (Hughes 1993, Desmond et al. 1995, Desmond and Savidge 1996, Griebel 2000, Knowles 2001, Livieri 2002). These findings are in contrast to the resource concentration hypothesis (Root 1973), which predicts animal population density is positively related to patch size. One plausible mechanism to explain this discrepancy is territoriality in burrowing owls. During the breeding season, burrowing owls actively defend nest territories ranging in size from 4.0 to 6.4 hectares (ha) (e.g., in North Dakota and Minnesota) from conspecifics (Grant 1965, Butts 1973, Martin 1973, Ross 1974, Moulton et al. 2004). Therefore, nest densities are often higher in small prairie dog colonies because all available territories are occupied; in large colonies where there is more available habitat nest densities are often lower because burrowing owls do not occupy all potential territories (Hughes 1993, Desmond et al. 1995, Desmond and Savidge 1996, Griebel 2000, Livieri 2002). Burrowing owls may prefer large colonies because they provide greater proportions of suitable nesting space (Desmond 1991, Ekstein 1999, Griebel 2000) and enable them to nest in groups, which collectively increases their vigilance of predators (Desmond et al. 1995). Additionally, predation risk to nesting owls may be reduced in large colonies ostensibly because predators are more easily detected and have a greater area to search (Clayton and Schmutz 1999).

Burrowing owls nesting in colonies with high densities of prairie dogs appear to benefit from the prairie dog sentinel system (Butts and Lewis 1982, MacCracken et al. 1985a, Whicker and Detling 1988, Plumpton and Lutz 1993, Toombs 1997, Weltzin et al. 1997, Ekstein 1999, Desmond et al. 2000, Griebel 2000, Restani et al. 2001, Lantz 2005). Prairie dogs selectively graze and clip tall vegetation, maintain burrow structure, and elicit alarm calls when predators approach. These activities provide burrowing owls with favorable nest sites, increased diversity of prey species, and also enhance predator detection and avoidance. Additionally, high densities of prairie dogs in an area may reduce the probability burrowing owls will be detected by their predators (e.g., the "dilution effect"; Wilkinson and English-Loeb 1982, Desmond et al. 2000).

The density and availability of burrows is important for the long-term persistence of burrowing owl populations (Zarn 1974, Desmond et al. 1995). Reproductive female owls depend on prairie dog burrows during the incubation and early brood rearing period, whereas male owls use satellite (or non-nest) burrows for resting, guard posts, and escape cover (Butts and Lewis 1982, Clayton and Schmutz 1999). Adults place young in several satellite burrows to reduce the risk of losing the entire brood to predation (Desmond and Savidge 1999). Once they emerge from the natal nest, fledglings use adjacent burrows to escape a crowded environment at the nest burrow, avoid nest parasites, seek refuge from the elements, catch or cache prey, and for protection during their dispersal period (Butts 1973, Butts and Lewis 1982, Haug 1985, Desmond 1991, Plumpton and Lutz 1993, King and Belthoff 2001).

In addition to the presence of burrows, short vegetation is an important habitat requirement of burrowing owls (McDonald et al. 2004). The patches of short-statured vegetation created by prairie dogs can influence nest placement and survival by providing good visibility to procure prey and avert predation (Green and Anthony 1989, Haug et al. 1993, Winter et al. 2005, Detling 2006). With repeated prairie dog grazing and clipping, many of the tall grass species within colonies are replaced by perennial short-grasses. Two warm-season grasses, buffalograss (*Buchloe dactyloides*) and blue grama grass (*Bouteloua gracilis*), consequently become abundant in and often dominate Great Plains prairie dog colonies (Bonham and Lerwick, 1976; Knowles, 1982; Archer et al., 1987). Because of their short growth forms, warm-season grasses within colonies may benefit burrowing owls. In South Dakota, MacCracken et al. (1985b) found greater percent canopy cover of a warm-season grass (i.e., buffalograss; *Buchloe dactyloides*) at occupied nest burrows versus adjacent, unoccupied burrows. As such, I hypothesized that burrowing owl nest density is positively related to the proportion of warm-season grasses within study colonies.

The distribution of prairie dog burrows and their longevity is primarily a function of soil textures within colonies. Consequently, soil texture may indirectly affect burrowing owl nest density (Toombs 1997). The well drained sandy-loam to loamy-clay soils in which prairie dogs generally construct their burrows (Koford 1958, Reading and Matchett 1997) also make suitable nest sites. Burrowing owl nests in South Dakota and Wyoming consisted of silty clay loam soils (Thompson 1984, MacCracken et al. 1985b), and nest burrows consisting of sandy loam soils had the highest rates of reuse in subsequent years (Griebel 2000, Holmes et al. 2003).

Landscape Scale Habitat Characteristics

The size and spatial distribution of colonies across a landscape can influence the persistence of co-occurring species like black-footed ferrets (*Mustela nigripes*) and burrowing owls. For example, black-footed ferrets depend on prairie dogs for survival (Minta and Clark 1989, Biggins et al. 1993). Ekstein (1999) suggested that landscape scale factors also influence the presence and survival of burrowing owls. She evaluated landscape variables (e.g., nearest neighboring colony and area of the largest colony) within a 3, 5, and 10 km radius of study colonies to estimate the distance(s) nest site selection occurred based on the presence or absence of burrowing owls. Colony size and the size of the largest colony within 10 km was positively correlated with the presence of nesting burrowing owls and similarly, the size of the largest colony within 3 km correlated positively with nest survival. Therefore, the presence of relatively large (i.e., >120 ha) colonies within a radius of 10 km may be related to occupancy by burrowing owls, and particularly, dispersing owls (Ekstein 1999).

Multiple prairie dog colonies aggregated in a complex (Biggins et al. 1993) might provide more nest, foraging, and dispersal habitat for burrowing owls than small, isolated colonies. Isolated populations have an increased risk of extinction from disease, inbreeding, and catastrophic events (Oldemeyer et al. 1993), but they may also serve as critical genetic refuges in the face of such events. This dichotomy complicates the design of a conservation network given the implications of many small versus a few large reserves in the context of disease pathways and isolation. Some researchers have recommended that few large reserves maximize species richness (Diamond 1975, Wilson and Willis 1975); others suggested that many small reserves might prevent species extinction or disease transmission (Simberloff and Abele 1976, Quinn and Hastings 1987). To limit further declines in burrowing owl populations, complexes containing both large and small colonies may be most desirable (Ekstein 1999, McNicoll 2005).

Finally, burrowing owl nest density in South Dakota may be affected by the habitat location of prairie dog colonies. The topography of my study area consisted of two physical settings that may have a strong influence on burrowing owl nest density: upland plateaus and lowland floodplains. The upland habitats consist of narrow strips of undulating plateaus divided by numerous intermittent creeks that drain southeast into the Bad River. The lowland habitats are relatively level, lower elevation floodplains. Study colonies located in lowland areas were often near watershed corridors lined by cottonwood trees (*Populus angustifolia*) that might increase exposure of burrowing owls to tree-dwelling predators (e.g., Great Horned Owls, *Bubu virginianus*) and flood events. Lowland colonies usually consisted of fine-textured soils susceptible to erosion, livestock trampling, and readily colonized by invasive herbaceous species. Upland colonies were located farther from river corridors, treeless, and had greater proportions of native vegetative species. Prairie dog colonies located on upland plateaus showed features strongly associated with burrowing owl nest habitat, including flat to gently sloping terrain, well-drained areas of short vegetation (i.e., <10 cm high) and bare ground (Butts 1973, MacCracken et al. 1985b, Green and Anthony 1989, Pezzolesi 1994, Deschant et al. 2001).

Methods

Study Area

The study population included prairie dog colonies located within the Bad River Ranches (hereafter "ranch"), which comprise about 570 km^2 in Stanley and Jones counties near Fort Pierre (44°21′N, 100°22′W), South Dakota (Figure 2.2). The ranch lies within the mixed-grass system of the Northern Great Plains (Kuchler 1975). The topography was composed of mixed-grass, flat to rolling uplands cut by the Bad River and intermittent drainages; elevations varied from about 457 m above sea level in lowland bottoms to 610 m on upland plateaus. Average annual precipitation was 48.29 cm, with 65% falling during the April – August breeding season. Mean monthly temperatures ranged from –7.47°C in January to 24°C in July (http://climate.sdstate.edu).

Soils were primarily clays derived from Creataceous Pierre Shale (Johnson et al. 1995). Kuchler (1975) characterized the area as a wheatgrass-needlegrass (*Stipa viridula*) community; buffalograss and blue grama grass also were widespread (K. Bly and J. Truett, unpublished data).

The ranch, owned by R. E. Turner, is managed for the sustainable production of bison and conservation of native species. At the time of this study the ranch supported approximately 5,000 bison divided among several herds that grazed pastures north and south of the Bad River on a rotating basis. During 2000 – 2004 the Turner Endangered Species Fund (a private, non-profit charity dedicated to conserving biodiversity on Turner lands) restored prairie dogs to selected sites on the ranch, largely by establishing new colonies and managing habitat to encourage colony growth. Including the reintroduced colonies, the ranch had 82 colonies occupying 765 ha in 2005, which grew to 87 colonies occupying 813 ha the following year.

I conducted this research from May – August 2005 and May – September 2006. Prairie dog study colonies were randomly selected from three size categories: small (0-20 ha), medium (20-40 ha), and large (>40 ha), and from two landscape types (i.e., colonies grouped in a complex and isolated) and habitats (i.e., lowland and upland colonies). In 2005, I surveyed 10 of the 82 colonies (pre-existing and reintroduced) ranging in size from 2.55 to 129.26 ha. In 2006, I surveyed 16 (the same 10 colonies plus an additional six) of the 87 ranch colonies ranging in size from 2.75 to 145.32 ha. All prairie dog colonies surveyed were active; no prairie dog poisoning or shooting occurred on study colonies for six years prior to and during the research period (K. Bly and J. Truett, unpublished data).

Nest Data Collection

Each study colony was surveyed for burrowing owl nests during May and June of 2005 and 2006. To locate nests, I visually inspected each prairie dog burrow by walking parallel line transects 10 – 25 m apart. To prevent resampling nests and burrows, I marked each burrow with flour or white chalk. Transect length depended on the width of individual colonies. I identified nests by the physical presence of burrowing owls, strands of shredded material (dung, yucca), feathers, prey remains, regurgitated castings, and whitewash at the entrance of nest burrow (Desmond 1991). I made repeated observations of each nest to confirm the presence of fledglings. Nests initiated after June 30th of each year were not included in my analyses. It was possible that on large colonies a few nests were not located. Although I did not obtain a nest detection probability, I believe detectability was similar among nests because of the intensive search effort conducted for each colony.

I marked all burrowing owl nest locations with two methods. First, I placed a round aluminum identification tag secured with a steel ground staple (www.forestry-suppliers.com) 1 m north of each nest burrow. Next, I obtained universal transverse mercator coordinates with a Garmin 12CX Global Positioning System (GPS) unit. The GPS waypoints were then downloaded into the GIS program ArcView 3.2a (ESRI 2000). To determine burrowing owl nest densities for each study colony, I divided the estimated number of nests by the size of the prairie dog colony in hectares (see “Colony Size” below).

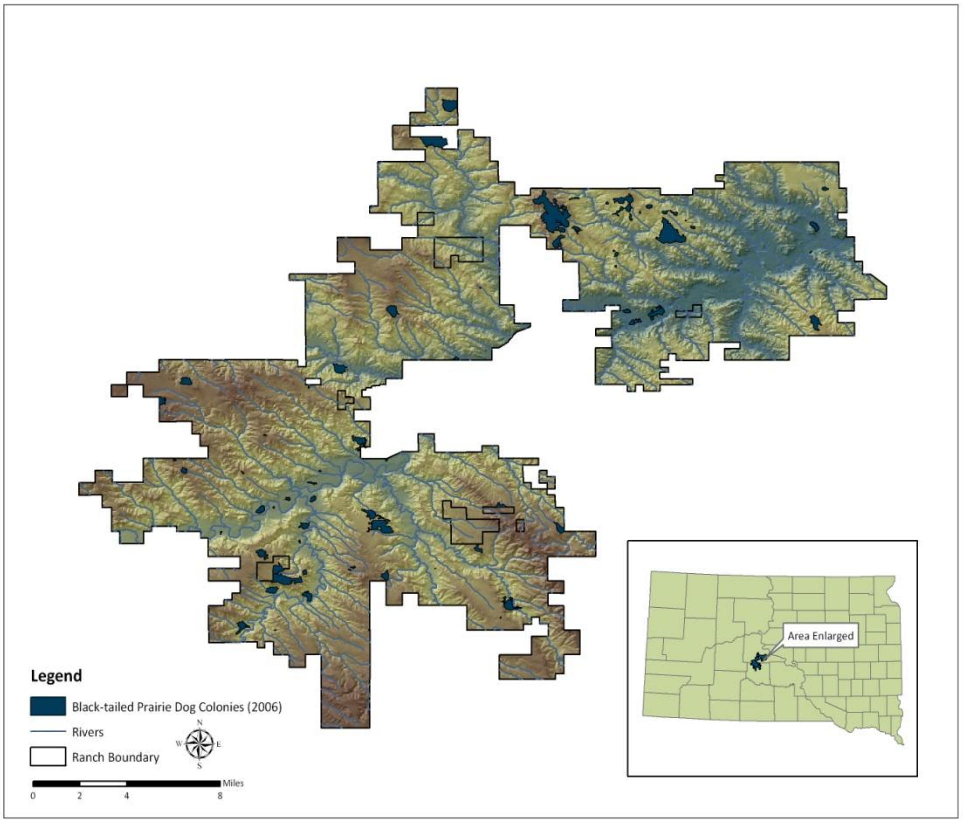

Figure 2.2. Location of prairie dog study colonies on the Bad River Ranches, South Dakota, 2005-2006. Dark blue polygons represent black-tailed prairie dog colonies.

Habitat Covariates

Colony Size. By walking or driving, I estimated the area occupied by a colony of prairie dogs by mapping the outermost, active burrow entrances (Hoogland 1995) with a Garmin 12CX GPS unit in August of each year. Active perimeter burrow entrances were marked as waypoints and then downloaded as shape files for analysis of area in hectares in the GIS program ArcView 3.2a (ESRI 2000).

Prairie Dog and Burrow Density. I estimated prairie dog density on study colonies during June – July of 2005 and 2006. These estimates were derived from counting a proportion (in 2005) or the total number (in 2006) of active and inactive burrows in each study colony. In 2005, I employed a modified version of the burrow sampling protocol described in Biggins et al. (1993). Because this methodology was designed for large prairie dog complexes, I modified the target proportion of each colony surveyed according to its size: 50% for colonies <10 ha, 20% for colonies 10-20 ha, 10% for colonies 20-40 ha, and 5% for colonies >40 ha. In 2006, I conducted comprehensive counts of active and inactive burrows in study colonies by walking parallel line transects 5 m apart. With both methods, I assumed the total number of burrows counted to be a minimum and a burrow detection rate of approximately 0.90 (Matchett 1994).

At each burrow entrance, I counted and classified burrows as active or inactive then marked each burrow with flour to prevent resampling. Burrows were classified as active based on the presence of a prairie dog, fresh prairie dog scat, or recent evidence of digging (Biggins et al. 1993, Dullum 2001), and inactive if it met two or more of the following criteria as stated in Desmond and Savidge (1996): (1) presence of unclipped live vegetation on the mound or in the burrow entrance, (2) spider webs over or in the burrow entrance, and (3) the absence of fresh prairie dog scat. I kept separate counts of active and inactive burrows on mechanical clicker counters.

Based on my counts of active burrows, I calculated prairie dog densities following the formula outlined in Biggins et al. (1993): *prairie dog density = (0.179 x active burrow density) / 0.566*. In this formula, 0.179 is the relation between counts of active burrows and prairie dogs and 0.566 is an observability index of black-tailed prairie dogs developed by D. E. Biggins and L. R. Hanebury (U. S. Fish and Wildlife Service, unpublished data).

<u>Vegetation Structure</u>. I measured total herbaceous vegetation cover, composition by category, and average height (per quadrat) in randomly located Daubenmire frames (i.e., 20 cm x 50 cm; Daubenmire 1959) along parallel line transects on colonies during July of each year. Vegetative categories included percent cover of warm-season grass, cool-season grass, forbs, litter, and bare ground. The total number of quadrats per colony increased with colony size: colonies <20 ha = 30 quadrats, 20 – 40 ha = 40 quadrats, and >40 ha = 50 quadrats. To capture the maximum amount of variation along vegetative gradients, I located transects perpendicular to topographic contours (Martin et al. 1997). I assigned the number of transects per colony based on colony size: 0 – 8 ha = 2 transects; 8 – 16 ha = 3 transects; 16 – 24 ha = 4 transects; 24 – 32 ha = 5 transects; 32 – 40 ha = 6 transects; and >40 ha = 10 transects. Finally, I obtained weighted averages of cover for each vegetative category per study colony.

Soil Texture. Soil texture data were acquired from the digitized STATSGO soils database (http://www.ncgc.nrcs.usda.gov; Stanley and Jones Counties). I imported soil layers into ArcView 3.2a (ESRI 2000), overlaid the burrowing owl nest locations, and systematically determined the soil texture underlying each burrowing nest. Since many study colonies consisted of more than one soil texture, soil textures were assigned rankings (Table 2.1) based on standard site evaluation criteria for farmsteads (http://www.uwex.edu/farmasyst), and averaged texture rankings on the colony level (i.e., one ranking per study colony).

Colony Isolation and Habitat. Using the colony mapping data, I placed study colonies into two spatial classifications: (1) *degree of isolation*: the distance in kilometers to a single colony or colony complex and (2) *habitat*: upland or lowland. A colony was considered part of a complex if it was within 2.4 km of two or more colonies; this distance encompassed both the average home-range size of burrowing owls (2.41 km^2; Haug and Oliphant 1990) and average dispersal distance of prairie dogs (2.4 km; Garrett and Franklin 1988). I considered colonies >2.4 km from other colonies to be isolated on the landscape. I classified colonies as upland or lowland based on their topographic location in relation to the Bad River, the predominant river bisecting the ranch. Lowland colonies were within or just above the Bad River floodplain; upland colonies were located on plateaus >500 m above the floodplain.

Table 2.1. Soil textures and associated rankings used to predict burrowing owl nest locations within black-tailed prairie dog colonies on the Bad River Ranches, South Dakota, 2005-2006.

Soil Rating	Texture of soil surface (A horizon)
9	Loam, silt loam, sandy clay loam, and silt
8	Clay, sandy clay, silty clay, clay loam, and silty clay loam
4	Loamy fine sand, loamy very fine sand, fine sandy loam, and very fine sandy loam
1	Sand, loamy sand, sandy loam, organic materials, and all textural classes with coarse fragment class modifiers (i.e., gravelly loam)

Data Analysis

Nest Density

I developed a suite of 10 *a priori* candidate models (Table 2.2) to investigate hypothesized associations between the log of burrowing owl nest density (lnOND) and six habitat covariates. My suite of candidate models included a global model containing the following explanatory variables: colony size (CS), prairie dog density (PD), total burrow density (B), proportion of warm-season grasses (WSG), degree of colony isolation (I), and colony habitat (H). (The soil texture variable was omitted from this model suite for reasons discussed below; see page 32.) To increase the predictive power of my models, I pooled data collected during the 2005 and 2006 field seasons.

Prior to evaluating my *a priori* hypothesized models, I calculated Pearson correlation coefficients to test for multicollinearity among habitat variables (Table 2.3). Because my response was counts of nests, I evaluated competing models of nest density using generalized linear Poisson regression with a log link function in R 2.5.1 (R: Copyright 2005, The R Foundation for Statistical Computing Version, 2005-12-20 r36812). I assessed the goodness-of-fit of my global model by estimating the dispersion parameter ϕ: $\hat{\phi} = \Sigma_i (y_i - \mu_i)^2 / \hat{\mu}_i / n - p$ (Faraway 2006). A $\phi > 1$ represents overdispersion, $\phi < 1$ is underdispersion, while $\phi = 1$ indicates that the variance in Y $= \phi$ EY $= \phi \mu$. Overdispersion indicates the presence of extra, unexplained variation in the response variable (e.g., nest density) and typically occurs when one or more important factors were not measured (McCullagh and Nelder 1989, Rotella et al. 2007).

I chose Poisson regression because my response variable consisted of discrete counts of burrowing owl nests that were independent in nature and thus likely to follow a Poisson distribution (Kutner et al. 2005, Faraway 2006). To translate my expected counts of nests into nest density, I took the log of colony size and set its coefficient equal to one: $\mu = \exp(\beta_0) \cdot CS \cdot \exp(\beta_2 \cdot CS)$; where μ is the expected count of nests for each study colony, and *CS* is colony size. More specifically, the first term following the intercept, CS, is a quantitative variate whereby its regression coefficient is forced to one; this term is called an offset (McCullagh and Nelder 1989). Thus, in R I added an offset term to my linear predictor with a known coefficient of one in lieu of an estimated coefficient. For notational convenience in the sequel, I suppressed the offset and denoted the first non-offset coefficient as β_1.

To assess support for my candidate models I employed a likelihood cross-validation (LCV) criterion (Sakamoto and Shirahata 1999, Liquet et al. 2007). This criterion estimates the expectation of the log likelihood (ELL) for a model by jackknife cross-validation (Sakamoto and Shirahata 1999, Liquet et al. 2007). The LCV criterion constructs a score, similar to the Akaike information criterion (AIC; Akaike 1973), but yields better results in the overall goodness-of-fit than AIC because it reduces the bias of estimates and performs better when sample size is small (Sakamoto and Shirahata 1999). I ran the suite of *a priori* models using a jackknife cross-validated generalized linear model (JackGLM) function (written by Mark L. Taper in program R; Appendix A). The JackGLM function used the prediction likelihood as the error measure. This method has been shown to be an effective estimator of the Kullback-Leibler distance (Liquet et al. 2007) and has been tested in model selection for Poisson regression (Sakamoto and Shirahata 1999). It should be noted that these information criteria are functions of the model's log-likelihood and the number of fitted parameters, k. In most analyses, k is equal to the number of regression parameters, including the intercept if there is one, plus one (i.e., 1) for the error variance. In Poisson regression, the error variance is not a distinct parameter so k is just the number of regression parameters.

I selected models with the smallest ELL, i.e., the product of -2ln(predicted likelihood), and ranked them in ascending order. Models with the lowest ELL values should better approximate burrowing owl nest density. To determine the strength of support for each candidate model I also calculated ΔELL (the amount each model in the suite differed from the model with the lowest ELL). Similar to information theoretic criterion, I considered models within $\Delta \text{ELL} \leq 2$ from the "top model" to be equally parsimonious (Burnham and Anderson 2002, Taper 2004) and assessed the biological importance of each covariate of the top models by calculating 95% confidence intervals.

Confidence intervals around beta estimates for each covariate that overlapped zero were not considered strong predictors of burrowing owl nest density.

After evaluating my *a priori* candidate models, I conducted an exploratory analysis of burrowing owl nest density and the selected habitat covariates to generate new hypotheses from the dataset (Taper and Gogan 2002). I evaluated subsets of single, additive, and interactive models using the jackknife prediction log likelihood as a model selection technique with the JackGLM function (discussed above) in R 2.5.1 (R: Copyright 2005, The R Foundation for Statistical Computing Version, 2005-12-20 r36812). As with ranking the candidate *a priori* models, I selected models with the smallest ELL and ranked them in ascending order. Finally, I used the same information-theoretic approach outlined above to determine the strength of support for each hypothesis generating model.

Table 2.2. *A priori* candidate model abbreviations, descriptions, structures, and hypothesized effects of prairie dog colony and landscape scale habitat covariates influencing the log of burrowing owl nest density (lnOND) on the Bad River Ranches, South Dakota, 2005-2006.

Abbreviation	Variable Description	Model Structure	Hypothesized Coefficient Result
CS	Prairie dog colony size (hectares)	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{CS})$	$\beta_1<0$
PD	Prairie dog density (# per hectare)	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{PD})$	$\beta_1>0$
B	Total burrow density (# active and inactive per colony)	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{B})$	$\beta_1>0$
WSG	Percent canopy cover of C4 grasses (weighted average % cover per colony)	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{WSG})$	$\beta_1>0$
I	Degree of colony isolation (kilometers)	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{I})$	$\beta_1<0$
H	Colony habitat (upland or lowland)	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{H})$	$\beta_1>0$ (upland)
CS + PD	Colony size + prairie dog density	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{CS}) + \beta_2(\mathrm{PD})$	$\beta_1>0$, $\beta_2>0$
I + H + CS	Isolation + habitat + colony size	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{I}) + \beta_2(\mathrm{H}) + \beta_3(\mathrm{CS})$	$\beta_1<0$, $\beta_2>0,\beta_3<0$
I * H	Isolation * habitat	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{I}) + \beta_2(\mathrm{H}) + \beta_3(\mathrm{I*H})$	$\beta_1<0$, $\beta_2>0,\beta_3>0$
GLOBAL	All variables	$\mathrm{lnOND} = \beta_0 + \beta_1(\mathrm{CS}) + \beta_2(\mathrm{PD}) + \beta_3(\mathrm{B}) + \beta_4(\mathrm{WSG}) + \beta_5(\mathrm{I}) + \beta_6(\mathrm{H}) + B_7(\mathrm{I*H})$	$\beta_1<0,\beta_2>0,\beta_3>0,$ $\beta_4>0,\beta_5<0,\beta_6>0,$ $\beta_7>0$

Predictions

Based on my literature review, I predicted that at the colony level burrowing owl nest density would be inversely related to prairie dog colony size. Previous studies reported that owl numbers increase but densities decrease with colony size (Hughes 1993, Desmond et al. 1995, Desmond and Savidge 1996, Griebel 2000, Livieri 2002) in response to territoriality or because there is more available nesting space in large versus small colonies. I also predicted burrowing owl nest density would be positively related to both prairie dog and total burrow density. Greater densities of prairie dogs in a colony would provide greater density of burrow sites for owl nests, increase owl predator detection, and create protection from inclement weather.

Further, I expected the proportion of warm-season grasses and sandy loam soils within colonies would be positively associated with burrowing owl nest density. Colonies with a greater proportion of warm-season grasses have greater total vegetative cover and shorter-stature grasses, both of which provide good forage habitat and detection of predators. Nest burrows consisting of sandy loam soils may have been favorable to burrowing owls because they were well drained and long-lived.

At the landscape scale, I predicted burrowing owl nest density would decrease with increasing colony isolation. Because colonies grouped in a complex provide a range of nesting options to burrowing owls, isolated colonies might be less suitable for nesting. Finally, I expected burrowing owl nest density would be greater in colonies located in upland areas because upland colonies were located farther from river corridors and woodland, which reduces the probability nest burrows will flood, and could reduce the presence of tree-dwelling predators.

Results

Nests

I surveyed 26 prairie dog colonies for burrowing owl nests during the 2005 (n =10) and 2006 (n = 16; the same 10 colonies as in 2005 plus an additional six colonies) breeding seasons. Overall, I identified 222 burrowing owl nests with fledglings: 80 nests on nine colonies in 2005, and 142 nests on 14 colonies in 2006 (Table 2.4). One colony (#27) showed no evidence of nesting owls in 2005 and two of the 16 colonies (#5 and #27) showed no nesting in 2006. These colonies were included in my analyses because they reflected the natural variation in my study area and were part of my statistical populations.

There was substantial variation among colonies in the number and density of burrowing owl nests. The number of nests per colony ranged from 0 to 21 ($\bar{x}$ = 8.54, SE = 13.33; Table 2.5) and burrowing owl nest densities (i.e., the number of nests per colony divided by size of the colony in hectares) ranged from 0.00 to 1.19 nests/ha ($\bar{x}$ = 0.24, SE = 1.35; Table 2.6). While the number of burrowing owl nests increased with colony size (Figure 2.3), nest densities declined (Figure 2.4).

Table 2.3. Pearson correlation coefficients among prairie dog colony and landscape level habitat variables used to explain burrowing owl nest density on the Bad River Ranches, South Dakota, 2005-2006.

	CS	PD	B	WSG	I	H
CS	1.00	-0.37	-0.39	0.39	-0.32	-0.40
PD		1.00	0.35	0.01	-0.07	-0.13
B			1.00	0.22	-0.22	-0.04
WSG				1.00	-0.51	-0.54
I					1.00	0.39
H						1.00

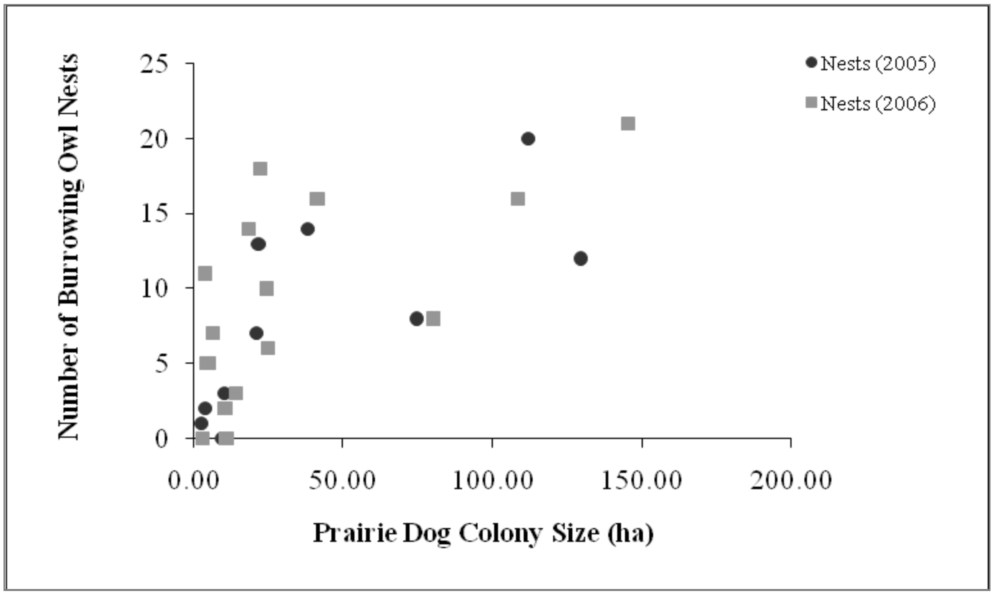

Figure 2.3. Scatterplot of the number of burrowing owl nests in relation to prairie dog colony size during the 2005 and 2006 field seasons.

Table 2.4. Prairie dog colonies studied during the 2005 (x = yes, o = no) and 2006 (y = yes, o = no) field seasons on the Bad River Ranches, South Dakota.

Colony ID	Surveyed in 2005	Confirmed nests 2005	Surveyed in 2006	Confirmed nests 2006
5	x	x	y	o
B	x	x	y	y
27	x	o	y	o
40	x	x	y	y
4	x	x	y	y
3	x	x	y	y
1	x	x	y	y
2	x	x	y	y
23	x	x	y	y
34	x	x	y	y
14	o	o	y	y
37	o	o	y	y
E	o	o	y	y
19	o	o	y	y
7	o	o	y	y
28	o	o	y	y
Total number of colonies:	*n = 10*	*n = 9*	*n = 16*	*n = 14*

Habitat Covariates

I observed burrowing owls nesting on prairie dog colonies ranging in size from 2.55 to 145.32 ha (Table 2.7). The size distribution of colonies used by burrowing owls favored small colonies, where 50% of colonies were 0-20 ha (small size category), 23% were 20-40 ha (medium), and 27% were >40 ha (large). From 2005 to 2006, the areal extent of all but one colony increased and one colony expanded out of the medium into the large category. Prairie dog density ranged from 6.66 to 64.09 dogs per ha and total burrow density ranged from 5.72 to 415.25 burrows per ha (Table 2.7).

Table 2.5. Number of burrowing owl nests located on prairie dog study colonies on the Bad River Ranches, South Dakota, 2005-2006.

2005			2006		
Colony ID	Colony Size (ha)	Number of Nests	Colony ID	Colony Size (ha)	Number of Nests
5	2.55	1	5	2.75	0
B	3.81	2	B	4.88	5
27	9.20	0	27	10.57	0
40	10.22	3	40	13.75	3
4	20.93	7	4	22.02	18
3	21.51	13	3	24.24	10
1	37.96	14	1	41.22	16
2	74.53	8	2	79.96	8
23	111.87	20	23	108.47	16
34	129.26	12	34	145.32	21
-	-	-	14	3.42	11
-	-	-	37	4.22	4
-	-	-	E	5.98	7
-	-	-	19	10.21	3
-	-	-	7	18.20	14
-	-	-	28	24.60	6
Total number of nests:		*n = 80*			*n = 142*

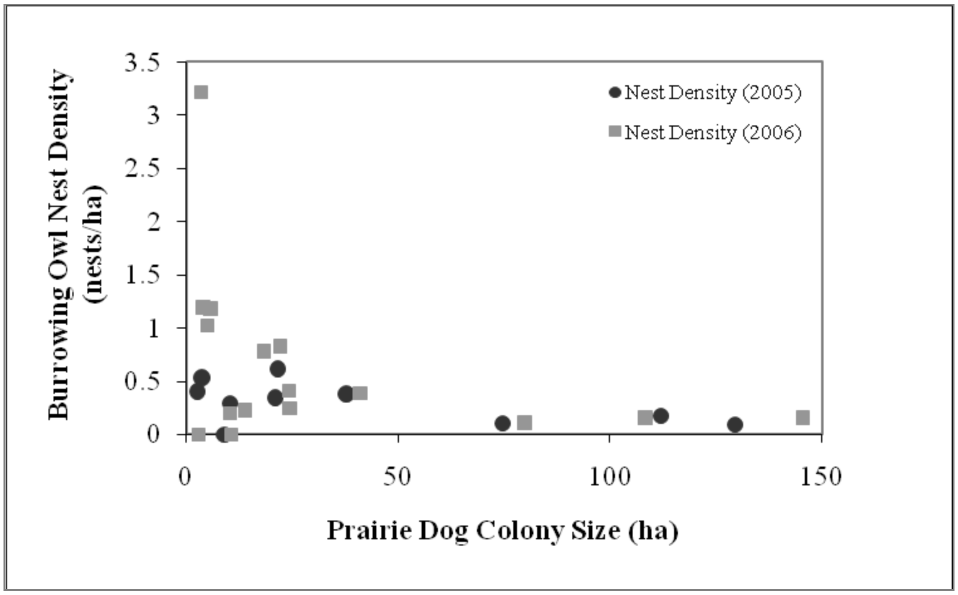

Figure 2.4. Scatterplot of burrowing owl nest density in relation to prairie dog colony size during the 2005 and 2006 field seasons.

Table 2.6. Burrowing owl nest densities in small (<20 ha), medium (20-40 ha), and large (>40 ha) prairie dog colonies on the Bad River Ranches, South Dakota, 2005-2006.

	Colony Size		
	Small (n = 13)	Medium (n = 7)	Large (n = 6)
Number Of Nests	53	84	85
Mean Nest Density	0.69	0.45	0.13
Standard Error	0.87	0.19	0.03
Range	0.00 to 3.22	0.24 to 0.82	0.09 to 0.18

With respect to vegetation cover within colonies, warm-season grasses comprised the smallest percentage ($\bar{x}$ = 10.0%, SE = 12.0; Table 2.7). Total average cover of cool-season grasses was 16.0% (SE = 12.0, range = 2.0 to 39.0), forb cover averaged 18.0% (SE = 13.0, range = 3.0 to 45.0), bare ground cover averaged 24.0% (SE = 15.0, range = 3.0 to 52.0), and the average cover of litter was 35.0% (SE = 9.0, range = 21.0 to 57.0). The average vegetative height among study colonies ranged from 1.19 to 16.46 cm ($\bar{x}$ = 5.10, SE = 3.42).

Soil textures within prairie dog colonies were not incorporated into my analysis. Soil textures underlying burrowing nests (observed) were compared to soil textures underlying 100 random points (expected) in each study colony. Based on my goodness-of-fit (i.e., $\sum [(O - E)^2/E]$, where O = observed values and E = expected values) results, there was not enough evidence ($\chi^2 = 0.08$, df = 2, $P = 0.10$) to conclude that burrowing owls selected certain soil textures within colonies. The majority (94.6%) of both observed and expected values were soil rating 8; soil ratings 9, 1, and 4 comprised 3.4%, 2.1%, and 0%, respectively.

At the landscape scale, seventy-five percent (n = 12) of the prairie dog study colonies were isolated on the landscape (i.e., >2.4 km from other colonies) and 25% (n = 4) were grouped in a complex (i.e., adjacent to ≥2 colonies within 2.4 km). The degree of colony isolation ranged from 0 to 4.14 km (Table 2.7). Of the 16 unique study colonies, 68.8% (n = 11) were located on upland plateaus and 31.2% (n = 5) were in lowland areas.

Table 2.7. Summary of continuous habitat and landscape level variables measured at burrowing owl nest colonies on the Bad River Ranches, South Dakota, 2005-2006.

Covariate	Mean (± SE)	Median	Range
Colony size (ha)	36.21 ± 43.43	19.56	2.55 to 145.32
Prairie dog density (dogs/ha)	30.81 ± 12.78	30.29	6.66 to 64.09
Total burrow density (burrows/ha)	117.89 ± 105.62	102.66	5.72 to 415.25
Warm season grasses (average %)	10.00 ± 12.00	3.00	0.00 to 32.00
Degree of colony isolation (km)	1.60 ± 1.62	1.13	0.00 to 4.14

Nest Density and Habitat Associations

I employed the LCV criterion instead of AIC, adjusted for small sample size (Sagiura 1978, Hurvich and Tsai 1989) and overdispersion (Anderson et al. 1994) because the dispersion parameter estimate for the global model was ≥1.0 (2.98 on 25 *df*). Generally, the estimate of the overdispersion parameter, $\hat{c}$, should be $1 \leq \hat{c} \leq 4$ (Burnham and Anderson 2002) and although 2.98 was within this range, there was clearly a structural lack of fit in this estimate. Therefore, I used the LCV criterion to obtain a better overall goodness-of-fit (Sakamoto and Shirahata 1999).

Colony size influenced burrowing owl nest density on the Bad River Ranches. The top supported *a priori* model (Table 2.2) of the log of burrowing owl nest density was $\text{lnOND} = \beta_0 + \beta_1(\text{CS})$ (Table 2.8). Parameter estimates for this model indicated that the log of burrowing owl nest density was inversely related to colony size, i.e., nest densities were higher in small prairie dog colonies (<20 ha) and lower in large colonies (>40 ha) (Figure 2.5). The confidence intervals of β_1 provide additional support as they did not encompass zero (Table 2.9). The equation representing the top model of the log of burrowing owl nest density was: *lnOND = -1.7188 - 0.0093 (Colony Size).* Colony size also appeared in the second, third, and fourth ranked hypothesized models in the suite, but these models were weakly supported (≥4.43 ΔELL units from the first-ranked model). Burrowing owl nest density was less influenced by single and multi-variable predictor models containing prairie dog total burrow density, cover of warm-season grasses, degree of colony isolation, and habitat (ΔELL scores ≥4.43; Table 2.9).

Table 2.8. *A priori* model selection results based on the expectation of log likelihood (ELL) of the log of burrowing owl nest density within prairie dog colonies (n = 26) on the Bad River Ranches, South Dakota, 2005-2006. The ELL was estimated by the likelihood cross-validation criterion and is the product of -2 and the predicted log likelihood. Models are ranked by the ascending ΔELL; *k* is the number of parameters in each model.

Candidate Model	*k*	ELL	ΔELL
CS	2	197.36	0.00
CS + PD	3	201.79	4.43
I + H + CS	4	205.99	8.63
GLOBAL	9	209.06	11.70
H	2	235.88	38.52
B	2	249.32	51.96
WSG	2	249.37	52.01
I	2	254.08	56.72
PD	2	255.12	57.76
I + H + (I * H)	4	260.79	63.43

Table 2.9. Parameter estimates from the top *a priori* model of the log of burrowing owl nest density within prairie dog colonies on the Bad River Ranches, South Dakota, 2005-2006.

Model = CS				
Parameter	Estimate	SE	95% LCI	95%UCI
Intercept (β_0)	-1.7188	0.0999	-1.5174	-1.9097
Colony size (β_1)	-0.0093	0.0013	-0.0067	-0.0118

Exploratory Analysis

Using variables included in the *a priori* models, I evaluated a combined suite of *a priori* and subsets of single, additive, and interactive exploratory models using a JackGLM function. Post-hoc exploratory analysis identified the interaction between the average percent cover of bare ground and colony habitat, $\ln\text{OND} = \beta_0 + \beta_1(\text{bare}) + \beta_2(\text{H}) + \beta_3(\text{bare*H})$, as the best approximating model for the log of burrowing owl nest density (Table 2.10). Habitat appeared to be the driving variable in this model since the slope on β_1(bare) overlapped zero. While the strong negative slope in β_2(H) indicated upland colonies were favored, the strong positive slope on β_3(bare*H) suggested that bare ground was important in lowland habitats (Table 2.11). The effective intercept in lowland habitats (β_0 + H) was less than the effective intercept in upland habitats (β_0).

Discussion

I investigated the relationship between a group of relevant habitat variables and burrowing owl nest density to better understand the owl's nesting ecology in South Dakota. I found, as hypothesized, that prairie dog colony size was a good predictor of burrowing owl nest density. My results were quite similar to nest density and colony size relationships found in other studies, e.g., in Colorado (Hughes 1993), Nebraska (Desmond 1991, Desmond et al. 1995, Desmond and Savidge 1996), New Mexico (Berardelli 2003), South Dakota (Griebel 2000, Knowles 2001, Livieri 2002), and Texas

Table 2.10. The log of burrowing owl nest density model ranking for 15 of the combined *a priori* and exploratory candidate models on the Bad River Ranches, South Dakota, 2005-2006. The expected log likelihood (ELL) is the product of -2 and the predicted log likelihood. Models are ranked by the ascending ΔELL; *k* is the number of parameters in each model.

Candidate Model	*k*	ELL	ΔELL
Bare + H + bare*H	4	176.57	0.00
CS + H + CS*H	4	192.79	16.22
CS	2	197.36	20.79
CS + CSG	3	197.50	20.93
B + bare + B*bare	4	197.50	20.93
CS + forbs	3	197.93	21.36
CS + height	3	198.53	21.96
CS + I	3	199.83	23.26
CS + litter + CS*litter	4	200.78	24.21
CS + WSG	3	201.04	24.47
CS + PD	3	201.79	25.22
CS + B	3	201.91	25.33
CS + litter	3	203.05	26.48
CS + bare	3	203.51	26.93

Table 2.11. Parameter estimates from the top exploratory model of the log of burrowing owl nest density within prairie dog colonies on the Bad River Ranches, South Dakota, 2005-2006.

Model = Bare*H				
Parameter	Estimate	SE	95% LCI	95%UCI
Intercept (β_0)	2.3048	0.1299	2.0438	2.5536
Bare (β_1)	0.1790	0.5297	-0.8758	1.2037
Habitat (β_2)	-5.5058	0.9662	-7.6070	-3.7841
Bare*Habitat (β_3)	11.4410	2.1164	7.5504	15.9208

(Pruett 2004). The mean estimate of nest density ($\bar{x}$ = 0.24) among colonies was higher than those reported in western South Dakota by Griebel (2000; $\bar{x}$ = 0.16 in 1999 and $\bar{x}$ = 0.15 in 2000), and lower than the 0.89 nests/ha and 1.26 nests/ha documented in southern New Mexico during 2000 and 2001 by Berardelli (2003). The general pattern of increasing number of nests but decreasing overall nest density as colony size increases was observed in my analysis.

Population density is a complex demographic characteristic that can vary among and within regions (Matter 1997, Mayor and Schaefer 2005). Furthermore, the inverse relationship observed between burrowing owl nest density and colony size may have resulted from ecological processes that vary among colonies (Matter 1997, Winter et al. 2005). For example, vegetation structure (Winter et al. 2005), local reproduction (Capman et al. 1990), predation (Risch et al. 1982), residence time (Root 1973), and dispersal (Turchin 1986, Bowman et al. 2002) could influence nest density of burrowing owls within and among colonies. Nest density may also be a function of prey availability and quality (Ross 1974, Warnock and James 1997), owl territoriality (Desmond and Savidge 1996), and habitat limitations (Desmond et al. 1995, Berardelli 2003). Desmond and Savidge (1996) found shorter mean nearest neighbor distances in small colonies (i.e., <35 ha) than in colonies ≥35 ha, suggesting that nesting space was limited in small-sized colonies. If the amount of suitable nest habitat is limited within a colony, the best territories are likely occupied first and defended while subsequent territories may be in less desirable areas and in close proximity to one another (e.g., ideal-despotic distribution; Fretwell 1972).

The spatial arrangement of burrowing owl nests within a colony has been shown to vary in relation to prairie dog colony sizes (Butts 1973, Ross 1974, Desmond 1991, Hughes 1993, Desmond and Savidge 1996, Toombs 1997, Berardelli 2003). On the Bad River Ranches, I observed that much of the variation in nest density occurred among the smaller colonies (<20 ha; Table 2.6), and a possible threshold in density may exist around 40 ha where larger colonies did not show dramatically lower nest densities. In western Nebraska, Desmond and Savidge (1996) noted a similar trend of variable densities among the small colonies they studied. Although sample sizes for medium and large colonies in my study were relatively small, the standard error I observed for nest density was substantially lower in large colonies (>40 ha) versus small and medium colonies (0 – 40 ha) on the Bad River Ranches in South Dakota.

Two key factors likely contributed to variation in density observed among small colonies in my study. First, and most obvious, the absence of burrowing owls from some colonies (two of the 13 small colonies were not occupied), and more importantly, the exceptionally high number of nests on a few small colonies. Both small, unoccupied colonies were in lowland areas where the predominant soil texture was Sandsarc clay. The unoccupied colonies may have been subjected to factors specific to their geographic position, including greater predation rates, or less favorable burrow sites. For example, in South Dakota, burrowing owls nested in burrows with greater sand content than non-nest burrows. MacCracken et al. (1985b) suggested that well drained sandy soils might facilitate enlargement of burrow tunnels. Furthermore, other small colonies with high numbers of nests were close to agricultural fields. Agricultural lands could provide both positive and negative effects on owl nesting. Field edges could attract predators and restrict owl movements, whereas adjacent nest sites could benefit if agricultural areas positively influence owl prey availability (Butts 1973).

Two other hypotheses have been proposed to explain why small colonies harbored greater nest densities than large colonies. First, small colonies may be important for nesting burrowing owls since they are central place foragers (Gervais et al. 2003). Small colonies often have greater edge-to-area ratios than large colonies thus nest-to-colony edge distances are shorter, which may allow better access to edge-related prey items and reduce the time and energy burrowing owls spend foraging (Desmond et al. 1995, Warnock and James 1997). Second, Knowles (2001) posited that the association between burrowing owl numbers might be correlated more with the length of colony perimeter than with colony size. Knowles stated that the inverse relationship between nest density and colony size might be explained by the differences in the way area and perimeter vary with size. Because burrowing owls appear to nest in a colony's periphery (Butts 1973, Desmond 1991, Toombs 1997, Ekstein 1999, Griebel 2000, Knowles 2001), I was intrigued by the potential influence of perimeter on burrowing owl nest density, thus I added it to a new model suite and assessed support for this suite using a LCV criterion (Sakamoto and Shirahata 1999, Liquet et al. 2007). Results from this new analysis, however, did not support the hypothesis that colony perimeter, $\ln\text{OND} = \beta_0 + \beta_1(\text{perimeter})$, was a better predictor of nest density than colony size (i.e., the model containing perimeter was >2 ΔELL units from the top model, $\ln\text{OND} = \beta_0 + \beta_1(\text{colony size})$).

The model results in my analyses did not support the idea that prairie dog density, burrow density, and cover of warm-season grasses were important habitat requirements for burrowing owls (McDonald et al. 2004). In contrast to my predictions, prairie dog density and total burrow density were negatively related to burrowing owl nest density, yet the parameter estimates indicated the influence of these two variables was weak. No correlation was documented between prairie dog density and burrowing owl density in studies by Desmond (1991) and Hughes (1993), suggesting the potential benefits owls derive from nesting in areas of high prairie dog densities did not drive nest density. Other studies relating total burrow density to the number of burrowing owl nests or pairs also found little to no significant correlation between the two variables (Desmond 1991, Hughes 1993, Toombs 1997). The slight change in my collection methods for total burrow densities (i.e., sampling a proportion of burrows in 2005 to surveying all burrows in 2006) may have contributed to the lack of this variable's influence on nest density. Observer error in burrow detection and classification may have played a role.

Contrary to my prediction, nest density was negatively correlated with the percent canopy cover of warm-season grasses. The confidence interval for this covariate included zero, indicating that it was not a good predictor in this study. In a study of variability in vegetation structure on grassland bird density and nesting success, Winter et al. (2005) found few vegetation variables (percent ground cover of litter, grass, forbs, woody vegetation, soil, height, and litter depth) that clearly affected the density of selected grassland bird species. They speculated that grazing regimes, choice of study sites, predation, and the short-term nature of their study could have contributed to the variation in vegetation structure and bird density.

At the landscape level, I predicted that habitat location and the degree of colony isolation would strongly influence nest density. In particular, I hypothesized that nest density would be positively related to upland colonies and colonies with less isolation. The effects of the landscape scale variables alone were negligible and coefficients for both were close to zero with confidence intervals including zero. However, in subsequent exploratory analysis, the interaction between bare ground and lowland habitat positively affected nest density. Burrowing owls consistently demonstrate a preference for nesting in areas containing bare ground and short vegetation (MacCracken et al. 1985b, Plumpton and Lutz 1993, McDonald et al. 2004). Bare ground appears to be beneficial to nesting owls by providing good horizontal visibility to detect approaching predators. This is important to the survival of burrowing owls, which spend much of their time on the ground where they are susceptible to predation (Butts 1973, Zarn 1974, Plumpton 1992). Moreover, study colonies containing the greatest average cover of bare ground in lowland habitats showed very high nest densities. Thus selection of nest sites may occur on a smaller scale than the landscape (i.e., nest or colony).

In my study area, nest densities were not different between isolated colonies and colonies grouped in a complex. In a large black-tailed prairie dog complex in Mexico, the number of nests in burrowing owl clusters was inversely related to the degree of colony isolation (McNicoll 2005). In Nebraska, the presence of burrowing owls was negatively related to the degree of colony isolation (Ekstein 1999). This suggests that although isolated colonies have an increased risk of extinction from disease, inbreeding, and catastrophic events (Oldemeyer et al. 1993), in some areas they are valuable to nesting burrowing owls.

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CHAPTER 3

FACTORS INFLUENCING BURROWING OWL COLONY PRODUCTIVITY IN BLACK-TAILED PRAIRIE DOG COLONIES IN SOUTH DAKOTA

Introduction

The availability and quality of nesting and foraging areas can influence the reproductive performance of burrowing owls (*Athene cunicularia*). Populations may be regulated by these and other variables such as territoriality and weather (Newton 1976, Raphael et al. 1996). For example, Newton (1976) found a correlation among population levels, reproductive success, and habitat quality in European Sparrowhawks (*Accipiter nisus*). Thus, quantifying reproductive parameters may be an effective approach to assess habitat quality and relevant for managing burrowing owl populations (Van Horne 1983, Martin 1992, Donovan et al. 2002).

Mean brood size has been used to assess reproductive performance in numerous burrowing owl nesting studies (Butts 1973, Ross 1974, Ekstein 1999, Desmond 1991, Plumpton 1992, Desmond et al. 2000, Griebel 2000, Restani et al. 2001, Berardelli 2003, Gorman et al. 2003, Lantz 2005, Teaschner 2005). However, Gorman et al. (2003) found that the mean number of young showed higher bias and lower precision than the maximum number observed. Given the importance of comparing demographic parameters among burrowing owl populations, Gorman et al. (2003) recommended future efforts report “the maximum number of juveniles observed during multiple censuses throughout the nesting season”.

With the observed habitat and population declines for burrowing owls at the edges of the species' distribution (Klute et al. 2003), it is important for managers to understand habitat characteristics that might affect breeding burrowing owls. Therefore, the primary objective of my research was to investigate hypothesized associations between burrowing owl colony productivity and prairie dog colony characteristics at two spatial scales: within colonies and across the greater landscape. I defined productivity as the total number of burrowing owl fledglings per colony. At the colony scale, productivity was assessed in relation to (1) colony size, (2) prairie dog density, (3) total burrow density, (4) mean nearest neighbor distance, (5) mean nest-to-colony edge distance, and (6) percent cover of warm-season grasses. At the landscape scale, burrowing owl colony productivity was assessed in relation to the degree of prairie dog colony isolation and the topographic setting of colonies (i.e., upland versus lowland).

Colony Scale Habitat Characteristics

Prairie dog colony size has been shown to be highly correlated with burrowing owl colony productivity within prairie dog colonies (Desmond and Savidge 1996, Ekstein 1999, Griebel 2000). Large colonies may contribute to nesting success by providing more habitat, greater food resources, and higher proportions of suitable nesting space than smaller colonies, particularly during drought years (Desmond and Savidge 1996, Ekstein 1999, Griebel 2000). Because large colonies support higher numbers of burrowing owls, predator detection may be enhanced in larger colonies and furthermore, prairie dogs themselves likely serve as alternate prey (Ekstein 1999).

High prairie dog densities have been linked with increased burrowing owl nest survival (Desmond et al. 2000). Burrowing owls often concentrate their nests in high density prairie dog patches because prairie dog activities (i.e., trimming tall vegetation, maintaining burrow structures, and eliciting calls warning of approaching predators) positively influence reproductive survival (Butts and Lewis 1982, MacCracken et al. 1985a, Haug et al. 1993, Plumpton and Lutz 1993, Toombs 1997, Ekstein 1999, Desmond et al. 2000, Griebel 2000, Restani et al. 2001, Lantz 2005). If burrowing owls receive cues and benefit from the prairie dog sentinel system, then fledgling survival should be positively correlated with prairie dog density.

Total burrow densities (i.e., active and inactive burrows used by prairie dogs) also appear to be important to the survival of burrowing owls. Both adults and young use "satellite" or non-nest burrows for protection from predators and inclement weather (Gleason 1978) in addition to sleeping and roosting (Haug et al. 1993). Reproductive females rely on prairie dog burrows during the incubation and early brood rearing periods whereas males use adjacent burrows for resting, guard posts, and escape cover (Butts and Lewis 1982, Clayton and Schmutz 1999). Once emerged from the natal nest, fledglings use satellite burrows to relieve crowding at the nest burrow, avoid nest parasites, reduce the risk of predation, seek refuge from the elements, and catch or cache prey (Butts 1973, Butts and Lewis 1982, Haug 1985, Desmond 1991, Plumpton and Lutz 1993, Desmond and Savidge 1999, King and Belthoff 2001). Consequently, the absence of burrows immediately surrounding the natal nest may compromise burrowing owl fledgling survival (Restani et al. 2001).

Nearest neighbor (Desmond and Savidge 2000, Griebel 2000) and nest-to-colony edge distances (Ekstein 1999) are two additional factors attributed to burrowing owl productivity at the colony scale. In Nebraska burrowing owl fledgling survival was higher for nests with nearest neighbor distances <100 m compared to those with neighbors >175 m (Desmond and Savidge 2000). In South Dakota, however, Griebel (2000) found that successful nests were those with the greatest nearest neighbor distances and lower numbers of nests within 250 m. These contrasting results may be attributed to differences in prairie dog colonies between study areas; colonies in Nebraska were smaller and more isolated than colonies in South Dakota and burrowing owls also nested in clusters, allowing them to alert one another to approaching predators. The large colony complexes found in South Dakota supported greater nearest neighbor distances potentially because there was less competition for nest sites and food resources, and owls may have relied on prairie dog alarm calls instead of adjacent burrowing owls (Griebel 2000). Distance of owl nests to colony edge did not appear to affect measured reproductive parameters in South Dakota (i.e., clutch and brood size, number fledged; Griebel 2000), but Ekstein (1999) found that burrowing owl nest survival was higher when nests were farther from the colony edge. She reasoned that nesting near colony edges may result in lower nest survival due to habitat edge effects. While colony perimeters could provide owls with more nest sites and closer proximity to foraging areas, owls may also be at greater risk of nest predation if predators frequent colony edges (Donovan et al. 1997).

Vegetation structure and composition within colonies may indirectly influence burrowing owl colony productivity. During wet years on the mixed-grass prairie vegetation surrounding burrows can grow tall as the growing season progresses if it is not clipped by prairie dogs. As burrowing owls often select vacant prairie dog burrows for nesting, such tall vegetation could affect survival of emerging young. Short-stature vegetation and bare ground ostensibly enhances predator detection and simplifies movement of pre-fledged juveniles to nearby satellite burrows (Butts 1973, Ross 1974, Haug 1985, MacCracken et al. 1985a, b, Green and Anthony 1989, Winter et al. 2005). Berardelli (2003) reported that nests with a lower percentage of forb cover produced more young.

Landscape Scale Habitat Characteristics

The connectivity or degree of isolation of individual prairie dog colonies has the potential to influence burrowing owl reproduction. Groups of prairie dog colonies in close proximity (i.e., colony complexes) may yield more productive and persistent burrowing owl populations because complexes afford greater habitat stability (McDonald et al. 2004). The less colonies are isolated the greater the probability that a dispersing burrowing owl will locate food, suitable habitat, or other owls to breed with (Warnock and James 1997, Ekstein 1999, McDonald et al. 2004).

Extensive prairie dog complexes were historically common in the Great Plains ecosystem. Early explorers Lewis and Clark reported an “infinite number” of prairie dogs and Merriam (1902) described a prairie dog complex that occupied nearly 65,000 km^2 in Texas. European settlement led to replacement of native grasslands with urban and agricultural development, and eradication of prairie dogs (Klute et al. 2003). Loss of this habitat resulted in the reduction, fragmentation, and isolation of large prairie dog complexes (Flath and Clark 1986, Lomolino and Smith 2003), leaving mostly small (~40 ha) and scattered colonies (Sidle et al. 2001).

Ekstein (1999) predicted owl-occupied colonies would be relatively large and imbedded in landscapes where surrounding colonies were less isolated. She found that colony size and the size of the largest colony within 10 km were positively correlated with the presence of nesting burrowing owls. In addition, the size of the largest colony within 3 km contributed positively to nest survival and a negative relationship between nest success and the distance to the nearest neighboring colony was observed (Ekstein 1999).

Habitat topology, the juxtaposition of prairie dog colonies, could also influence burrowing owl colony productivity on the Bad River Ranches. The topography on the ranch consisted of two physical settings that may have a strong influence on colony productivity: upland plateaus and lowland floodplains. The upland habitats consist of narrow strips of undulating plateaus divided by numerous intermittent creeks that drain southeast into the Bad River. The lowland habitats are relatively level, lower elevation floodplains. Study colonies located in lowland areas were often near watershed corridors lined by cottonwood trees (*Populus angustifolia*) that might increase exposure of burrowing owls to tree-dwelling predators (e.g., Great Horned Owls, *Bubu virginianus*) and flood events. Lowland colonies usually consisted of fine-textured soils susceptible to erosion, livestock trampling, and readily colonized by invasive herbaceous species. Upland colonies were located farther from river corridors, treeless, and had greater proportions of native vegetative species. Prairie dog colonies located on upland plateaus showed features strongly associated with burrowing owl nest habitat, including flat to gently sloping terrain, well-drained areas of short vegetation (i.e., <10 cm high) and bare ground (Butts 1973, MacCracken et al. 1985b, Green and Anthony 1989, Pezzolesi 1994, Deschant et al. 2001).

Methods

Study Area

The study population included prairie dog colonies located within the Bad River Ranches (hereafter "ranch"), which comprise about 570 km² in Stanley and Jones counties near Fort Pierre (44°21′N, 100°22′W), South Dakota. The ranch lies within the mixed-grass system of the Northern Great Plains (Kuchler 1975). The topography was composed of mixed-grass, flat to rolling uplands cut by the Bad River and intermittent drainages; elevations varied from about 457 m above sea level in lowland bottoms to 610 m on upland plateaus. Average annual precipitation was 48.29 cm, where 65% fell during the April – August breeding season. Mean monthly temperatures ranged from –7.47ºC in January to 24ºC in July (http://climate.sdstate.edu). Soils were primarily clays derived from Createaceous Pierre Shale (Johnson et al. 1995). Kuchler (1975) characterized the area as a wheatgrass-needlegrass (*Stipa viridula*) community; buffalograss and blue grama grass also were widespread (K. Bly and J. Truett, unpublished data).

The ranch, owned by R. E. Turner, is managed for the sustainable production of bison and conservation of native species. At the time of this study, the ranch supported approximately 5,000 bison divided among several herds that grazed pastures north and south of the Bad River on a rotating basis. During 2000 – 2004 the Turner Endangered Species Fund (a private, non-profit charity dedicated to conserving biodiversity on Turner lands) restored prairie dogs to selected sites on the ranch, largely by establishing new colonies and managing habitat to encourage colony growth. Including the reintroduced colonies, the ranch had 87 colonies occupying 813 ha in 2006.

I conducted my field research from May – September 2006. Prairie dog study colonies were randomly selected from three size categories: small (0-20 ha), medium (20-40 ha), and large (>40 ha), and from two landscape types (i.e., colonies grouped in a complex and isolated colonies) and habitats (i.e., lowland and upland colonies). I surveyed 16 of the 82 colonies (pre-existing and reintroduced) ranging in size from 2.75 to 145.32 ha. All prairie dog colonies surveyed were active; no prairie dog poisoning or shooting occurred on study colonies for six years prior to and during the period of my research (K. Bly and J. Truett, unpublished data).

Nest Data Collection

I surveyed each study colony for burrowing owl nests during May and June of 2006. To locate nests, I visually inspected each prairie dog burrow by walking parallel line transects 10 – 25 m apart. To prevent resampling nests and burrows, I marked each burrow with flour or white chalk. Transect length depended on the width of individual colonies. I identified nests by the physical presence of burrowing owls, strands of shredded material (dung, yucca), feathers, prey remains, regurgitated castings, and whitewash at the entrance of nest burrow (Desmond 1991). Nests initiated after June 30th of each year were not included in my analyses. It was possible that on large colonies a few nests were not located. Although I did not obtain a nest detection probability, I believe detectability was similar among nests because of the intensive search effort conducted for each colony.

I marked all burrowing owl nest locations with two methods. First, I placed a round aluminum identification tag secured with a steel ground staple (www.forestry-suppliers.com) 1 m north of each nest burrow. Next, I obtained universal transverse mercator coordinates with a Garmin 12CX Global Positioning System (GPS) unit. The GPS waypoints were then downloaded into the GIS program ArcView 3.2a (ESRI 2000).

Burrowing Owl Fledgling Counts

Because I estimated the number of fledglings for each known nest at the colony scale, I defined burrowing owl colony productivity as the total number of burrowing owl fledglings per colony. The total was obtained by summing the maximum number of fledglings observed during multiple census periods for burrows where fledglings were known to be present during the breeding season. To minimize the inherent bias in raptor nesting studies based on single counts (Steenhof 1987) I counted the maximum number of burrowing owl fledglings at each nest during a 60-minute period from ≥100 m away using a spotting scope and binoculars for three independent censuses: June, July, and August 2006. Each observation period was conducted during the early morning (i.e., 0.5 hr before sunrise until 1000 hr) and evening hours (i.e., 1700 hr until 0.5 hr after sunset) when vocalization and aboveground activity of burrowing owls was often highest (Johnsgard 1988, Conway and Simon 2003). Adults were delineated from young based on chest plumage and barring (Priest 1997).

Although each nest received equal observation effort, some visual obstructions (e.g., vegetation, burrows) did preclude accurate fledgling counts for some nests. Therefore, I assumed a 0.71 detection probability of fledglings of known ($\bar{x}$ = 4.5, SE = 0.6, range 1 to 9) versus observed ($\bar{x}$ = 3.2, SE = 0.4, range 1 to 7) mean number of fledglings reported by Gorman et al. (2003).

Habitat Covariates

Colony Size.

By walking or driving, I estimated the area occupied by a colony of prairie dogs by mapping the outermost, active burrow entrances (Hoogland 1995) with a Garmin 12CX GPS unit in August of each year. Active perimeter burrow entrances were marked as waypoints and then downloaded as shape files for analysis of area in hectares in the GIS program ArcView 3.2a (ESRI 2000).

Prairie Dog and Burrow Density.

I estimated prairie dog density on study colonies during June – July of 2006. These estimates were derived from counting the total number of active and inactive burrows in each study colony. I conducted comprehensive colony counts of active and inactive burrows by walking parallel line transects 5 m apart. I assumed the total number of burrows counted to be a minimum and a burrow detection rate of approximately 0.90 (Matchett 1994).

At each burrow entrance, I counted and classified burrows as active or inactive then marked each burrow with flour to prevent double counts. Burrows were classified as active based on the presence of a prairie dog, fresh prairie dog scat, or recent evidence of digging (Biggins et al. 1993, Dullum 2001) and inactive if it met two or more of the following criteria as stated in Desmond and Savidge (1996): (1) presence of unclipped live vegetation on the mound or in the burrow entrance, (2) spider webs over or in the burrow entrance, and (3) the absence of fresh prairie dog scat. I kept separate counts of active and inactive burrows on mechanical clicker counters.

Based on my counts of active burrows, I calculated prairie dog densities following the formula outlined in Biggins et al. (1993): *prairie dog density = (0.179 x active burrow density) / 0.566*. In this formula, 0.179 is the relation between counts of active burrows and prairie dogs and 0.566 is an observability index of black-tailed prairie dogs developed by D. E. Biggins and L. R. Hanebury (U. S. Fish and Wildlife Service, unpublished data).

Mean Nearest Neighbor and Mean Nest-to-Edge Distances. Nearest neighbor distances within all prairie dog study colonies were determined in meters using GIS. I defined nearest neighbor distance as the next closest active nest site, either within the same colony or in a different colony (Griebel 2000). The distance from a nest location to the edge of a prairie dog colony was determined using GIS. Both nearest neighbor and nest-to-colony edge distances were averaged by colony.

Vegetation Structure. I measured total herbaceous vegetation cover, composition by category, and average height (per quadrat) in randomly located Daubenmire frames (i.e., 20 cm x 50 cm; Daubenmire 1959) along parallel line transects on colonies during July 2006. Vegetative categories included percent cover of warm-season grass, cool-season grass, forbs, litter, and bare ground. The total number of quadrats per colony increased with colony size: colonies <20 ha = 30 quadrats, 20 – 40 ha = 40 quadrats, and

>40 ha = 50 quadrats. To capture the maximum amount of variation along vegetative gradients, I located transects perpendicular to topographic contours (Martin et al. 1997). I assigned the number of transects per colony based on colony size: 0 – 8 ha = 2 transects; 8 – 16 ha = 3 transects; 16 – 24 ha = 4 transects; 24 – 32 ha = 5 transects; 32 – 40 ha = 6 transects; and >40 ha = 10 transects. Finally, I obtained weighted averages of cover for each vegetative category per study colony.

Colony Isolation and Habitat. Using the colony mapping data, I placed study colonies into two spatial classifications: (1) *degree of isolation*: the distance in kilometers to a single colony or colony complex and (2) *habitat*: upland or lowland. A colony was considered part of a complex if it was within 2.4 km of two or more colonies; this distance encompassed both the average home-range size of burrowing owls (2.41 km^2; Haug and Oliphant 1990) and average dispersal distance of prairie dogs (2.4 km; Garrett and Franklin 1988). I considered colonies >2.4 km from other colonies to be isolated on the landscape. I classified colonies as upland or lowland based on their topographic location in relation to the Bad River, the predominant river bisecting the ranch. Lowland colonies were within or just above the Bad River floodplain; upland colonies were located on plateaus >500 m above the floodplain.

Data Analysis

Burrowing Owl Colony Productivity

I developed a suite of 13 *a priori* candidate models (Table 3.1) to investigate hypothesized associations between the log of burrowing owl colony productivity (lnOP;

mean number of fledglings counted per colony) and eight habitat covariates at the colony and landscape scales. My suite of candidate models included a global model containing the following explanatory variables: colony size (CS), prairie dog density (PD), total burrow density (B), mean nearest neighbor distance (NN), mean nest-to-colony edge distance (NE), proportion of warm-season grasses (WSG), degree of colony isolation (I), and colony habitat (H). Prior to evaluating these models, I calculated Pearson correlation coefficients to test for multicollinearity among habitat variables (Table 3.2). I assessed the goodness-of-fit of the global model by estimating the dispersion parameter ϕ: $\hat{\phi} = \Sigma_i (y_i - \mu_i)^2 / \hat{\mu}_i \big/ n - p$ (Faraway 2006). A $\phi > 1$ represents overdispersion, $\phi < 1$ is underdispersion, while $\phi = 1$ indicates variance in $\mathrm{Y} = \phi \, \mathrm{EY} = \phi \, \mu$. Overdispersion indicates the presence of extra, unexplained variation in the response variable (e.g., burrowing owl colony productivity) and typically occurs when one or more important factors were not measured (McCullagh and Nelder 1989, Rotella et al. 2007).

To assess support for my candidate models I employed a LCV criterion (Sakamoto and Shirahata 1999, Liquet et al. 2007). This criterion estimates the expectation of the log likelihood (ELL) for a model by jackknife cross-validation (Sakamoto and Shirahata 1999, Liquet et al. 2007). The LCV criterion constructs a score, similar to the Akaike information criterion (AIC; Akaike 1973), but yields better results in the overall goodness-of-fit than AIC because it reduces the bias of estimates and performs better when sample size is small (Sakamoto and Shirahata 1999).

I ran the suite of *a priori* models using a jackknife cross-validated generalized linear model (JackGLM) function (written by Mark L. Taper in program R; Appendix A).

The JackGLM function used the prediction likelihood as the error measure. This method has been shown to be an effective estimator of the Kullback-Leibler distance (Liquet et al. 2007) and has been tested in model selection for Poisson regression (Sakamoto and Shirahata 1999). I chose Poisson regression because my response variable consisted of discrete counts of burrowing owl fledglings that were independent in nature and thus likely to follow a Poisson distribution (Kutner et al. 2005, Faraway 2006). It should be noted that these information criteria are functions of the model's log-likelihood and the number of fitted parameters, k. In most analyses, k is equal to the number of regression parameters, including the intercept if there is one, plus one (i.e., 1) for the error variance. In Poisson regression, the error variance is not a distinct parameter so k is just the number of regression parameters.

I selected models with the smallest ELL, i.e., the product of -2ln(predicted likelihood), and ranked them in ascending order. I believed that models with the lowest ELL values would better approximate burrowing owl colony productivity. To determine the strength of support for each candidate model I also calculated $\Delta \mathrm{ELL}$ (the amount each model in the suite differed from the model with the lowest ELL). Similar to information theoretic criterion, I considered models within $\Delta \mathrm{ELL} \leq 2$ from the "top model" to be equally parsimonious (Burnham and Anderson 2002, Taper 2004) and assessed the biological importance of each covariate of the top models by calculating 95% confidence intervals. Confidence intervals around beta estimates for each covariate that overlapped zero were not considered strong predictors of burrowing owl colony productivity.

After evaluating my *a priori* candidate models, I conducted an exploratory analysis of burrowing owl colony productivity and the selected habitat covariates to generate new hypotheses from the dataset (Taper and Gogan 2002). I evaluated subsets of single, additive, and interactive models using the jackknife prediction log likelihood as a model selection technique with the JackGLM function (discussed above) in R 2.5.1 (R: Copyright 2005, The R Foundation for Statistical Computing Version, 2005-12-20 r36812). As with ranking the candidate *a priori* models, I selected models with the smallest ELL and ranked them in ascending order. Finally, I used the same information-theoretic approach outlined above to determine the strength of support for each hypothesis generating model.

Predictions

At the colony scale, burrowing owl productivity is positively influenced by the availability of suitable nesting habitat, prairie dog densities, and the presence of nest and satellite burrows (Butts and Lewis 1982, Desmond 1991, Ekstein 1999, Griebel 2000). Large colonies can harbor more breeding pairs of burrowing owls, greater mean nesting space, and increased hunting opportunities (Desmond 1991, Griebel 2000). High densities of prairie dogs may increase productivity by alerting burrowing owls to approaching predators, maintaining burrow structure, and clipping tall vegetation around burrows (Butts and Lewis 1982). High burrow density provides burrowing owls with favorable nest sites, perches, shelter, and escape cover (Butts 1973). Thus, I predicted that burrowing owl colony productivity would be positively related to prairie dog colony size, prairie dog density, and total burrow density.

I hypothesized that mean nearest neighbor and mean nest-to-colony edge distances would be contingent upon colony size. Given the skewed distribution toward small-sized colonies (<20 ha) in my study area, I predicted burrowing owl colony productivity would be greater for mean nearest neighbor distances <100 m. Colonies <35 ha in Nebraska had shorter mean nearest neighbor distances (105 m) and had higher fledging survival than those with neighbors >175 m (Desmond and Savidge 2000). Nest success was positively related to nest distance from colony edge in Colorado (Ekstein 1999); similarly, I expected productivity would be greater for burrowing owls nesting farther from colony edges where predators may lurk.

Table 3.1. *A priori* candidate model abbreviations, descriptions, structures, and hypothesized effects of prairie dog colony and landscape scale habitat covariates influencing the log of burrowing owl colony productivity (lnOP) in 2006 on the Bad River Ranches, South Dakota.

Abbreviation	Variable Description	Model Structure	Hypothesized Coefficient Result
CS	Prairie dog colony size (hectares)	$\ln OP = \beta_0 + \beta_1(CS)$	$\beta_1>0$
PD	Prairie dog density (# per hectare)	$\ln OP = \beta_0 + \beta_1(PD)$	$\beta_1>0$
B	Total burrow density (#active and inactive per colony)	$\ln OP = \beta_0 + \beta_1(B)$	$\beta_1>0$
NN	Mean nearest neighbor distance (meters)	$\ln OP = \beta_0 + \beta_1(NN)$	$\beta_1>0$
NE	Mean nest-to-colony edge distance (meters)	$\ln OP = \beta_0 + \beta_1(NE)$	$\beta_1>0$
WSG	Percent canopy cover of C4 grasses (weighted average % cover per colony)	$\ln OP = \beta_0 + \beta_1(WSG)$	$\beta_1>0$
I	Degree of colony isolation (kilometers)	$\ln OP = \beta_0 + \beta_1(I)$	$\beta_1<0$
H	Colony habitat (upland or lowland)	$\ln OP = \beta_0 + \beta_1(H)$	$\beta_1>0$ (upland)
NN * CS	Mean nearest neighbor * colony size	$\ln OP = \beta_0+\beta_1(NN)+\beta_2(CS)+ \beta_3(NN*CS)$	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$
NE * CS	Mean nest-to-colony edge * colony size	$\ln OP = \beta_0+\beta_1(NE)+\beta_2(CS)+ \beta_3(NE*CS)$	$\beta_1>0$, $\beta_2>0$, $\beta_3>0$
I + H + CS	Isolation + habitat + colony size	$\ln OP = \beta_0 + \beta_1(I) + \beta_2(H) + \beta_3(CS)$	$\beta_1<0$, $\beta_2>0$, $\beta_3>0$
I * H	Isolation* habitat	$\ln OP = \beta_0 + \beta_1(I) + \beta_2(H) + \beta_3(I*H)$	$\beta_1<0$, $\beta_2>0$, $\beta_3>0$
GLOBAL	All variables	$\ln OP = \beta_0+\beta_1(CS)+\beta_2(PD)+ \beta_3(B) +\beta_4(NN)+\beta_5(NE) +\beta_6(WSG)+ \beta_7(I)+ \beta_8(H)\ \beta_9(NN*CS)+ \beta_{10}(NE*CS)+ \beta_{11}(I+H+CS)+ \beta_{12}(I*H)$	$\beta_1>0$, $\beta_2>0$,$\beta_3>0$, $\beta_4>0$,$\beta_5>0$, $\beta_6>0$, $\beta_7<0$, $\beta_8>0$,$\beta_9>0$, $\beta_{10}>0$, $\beta_{11}<0$, $\beta_{12}>0$

Furthermore, I predicted the proportion of warm-season grasses within colonies would be positively associated with burrowing owl colony productivity. Productivity and survival of pre-fledged juveniles may be enhanced by the presence of short-stature vegetation (e.g., warm-season grasses such as buffalograss) and bare ground surrounding burrows by increasing predator detection and simplifying movement among satellite burrows (Butts 1973, Ross 1974, Haug 1985, MacCracken et al. 1985a, b, Green and Anthony 1989, Winter et al. 2005).

At the landscape scale, the degree of colony isolation may indirectly influence burrowing owl colony productivity. Burrowing owls nesting in isolated colonies may have more difficulty finding or replacing mates, and locating other colonies during dispersal to than colonies grouped in a complex. Therefore, I predicted an inverse relationship between burrowing owl colony productivity and the degree of colony isolation. Finally, I expected burrowing owl colony productivity would be greater in colonies located in upland areas. Upland colonies are typically located farther from river corridors and are treeless, which reduces the probability nest burrows will flood or young will be exposed to tree-dwelling predators.

Results

Burrowing Owl Fledgling Counts

Fourteen of the 16 prairie dog colonies surveyed in 2006 were occupied by burrowing owls. I monitored 142 successful burrowing owl nests and recorded a total of 700 fledglings (Table 3.3). The maximum number of fledglings observed at successful nests ranged from 1 to 13 fledglings ($\bar{x} = 5$, SD = 2.54), whereas the mean number of fledglings per colony was 50 (range = 11 to 103, SD = 31.26).

Habitat Covariates

The Pearson correlation coefficients, which indicate the strength and direction of a linear relationship between two random variables, suggested several habitat variables were highly correlated ($r > 0.5$; Table 3.2). Prairie dog density and total burrow density had the highest correlation ($r = 0.87$; n = 14), followed by colony size with mean nearest neighbor distance ($r = 0.58$; n = 14).

The habitat variables I measured in 2006 varied among study colonies (Table 3.4). I observed burrowing owl fledglings occupying prairie dog study colonies that ranged in size from 3.42 to 145.32 ha. Prairie dog density ranged from 6.66 to 64.09 (dogs/ha) and total burrow density ranged from 58.38 to 415.25 (burrows/ha). Burrowing owls showed a mean nearest neighbor distance of 117.57 m (SE = 40.04) and mean nest-to-nearest colony edge distance of 70.93 m (SE = 18.83). Compared with the percentage of vegetation in each category, warm-season grasses comprised the smallest average cover ($\bar{x} = 11.0\%$, SE = 12.0) per colony. Total average cover of cool-season grasses was 14.0% (SE = 9.0, range = 2.0 to 30.0), forb cover averaged 12.0% (SE = 9.0, range = 3.0 to 30.0), bare ground cover averaged 26.0% (SE = 15.0, range = 3.0 to 52.0), and the average cover of litter was 37.0% (SE = 10.0, range = 22.0 to 57.0). The average height of vegetation among study colonies ranged from 13.54 to 25.19 cm ($\bar{x} = 22.07$, SE = 3.04).

At the landscape scale, 50.0% (n = 7) of the prairie dog study colonies were isolated on the landscape (i.e., >2.4 km from other colonies) and 50.0% (n = 7) formed a complex (i.e., colonies within 2.4 km of two or more other colonies). The mean number of fledglings per colony was greater in isolated colonies (n = 422 fledglings, $\bar{x}$ = 60.29, SE = 25.58, range = 25 to 103) than in colony complexes (n = 278 fledglings, $\bar{x}$ = 39.72, SE = 34.87, range = 11 to 103). The degree of colony isolation ranged from 0 to 4.13 km (Table 3.4). Of the 14 study colonies containing burrowing owl fledglings, 78.6% (n = 11) were located on upland plateaus and 21.4% (n = 3) were in lowland areas.

Table 3.2. Pearson correlation coefficients among prairie dog colony and landscape level habitat variables used to explain burrowing owl colony productivity in 2006 on the Bad River Ranches, South Dakota.

	CS	PD	B	NN	NE	WSG	I	H
CS	1.00	-0.66	-0.55	0.58	0.37	0.20	-0.18	-0.29
PD		1.00	0.87	-0.60	-0.06	0.10	-0.15	0.15
B			1.00	-0.68	-0.02	0.24	-0.29	-0.03
NN				1.00	-0.05	0.05	0.10	-0.26
NE					1.00	-0.16	-0.35	0.11
WSG						1.00	-0.34	-0.51
I							1.00	0.12
H								1.00

Table 3.3. The total number of burrowing owl fledglings counted at nests within prairie dog study colonies (n = 14) during the 2006 breeding season on the Bad River Ranches, South Dakota.

Colony ID	Colony size (ha)	Total number of nests located	Total number of fledgling owls
37	4.22	4	25
B	4.88	5	11
14	3.42	11	29
E	5.98	7	26
19	10.21	3	18
40	13.75	3	17
7	18.20	14	73
4	22.02	18	103
3	24.24	10	68
28	24.60	6	39
1	41.22	16	66
2	79.96	8	48
23	108.47	16	74
34	145.32	21	103
Total number of nests and fledglings:		*n = 142*	*n = 700*

Table 3.4. Summary of continuous habitat and landscape level variables measured at burrowing owl nest colonies during 2006 on the Bad River Ranches, South Dakota.

Covariate	Mean (± SE)	Range
Colony size (ha)	36.18 ± 43.89	3.42 to 145.32
Prairie dog density (dogs/ha)	28.57 ± 13.80	6.66 to 64.09
Total burrow density (burrows/ha)	175.30 ± 95.56	58.38 to 415.25
Mean nearest neighbor distance (m)	117.57 ± 40.04	51.80 to 192.50
Mean nest-to- edge distance (m)	70.93 ± 18.83	45.58 to 108.76
Warm season grasses (average %)	11.00 ± 12.00	0.00 to 29.00
Degree of colony isolation (km)	1.37 ± 1.53	0.00 to 4.13

Burrowing Owl Colony Productivity and Habitat Associations

The log of burrowing owl colony productivity (lnOP) was predicted by *a priori* models (Table 3.1) containing both habitat and landscape level covariates. Based on the minimum expected log-likelihood value, model $\ln OP = \beta_0 + \beta_1(I) + \beta_2(H) + \beta_3(CS)$ was the top-ranking *a priori* model. This model received more support than any alternative model in the suite (Table 3.5) and indicated productivity was positively influenced by the additive effect of prairie dog colony size, isolation, and habitat. As suggested by the confidence intervals of the covariates, the effects were real (Table 3.6). The equation representing the top model of the log of burrowing owl colony productivity on the Bad River Ranches was: $\ln OP = 3.0312 + 0.2277\ (Degree\ of\ Colony\ Isolation) + 0.2338\ (Colony\ Habitat) + 0.0108\ (Colony\ Size)$.

The remaining colony and landscape level habitat variables poorly predicted burrowing owl colony productivity. Single predictor models containing covariates of colony size, prairie dog density, total burrow density, mean nest-to-edge distance, the degree of isolation, mean nearest neighbor distance, cover of warm-season grass, and colony habitat received little support (i.e., ΔELL ≥ 9.81). I also found little evidence of interactive effects of colony size and mean nest-to-colony edge distance (CS*NE; 95% CI: -0.0001 to 0.0001), degree of isolation and habitat (I*H; 95% CI: 0.3023 to 0.5415), and colony size and mean nearest neighbor distance (CS*NN; 95% CI: -0.0004 to 0.0000) on burrowing owl colony productivity.

Table 3.5. *A priori* model selection results based on jackknife prediction log likelihood of the log of burrowing owl colony productivity within prairie dog colonies (n = 14) in 2006 on the Bad River Ranches, South Dakota. The expected log likelihood (ELL) is the product of -2 and the predicted log likelihood. Models are ranked by the ascending ΔELL; *k* is the number of parameters in each model.

Candidate Model	*k*	ELL	ΔELL
I + H + CS	4	278.95	0.00
CS	2	288.75	9.81
PD	2	321.08	42.13
B	2	323.24	44.29
CS + NE + CS * NE	4	392.45	113.50
NE	2	397.27	118.33
I	2	397.74	118.80
NN	2	405.71	126.76
WSG	2	439.94	161.00
H	2	515.73	236.79
I + H + I * H	4	751.88	472.93
CS + NN + CS * NN	4	3477.29	3198.34
Global	12	1.65E+53	1.65E+53

Table 3.6. Parameter estimates from the top *a priori* model of the log of burrowing owl colony productivity within prairie dog colonies in 2006 on the Bad River Ranches, South Dakota.

Model = I + H + CS

Parameter	Estimate	SE	95% LCI	95%UCI
Intercept (β_0)	3.0312	0.2854	2.8473	3.2080
Degree of isolation (β_1)	0.2277	0.0261	0.1766	0.2789
Habitat (β_2)	0.2338	0.3124	0.0340	0.4289
Colony Size (β_3)	0.0108	0.0028	0.0090	0.0126

Exploratory Analysis

Based on the variables included in the *a priori* models, I evaluated subsets of single, additive, and interactive exploratory models. Post-hoc exploratory analysis revealed one top supported model of burrowing owl colony productivity (Table 3.7). This model, $\ln OP = \beta_0 + \beta_1(CS) + \beta_2(I)$, suggested the additive influence of colony size and the degree of isolation had a positive effect on burrowing owl colony productivity. The confidence intervals of each coefficient did not overlap zero, which suggested their slopes were different from zero (Table 3.8). When this model was evaluated in a suite containing the *a priori* models, it was clearly the best approximation of burrowing owl colony productivity (Table 3.7). The second-ranked model, $\ln OP = \beta_0 + \beta_1(CS) + \beta_2(I) + \beta_3(CS*I)$, was >2 ΔELL (i.e., ΔELL = 4.83) from the top exploratory model and the best approximating *a priori* model was nearly >48 ΔELL units from the top exploratory model.

Discussion

While the results of my analyses must be viewed within the boundaries of this data set, they are comparable to reported parameters in other populations of breeding burrowing owls. The mean number of fledglings I observed at successful nests (i.e., 5.0 fledglings per total nests) on the Bad River Ranches was greater than that reported for prairie dog colonies in Colorado (4.4; Plumpton 1992), Nebraska (4.0; Desmond 1991),

Table 3.7. The log of burrowing owl colony productivity model ranking for 15 of the combined *a priori* and exploratory candidate models on the Bad River Ranches, South Dakota, 2006. The expected log likelihood (ELL) is the product of -2 and the predicted log likelihood. Models are ranked by the ascending ΔELL; *k* is the number of parameters in each model.

Candidate Model	*k*	ELL	ΔELL
CS + I	3	229.97	0.00
CS + I + CS*I	4	234.80	4.83
CS + forbs + CS*forbs	4	238.14	8.17
PD + forbs + PD*forbs	4	266.87	36.90
PD + litter + PD*litter	4	277.22	47.25
I + H + CS	4	278.95	48.98
CS	2	288.75	58.78
B + forbs + B*forbs	4	290.29	60.32
CS + WSG	3	296.47	66.50
CS + forbs	3	300.82	70.85
B + NN	3	300.94	70.97
CS + height	3	301.72	71.75
CS + NE	3	304.10	74.13
B + bare + B*bare	4	304.10	74.13
CS + CSG	3	305.24	75.27

Table 3.8. Parameter estimates from the top exploratory model of the log of burrowing owl colony productivity within prairie dog colonies on the Bad River Ranches, South Dakota, 2006.

Model = CS + I				
Parameter	Estimate	SE	95% LCI	95%UCI
Intercept (β_0)	3.1023	0.0859	2.9303	3.2670
CS (β_1)	0.0102	0.0009	0.0085	0.0119
Degree of Isolation (β_2)	0.2317	0.0260	0.1807	0.2827

North Dakota (4.0; Konrad and Gilmer 1984), Oklahoma (4.7; Butts 1973), South Dakota (4.0; Griebel 2000), and Wyoming (4.5; Lantz 2005).

The best approximating models of burrowing owl colony productivity on the Bad River Ranches included both prairie dog colony and landscape level habitat variables. The model results suggested the additive influence of the colony size and the degree of isolation was a positive predictor of productivity. In Nebraska and South Dakota, nest productivity was also positively influenced by prairie dog colony size where habitat was not limited (i.e., larger colonies fledged more chicks than small colonies; Desmond 1991, Ekstein 1999, Griebel 2000). Predation risk to fledglings may be reduced in large colonies because ostensibly there are more prairie dogs and other burrowing owls to aid in detecting predators, more burrows to seek escape cover, and predators have a greater area to search for prey (Desmond et al.1995, Clayton and Schmutz 1999). In contrast to my prediction and to observations by Ekstein (1999), productivity was positively related to the degree of colony isolation. It may be that isolated prairie dog colonies on the ranch were not saturated with nesting owls, such that each breeding pair was able to rear young in optimal nest locations and in turn, this translated into higher productivity.

The variable topography on the Bad River Ranches led me to predict burrowing owls nesting in large, upland colonies surrounded by other colonies would have greater productivity. The results from my *a priori* analysis, however, demonstrated productivity was positively influenced by the additive effect of colony isolation, lowland habitats, and colony size. Although reasons for this relationship are uncertain, these three factors combined may outweigh the negative features I associated with isolated, lowland colonies. For example, a medium-sized colony (#4) that was located in a lowland area, and isolated from other colonies produced the greatest number of fledglings (n = 103).

Models including the remaining colony-level habitat covariates had negligible effects on burrowing owl colony productivity. In other studies of burrowing owl nest ecology (Plumpton 1992, Ronan 2002, Lantz 2005), site characteristics also had little influence on reproductive parameters. While I referenced results of previous studies to select biologically relevant, *a priori* covariates, it may be that I failed to measure one or more factors important to breeding burrowing owls.

I expected a positive association between owl productivity and prairie dog density and total burrow density, but my analysis indicated a weak negative effect of both variables. Prairie dog density and total burrow density were highly correlated; prairie dog density was derived from counts of active and inactive burrows in each study colony, and I expected this measure to covary with total burrow density. Research relating total burrow density to nest productivity has yielded disparate results. In Nebraska, Ekstein (1999) found that nest success and total burrow density within 50 m of the nest were negatively related, whereas Desmond and Savidge (1999) and Desmond et al. (2000) found a positive relationship between burrow density surrounding nests and the number of fledglings produced. In Montana and North Dakota, productivity and juvenile survival was not correlated to the total number of burrows within a 30-m radius of the nest (Restani 2001, Restani et al. 2001, Davies and Restani 2006). Alternatively in South Dakota, total burrow density was positively related to the mean number of young fledged (Griebel 2000) and nests surrounded by high numbers of active satellite burrows had significantly greater reproductive success (Desmond and Savidge 1999). In Colorado, Plumpton (1992) reported a negative correlation ($r = -0.0237$, $P = 0.9125$) between the mean number of young fledged and density of available burrows in one year, but a positive correlation ($r = 0.0553$, $P = 0.7884$) the following year; neither of these correlations were significant, however, and the observed difference is likely attributed to sampling noise.

Mean inter-nest distances and the average distance of owl nests to colony edge had a slight, positive influence on burrowing owl colony productivity. Given the skewed distribution of small-sized colonies (<20 ha) in my study area, I predicted burrowing owl colony productivity would be greater for mean nearest neighbor distances <100 m. The relationship between productivity and mean nearest neighbor distance was not significant and the model containing the interaction between colony size and mean nearest neighbor distance received little support. Similar to results documented by Griebel (2000), nest distance from the nearest colony edge did not appear to affect burrowing owl colony productivity in South Dakota.

Despite the benefits of short vegetation to burrowing owls, its structure and composition within colonies do not appear to strongly influence their productivity (Desmond 1991, Teaschner 2005). Productivity was not related to vegetation height in Nebraska (Desmond 1991), nor was it correlated with measures of visual obstruction and vegetative composition in Texas (Teaschner 2005). Because vegetation within colonies is typically short as a result of grazing by prairie dogs and livestock or drought conditions, the relationship between composition or structure and burrowing owl colony productivity may not be important.

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CHAPTER 4

SPATIAL DISTRIBUTION OF BURROWING OWL NESTS WITHIN BLACK-TAILED PRAIRIE DOG COLONIES IN SOUTH DAKOTA

Introduction

The primary habitat requirement for breeding burrowing owls (*Athene cunicularia*) is subterranean burrows excavated and maintained by burrowing mammals (McDonald et al. 2004). In the Great Plains ecosystem, burrowing owls most often nest in black-tailed prairie dog (*Cynomys ludovicianus*; hereafter “prairie dog”) burrows (Butts 1973, Ross 1974). Burrows not only provide refuge from inclement weather, but also serve as focal locations for roosting, attracting mates, nesting, rearing young, and avoiding predators (O’Meila et al. 1982, Desmond 1991, Desmond and Savidge 1996, Desmond et al. 2000).

Burrowing owls are often affiliated with particular patches within active prairie dog colonies for establishing nesting territories. Areas of high burrow and prairie dog densities appear to explain this habitat specificity (Plumpton 1992, Haug et al. 1993, Toombs 1997, Ekstein 1999, Griebel 2000, Restani et al. 2001, Ronan 2002, Lantz 2005). Prairie dog and burrow densities within a colony are naturally heterogeneous due, in part, to forage availability, predator densities, and soil type (Hoogland 1995). Vegetation height and productivity within colony centers has been shown to decline over time (Detling 2006), which often leads to an increase in prairie dog densities at colony edges (Koford 1958). As prairie dogs expand toward colony perimeters, burrows located within colony interiors may degrade over time in the absence of prairie dog maintenance. For this reason, burrowing owls appear to exploit burrows at the edge of colonies as nest sites in lieu of colony centers (Butts 1973, Desmond et al. 1995, Ekstein 1999). Their apparent edge preference may also be a function of the number of available burrows (Butts 1973, Agnew et al. 1986, Desmond 1991) or nearness to the abundance and diversity of prey items (e.g., grasshoppers, small mammals) along colony edges.

Various spatial patterns of burrowing owl nests within and among prairie dog colonies have been documented in previous studies (Butts 1973, Desmond 1991, Desmond et al. 1995). In Oklahoma, Butts (1973) observed the spatial organization of nests on some colonies to be clumped while others were located at colony perimeters. In Nebraska, Desmond (1991) and Desmond et al. (1995) concluded that burrowing owls favored nesting in loose aggregations or “clusters” where habitat was not limited (i.e., colonies >35 ha) and exhibited a random distribution where habitat was limited (i.e., colonies <35 ha). Subsequent studies have assessed reproductive parameters in relation to nest distance from the colony edge. Ekstein (1999) found that nest success increased with distance from colony edge, while reproductive parameters measured by Griebel (2000; clutch size, brood size, and number of chicks fledged) were not significantly influenced by the proximity to colony perimeters.

The goal of this chapter was to evaluate the spatial distribution of burrowing owl nests within prairie dog colonies in South Dakota. Given the variation in prairie dog and burrow densities within colonies, and the potential benefits to owls nesting near colony edges, I hypothesized that nests would be distributed along colony perimeters. Biologically, peripheral nesting may contribute to productivity by allowing for better access to prey items and reducing the time and energy adults spend foraging (Desmond et al. 1995, Warnock and James 1997), thus I predicted burrowing owl nest productivity would decline with distance from colony edges. I defined nest productivity as the maximum number of burrowing owl fledglings counted per nest during multiple census periods.

Methods

Study Area

The study population included prairie dog colonies located within the Bad River Ranches (hereafter "ranch"), which comprise about 570 km² in Stanley and Jones counties near Fort Pierre (44°21′N, 100°22′W), South Dakota. The ranch lies within the mixed-grass system of the Northern Great Plains (Kuchler 1975). The topography was composed of mixed-grass, flat to rolling uplands cut by the Bad River and intermittent drainages; elevations varied from about 457 m above sea level in lowland bottoms to 610 m on upland plateaus. Average annual precipitation was 48.29 cm, with 65% falling during the April – August breeding season. Mean monthly temperatures ranged from –7.47ºC in January to 24ºC in July (http://climate.sdstate.edu). Soils were primarily clays derived from Createaceous Pierre Shale (Johnson et al. 1995). Kuchler (1975) characterized the area as a wheatgrass-needlegrass (*Stipa viridula*) community; buffalograss and blue grama grass also were widespread (K. Bly and J. Truett, unpublished data).

The ranch, owned by R. E. Turner, is managed for the sustainable production of bison and conservation of native species. At the time of this study the ranch supported approximately 5,000 bison divided among several herds that grazed pastures north and south of the Bad River on a rotating basis. During 2000 – 2004 the Turner Endangered Species Fund (a private, non-profit charity dedicated to conserving biodiversity on Turner lands) restored prairie dogs to selected sites on the ranch, largely by establishing new colonies and managing habitat to encourage colony growth. Including the reintroduced colonies, the ranch had 82 colonies occupying 765 ha in 2005, which grew to 87 colonies occupying 813 ha the following year.

I conducted this research from May – August 2005 and May – September 2006. Prairie dog study colonies were randomly selected from three size categories: small (0-20 ha), medium (20-40 ha), and large (>40 ha), and from two landscape types (i.e., colonies grouped in a complex and isolated) and habitats (i.e., lowland and upland colonies). In 2005, I surveyed 10 of the 82 colonies (pre-existing and reintroduced) ranging in size from 2.55 to 129.26 ha. In 2006, I surveyed 16 (the same 10 colonies plus an additional six) of the 87 ranch colonies ranging in size from 2.75 to 145.32 ha. All prairie dog colonies surveyed were active; no prairie dog poisoning or shooting occurred on study colonies for six years prior to and during the research period (K. Bly and J. Truett, unpublished data).

Nest Data Collection

Each study colony was surveyed for burrowing owl nests during May and June of 2005 and 2006. To locate nests, I visually inspected each prairie dog burrow by walking parallel line transects 10 – 25 m apart. To prevent resampling nests and burrows, I marked each burrow with flour or white chalk. Transect length depended on the width of individual colonies. I identified nests by the physical presence of burrowing owls, strands of shredded material (dung, yucca), feathers, prey remains, regurgitated castings, and whitewash at the entrance of nest burrow (Desmond 1991). I made repeated observations of each nest to confirm the presence of fledglings. Nests initiated after June 30th of each year were not included in my analyses. It was possible that on large colonies a few nests were not located. Although I did not obtain a nest detection probability, I believe detectability was similar among nests because of the intensive search effort conducted for each colony.

I marked all burrowing owl nest locations with two methods. First, I placed a round aluminum identification tag secured with a steel ground staple (www.forestry-suppliers.com) 1 m north of each nest burrow. Next, I obtained universal transverse mercator coordinates with a Garmin 12CX Global Positioning System (GPS) unit. The GPS waypoints were then downloaded into the GIS program ArcView 3.2a (ESRI 2000). To determine burrowing owl nest densities for each study colony, I divided the estimated number of nests by the size of the prairie dog colony (see "Habitat Covariates" below for description of colony size).

Burrowing Owl Fledgling Counts

Burrowing owl nest productivity was estimated at each nest within study colonies during 2006 only. I defined nest productivity as the maximum number of fledglings observed during multiple censuses for burrows where fledglings were known to be present throughout the nesting season. To minimize the inherent bias in raptor nesting studies based on single counts (Steenhof 1987) I counted the maximum number of burrowing owl fledglings at each nest during a 60-minute period from ≥100 m away using a spotting scope and binoculars for three independent censuses: June, July, and August 2006. Each observation period was conducted during the early morning (i.e., 0.5 hr before sunrise until 1000 hr) and evening hours (i.e., 1700 hr until 0.5 hr after sunset) when vocalization and aboveground activity of burrowing owls was often highest (Johnsgard 1988, Conway and Simon 2003). Adults were delineated from young based on chest plumage and barring (Priest 1997).

Although each nest received equal observation effort, some visual obstructions (e.g., vegetation, burrows) did preclude accurate fledgling counts for some nests. Therefore, I assumed a 0.71 detection probability of fledglings of known ($\bar{x}$ = 4.5, SE = 0.6, range 1 to 9) versus observed ($\bar{x}$ = 3.2, SE = 0.4, range 1 to 7) mean number of fledglings reported by Gorman et al. (2003).

Habitat Covariates

Using GIS, I determined prairie dog colony size, nest-to-colony edge distance, and the degree of colony isolation. By walking or driving, I estimated the area occupied by a colony of prairie dogs by mapping the outermost, active burrow entrances (Hoogland 1995) with a Garmin 12CX GPS unit in August of each year. Active perimeter burrow entrances were marked as waypoints and then downloaded as shape files for analysis of area in hectares in the GIS program ArcView 3.2a (ESRI 2000). The distance from each nest location to the nearest prairie dog colony edge was measured in meters and the distance each colony was from the next closest colony (i.e., the degree of colony isolation) was measured in kilometers.

Data Analysis

I assessed the spatial distribution of burrowing owls nests within colonies using a Chi-square analysis. First, I obtained the observed and expected distances of nests to nearest colony edges for each study colony. I pooled unique nest locations from 2005 and 2006 and performed a spatial join of each nest to the nearest colony edge (observed distribution) in ArcView 3.2a (ESRI 2000). I then generated 1,000 random points without replacement within each study colony and performed another spatial join of each random point to the nearest colony edge (expected distribution).

Second, in program R 2.5.1 (R: Copyright 2005) I created histograms of the observed versus the expected distances to nearest colony edges. A requirement for Chi-square analysis of categorical data is that the minimum expected cell frequency is ≥ 5. Thus, I conducted analyses for colonies with ten or more nests. For colonies containing

$\geq$15 nests I used three bins, and for colonies containing more than nine but less than 15 nests I used two bins. Distances of nearest colony edge to nests were divided into three bins of approximately equal areas by sorting the random points on distance to nearest edge and creating a distance to edge cut point between (1) the 333rd and the 334th ranked random points and (2) the 666th and 667th ranked random points.

Third, I obtained chi-squared deviates for each of the three bins per colony and produced hanging bar plots of the Pearson's Residuals to determine whether significant differences existed at the 10% critical level. I calculated chi-squared deviates as $(O - E)/\sqrt{E}$; where O is the observed number of nests in each bin and E is the expected number of nests calculated as the total number of nests multiplied by the proportion of random points in each bin. Finally, chi-squared deviate values were squared and then summed to obtain the chi-squared values. For each colony, bins of nest locations exceeding the critical value (±0.10) were considered a significant deviation from the random expectation.

I also assessed the relationship between the spatial location of nests within colonies and burrowing owl nest productivity using linear model regression in program R 2.5.1 (R: Copyright 2005). To account for potential variation in productivity among colonies, I allowed individual colonies to have different intercepts but a common slope for the effect of distance from edge on individual nest productivity. I created an additive linear model including the covariates from the best approximating model of the log of burrowing owl productivity (lnOP) at the colony scale in Chapter 3. The model included colony size (CS) and the degree of colony isolation (I), plus distance from nest to colony edge (NE) variable: lnOP ~ CS + I + NE. I quantified support for the hypothesized relationship between nest productivity and distance to colony edge by evaluating the basic summary statistics associated with this model, including: estimates of the coefficients, standard error, and 95% confidence intervals.

Results

As predicted, burrowing owls displayed a preference for nesting near colony perimeters (Figures 4.1, 4.2, and 4.3). Seven of 16 prairie dog study colonies contained ≥15 nests. Five of these seven colonies demonstrated significant Chi-Squared values at the 0.10 critical level (i.e., ≥4.61; Table 4.1). Nests in the nine remaining colonies appeared to be randomly distributed. Burrowing owl nest densities for the five colonies of significance were ≥0.15 nests/ha (range 0.15 to 0.82 nests/ha). Burrowing owl nest densities for the nine colonies with random nest distributions were ≥0.10 nests/ha (range 0.10 to 3.22 nests/ha). Burrowing owls showed a mean nest-to-nearest colony edge distance of 70.93 m (SE = 18.83, range 45.58 to 108.76).

There was not a significant relationship between nest productivity and nest distance to colony edge (Table 4.2). The linear model regression confirmed the visual impression of Figure 4.4, which displayed the regression between the maximum number of fledglings per nest against nest-to-colony edge distance for each colony. Fourteen of the 16 prairie dog colonies surveyed in 2006 were occupied by burrowing owls. I monitored 142 successful burrowing owl nests and recorded a total of 700 fledglings (Table 3.3). The maximum number of fledglings observed at successful nests ranged from 1 to 13 fledglings ($\bar{x}$ = 5, SD = 2.54), whereas the mean number of fledglings per colony was 50 (range = 11 to 103, SD = 31.26).

Table 4.1. Chi-squared values resulting from observed (i.e., nests) and expected (i.e., random points) distances to nearest colony perimeter. Unique burrowing owl nests located in 2005 and 2006 were pooled. Values exceeding 4.61 were considered significant at the 0.10 chi-squared critical level.

Colony ID	Size Class	Number of nests	$\chi^2 = \Sigma \frac{(x_i - E_i)^2}{E_i}$
7	small	29	8.5816*
4	medium	24	12.0300*
3	medium	22	6.1174*
1	medium	28	16.2856*
2	large	15	1.2066
23	large	37	5.2768*
34	large	33	0.7281

*Significant at the 0.10 chi-squared critical value.

Table 4.2. Parameter estimates from the linear model regression of the effects of nest distance to colony edge on the log of burrowing owl nest productivity within prairie dog colonies in 2006 on the Bad River Ranches, South Dakota.

Model = CS + I + NE

Parameter	Estimate	SE	95% LCI	95%UCI
Intercept (β_0)	3.7160	0.4887	2.7494	4.6825
Colony Size (β_1)	0.0048	0.0047	-0.0045	0.0142
Degree of isolation (β_2)	0.5727	0.1533	0.2695	0.8759
Nest-to-Colony Edge (β_3)	0.0032	0.0043	-0.0053	0.0117

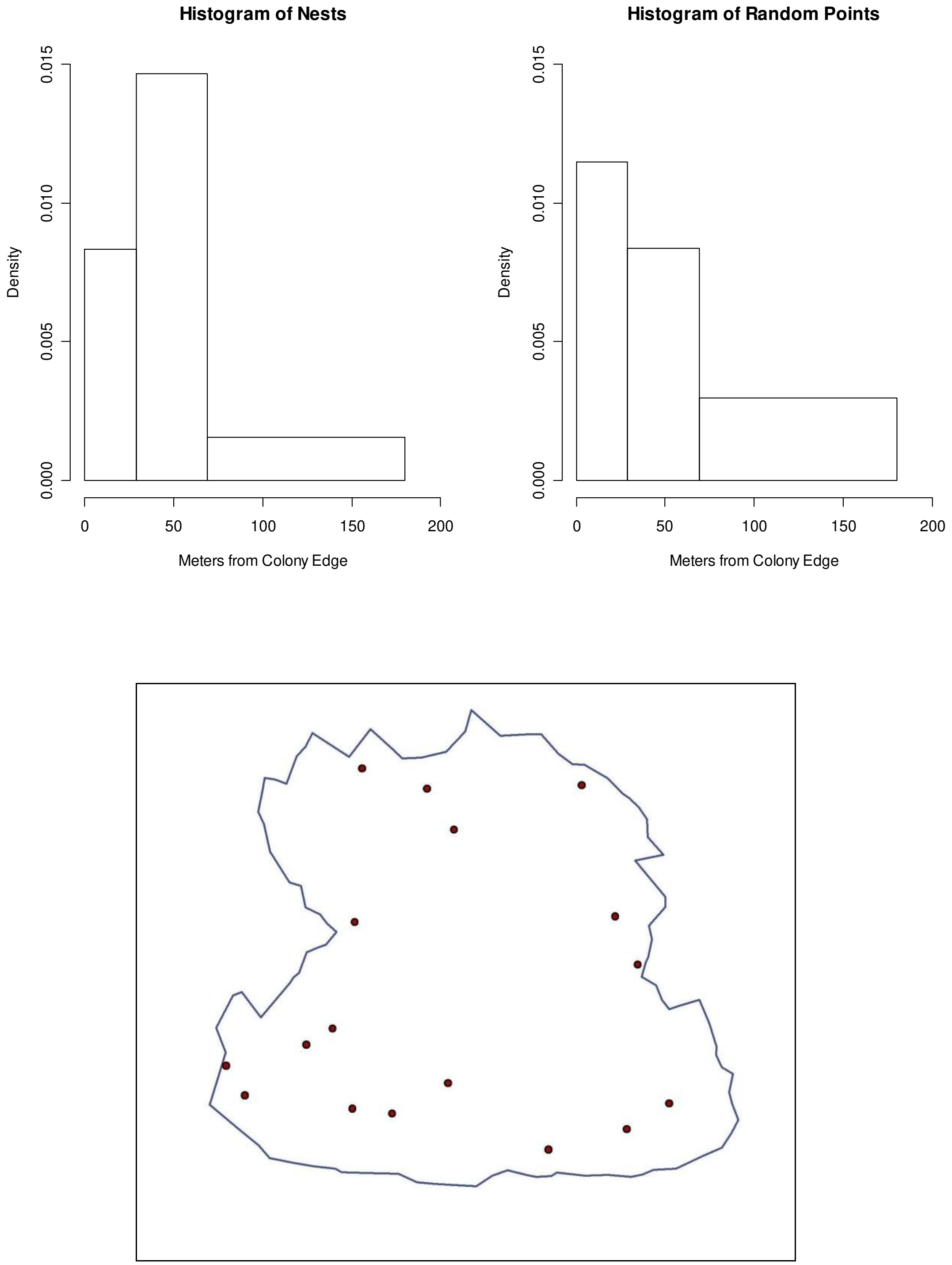

Figure 4.1. Histograms of distance from burrowing owl nests and random points to nearest colony edge compared with 2005 nest locations in prairie dog study colony #7 (small-sized colony, 18.20 ha). Density on the x-axis represents the relative frequency of nests or random points in bins divided by bin width.

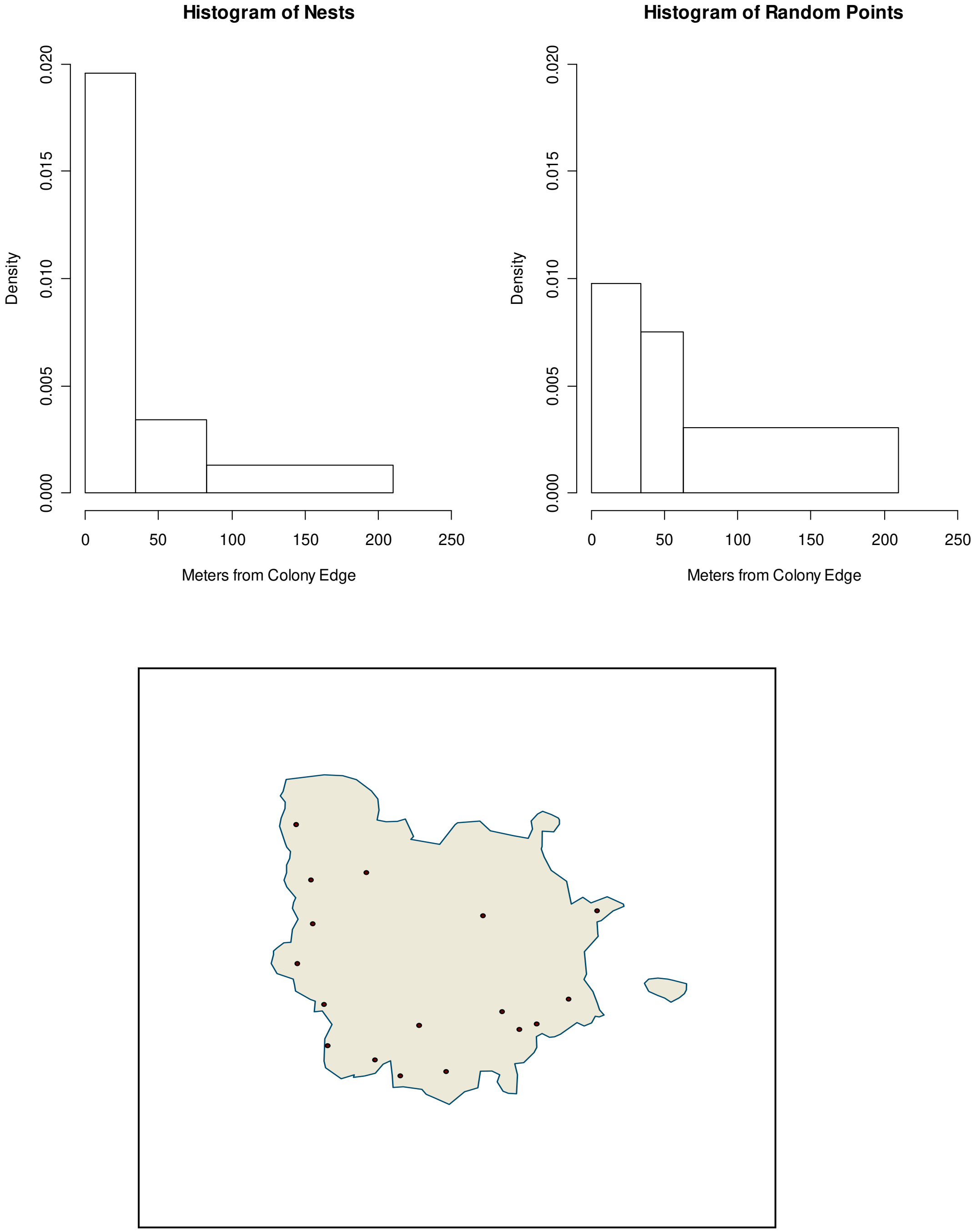

Figure 4.2. Histograms of distance from burrowing owl nests and random points to nearest colony edge compared with 2005 nest locations in prairie dog study colony #4 (medium-sized colony, 22.02 ha). Density on the x-axis represents the relative frequency of nests or random points in bins divided by bin width.

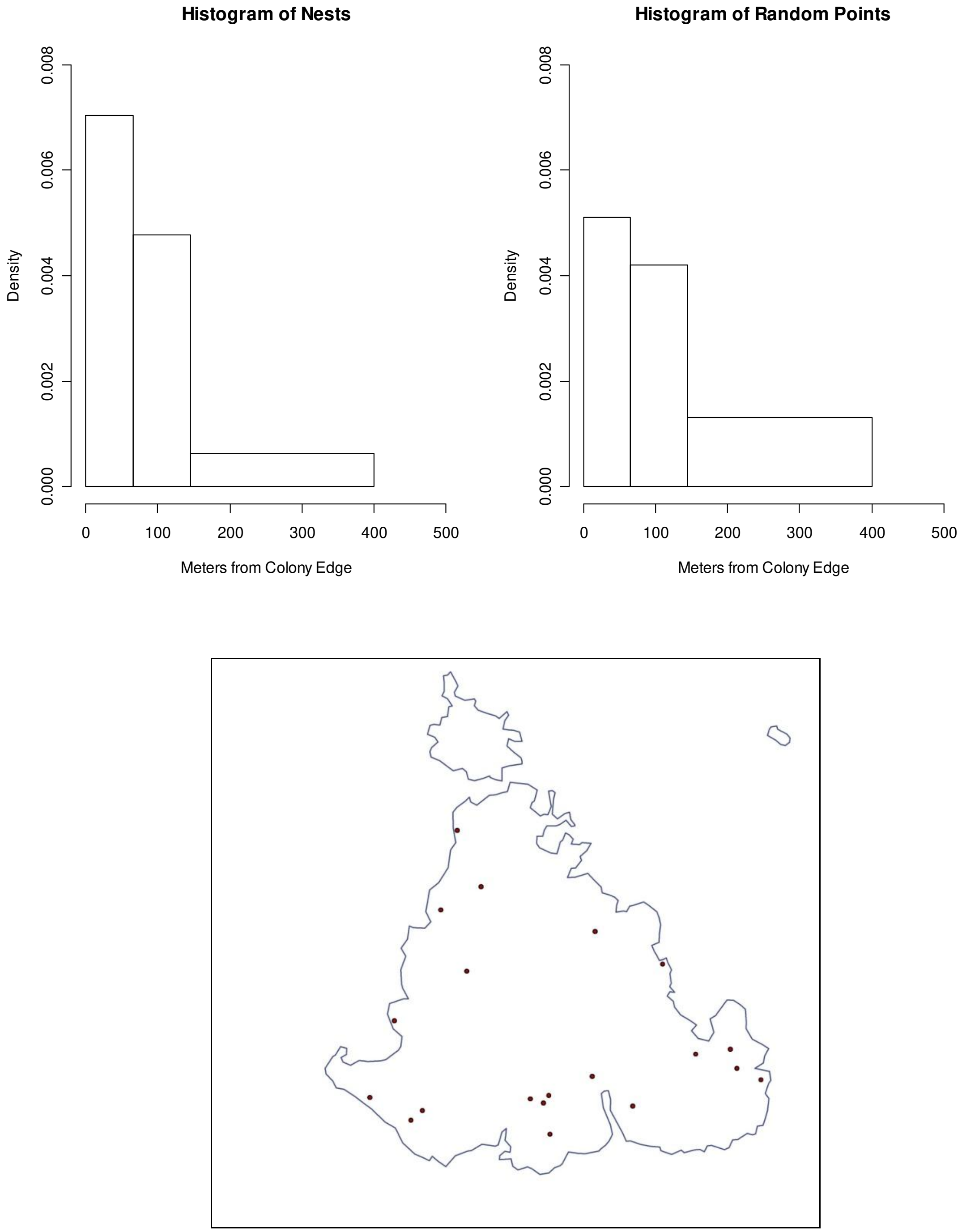

Figure 4.3. Histograms of distance from burrowing owl nests and random points to nearest colony edge compared with 2005 nest locations in prairie dog study colony #23 (large-sized colony, 108.47 ha). Density on the x-axis represents the relative frequency of nests or random points in bins divided by bin width.

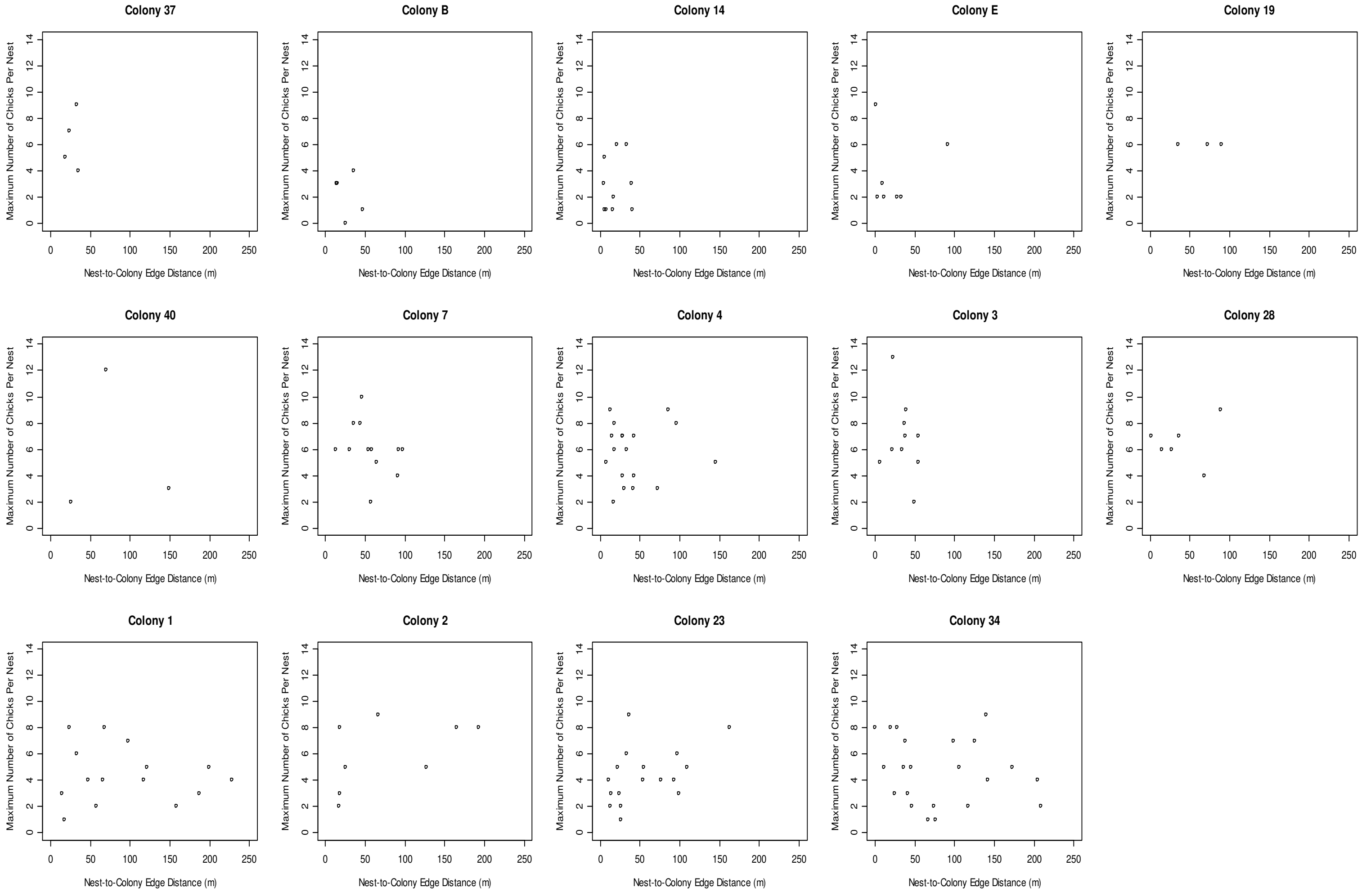

Figure 4.4. Plot of the linear regression between the maximum number of fledglings per nest against the nest-to-colony edge distance for each prairie dog colony in 2006 on the Bad River Ranches, South Dakota.

Discussion

In prairie dog colonies on the Bad River Ranches, burrowing owls nested close to colony edges but this did not translate into higher productivity. As colony size increased, the effect of the distance from the nest burrow to colony edge on burrowing owl colony productivity became more negative. If productivity was strictly a function of the distance from colony edge, however, the relationship between productivity and distance to nearest edge may be the same in both small and large colonies. Distance of owl nests to colony edge did not appear to affect measured reproductive parameters in South Dakota (i.e., clutch and brood size, number fledged; Griebel 2000). Mean nest distances to colony edge in one year of that study were 74.4 m (1999; range: 5.0 to 347.0 m) and 82.2 m (range: 1.0 to 500.0 m) in 2000. Ekstein (1999) found that burrowing owl nest survival was higher when nests were farther from the colony edge. She reasoned that nesting near colony edges may result in lower nest survival due to habitat edge effects. While colony perimeters could provide owls with more nest sites and closer proximity to foraging areas, owls may also be at greater risk of nest predation if predators frequent colony edges (Donovan et al. 1997). This, in part, might explain the minimal effect of nest distance to colony edge on productivity observed in my study.

Unlike results reported by Desmond (1991) and Desmond et al. (1995), spatial patterns of nests relating to small (<35 ha) versus large (≥35 ha) prairie dog colonies did not emerge in my analysis. The authors in both studies suggested that habitat in small colonies was limited and thus nests were distributed randomly, while in large colonies where nesting space was not in short supply burrowing owls nested in clusters. Butts

(1973) also reported aggregations of nests on some colonies and a preference for nesting near colony perimeters on others, but prairie dog colony sizes were not reported. Although I did not test for patterns of clustering, I observed a range of colony sizes (18.20 ha to 108.47 ha) in which burrowing owls concentrated their nests at colony edges.

The apparent edge preference exhibited by breeding burrowing owls nesting in colonies on the Bad River Ranches raises questions about the potential nest-level effects on productivity. Although this study did not evaluate this, future research at the nest level would be valuable as some variables influential to burrowing owl nest productivity may be masked at the colony and landscape levels. For example, why does an edge nesting pattern exist if there isn’t a corresponding fitness effect? I propose several hypotheses: (1) there are fitness effects but they are subtle and emerge after the maximum number of fledglings is counted at each nest or because all possible nest territories are not occupied, (2) the pattern is due to habitat surrounding nest burrows (nest level effects), or (3) predation of burrowing fledglings at colony edges counteracts the potential benefits of increased prey availability.

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CHAPTER 5

THESIS SUMMARY

Research and Management Implications

The objective of this research was to evaluate prairie dog colony habitat factors influencing a population of burrowing owls at the eastern extent of their range in South Dakota. I modeled hypothesized associations between two response variables, burrowing owl nest density (Chapter 2) and colony productivity (Chapter 3), and prairie dog habitat characteristics at the colony and landscape scales. I also evaluated the spatial distribution of owls and their nests within colonies at the nest scale (Chapter 4).

The results of this study suggest that many small (0 – 20 ha) and medium (20 – 40 ha) prairie dog colonies are needed to maximize the number of burrowing owls per hectare in this region. Beyond the Bad River Ranches, across South Dakota, small and medium-sized prairie dog colonies are common ($\bar{x}$ = 28.60 ha, SD = 137.39 ha, range = 0 to 7,593.93 ha, n = 7,703 colonies; Kempema 2007). Colonies on the Lower Brule Indian Reservation southeast of the Bad River Ranches averaged 25.97 ha (n = 68, range = 0.08 to 209.13 ha, SE = 37.80 ha; S. Grassel, Lower Brule Sioux Tribe, personal communication). The importance of retaining small and medium-sized colonies for nesting burrowing owls was highlighted by my observations that small colonies harbored higher nest densities of burrowing owls than did large (>40 ha) colonies. Actively managing for small and medium colonies could help generate increasing amounts of suitable owl nest habitat. In addition, managing for and protecting many isolated colonies

(>2.4 km away from other colonies) would ensure redundancy of burrowing owl in the event of disease outbreaks.

The need for managers to consider both colony and landscape scale habitat characteristics is reinforced by the results of my model selection analysis. Among the habitat variables considered, the most notable *a priori* relationships were between: (1) nest density and colony size and (2) colony productivity and the additive effect of colony size, the degree of isolation, and the topographic location of colonies. Exploratory analysis showed the percent cover of bare ground in lowland habitats was important to nest density and that simply the additive influence of colony size and the degree of isolation mattered to colony productivity. The apparent edge preference exhibited by owls nesting in colonies on the Bad River Ranches raises questions about nest-level effects on productivity, and additional research at this scale is needed to assess this association.

This study demonstrates the importance of prairie dog colonies on the Bad River Ranches in central South Dakota to breeding burrowing owls. Little information existed previously on the Bad River Ranches regarding the status of burrowing owls. This landscape has particular relevance to conservation of burrowing owls because it is one of the few plague-free zones that may support the long-term persistence of prairie dog colonies in the region. The results of this research provide baseline data on burrowing owl nest density and colony productivity within black-tailed prairie dog colonies on the ranch, which can help inform management decisions.

Compared with other burrowing owl populations in the Great Plains, nest density and nest productivity per hectare was high suggesting that ongoing management practices facilitated burrowing owl colony productivity. At the time of my study, management of prairie dog colonies on the Bad River Ranches encouraged colony expansion by intensive early (May and June) grazing by bison (*Bison bison*), mechanical mowing of tall grass in colonies that were not grazed, and the strict prohibition of prairie dog shooting and poisoning. To ensure the persistence of burrowing owl populations in this area, I recommend annual measurements of reproductive parameters and continuity of the successful management practices listed above.

I measured maximum counts of fledglings for only one breeding season. To effectively assess associations between burrowing owl colony productivity and multi-scale habitat variables repeated, reliable measurements are necessary. I suggest future research examine additional demographics including fledgling survival and dispersal in relation to nest and colony scale habitat variables. I also recommend implementing standardized census protocols and detection probabilities into study design and statistical analyses of data in order to provide managers and policy makers with unbiased estimates of burrowing owl reproductive rates (Gorman et al. 2003).

Sylvatic plague, unregulated shooting, and poisoning continue to threaten black-tailed prairie dog populations throughout much of their range. Given their reliance on prairie dog colonies for nesting and foraging habitat, burrowing owl populations directly and indirectly face similar threats. Burrowing owls apparently benefited from the shooting restrictions put in place by the U.S. Forest Service for black-footed ferret recovery in Buffalo Gap National Grassland in western South Dakota (Griebel 2000). Implementing and enforcing shooting and poisoning closures on prairie dog colonies would help ensure the persistence of both burrowing owls and prairie dogs.

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APPENDIX A

JACKKNIFE CROSS-VALIDATED GENERALIZED LINEAR MODEL (JACKGLM) CODE

Appendix A. Jackknife cross-validated generalized linear model (JackGLM) code written by Mark L. Taper in program R.

```
jackglm <- function(fo,yname,datf,fam='poisson',offst="NoOffset")
  # the function jackglm calculates a jackknife prediction deviance for a glm
  # Mark L. Taper 1/11/2008
  # NOTE as of 1/11/2008 this is only functional for fam='poisson'
  # Note Prediction log relative error uses a continuity correction of .5 added to both yi &
yiht
  # input fo=string containing model formula
  # input datf=dataframe containing observations
  # input error distribution family
  # input offset as a object, the default is no offset i.e. NULL
  # return value = list of 1) vector of jackknifed observations
  #                  2) vector of jackknife predictions
  #                  3) vector of indicator variables for zero observations
  #                  4) total number of observations
  #                  5) number of zero observations
  #                  6) jackknife prediction deviance - closer to zero is better
  #                  7) jackknife prediction log likelihood - closer to +inf is better
  #                  8) Jackknife prediction log relative error - closer to 0 is better
  #                  9) vector of Poisson Anscombe resdiduals
  #                  10) vector of Poisson Deviance residuals
  #                  11) Vector of log(yi/yht)

{  obs=dim(datf)[1]  #number of observations in dataframe
  PredDev=0           #variable into which to sum prediction deviance
  PredLL=0            #variable into which to sum prediction likelihood
  PredLRE=0           #variable into which to sum log relative error
  AnscRes=rep(NA,times=obs)  #vector to hold Poisson Anscombe residuals
  DevRes=rep(NA,times=obs)  #vector to hold Poisson deviance residuals
  LRERes=rep(NA,times=obs)  #vector to hold log relative error residuals
  isZero=rep(0,times=obs)  #vector to hold posistions of zero observations
  numZero=0              #variable to hold number of zeros
  output=as.list(rep("NULL",times=11))  #list to hold output

names(output)=list("Yi","Yiht","isZero","numObs","numZeros","PredDev","PredLL","Pr
edLRE","AnscRes",
                  "DevRes","LRERes")
  Yi=rep(NA,times=obs)
  Yiht=rep(NA,times=obs)

  for (i in 1:obs)
  {   dtfi=datf[-i,]  #dataframe - ith observation
```

```
    prddtf=datf[i,]  #dataframe of ith observation
    yi=prddtf[,yname]
    if (offst=="NoOffset") mod=glm(formula=fo,family=fam,data=dtfi)
    else mod=glm(formula=fo,family=fam,data=dtfi, offset=offst)
    yiht=predict(mod,newdata=prddtf,type='response')
    Yi[i]=yi
    Yiht[i]=yiht
    if (yi>0)
    {
       pdi=(2*(yi*log(yi/yiht)-(yi-yiht)))   #prediction deviance for element i
       prei=(log(yi+.5)-log(yiht+.5))        #prediction log relative error for element i
    }
    else
    {   isZero[i]=1
       pdi=2*yiht      # 0 is the limit value of yi*log(yi/yiht) as yi->0
       prei=log(.5)-log(yiht+.5)
    }
    plli=dpois(yi,yiht,log=TRUE)
    PredDev=PredDev+ pdi
    PredLL=PredLL+plli
    PredLRE=PredLRE+prei^2
    AnscRes[i]=3*((yi^.666667)-(yiht^.666667))/(2*yiht^0.1666667)
#McCullagh&Nelder (1989) p.38
    DevRes[i]=sign(yi-yiht)*sqrt(pdi)                   #McCullagh&Nelder (1989) p. 39
    LRERes[i]=prei
  }
  output[[1]]=Yi
  output[[2]]=Yiht
  output[[3]]=isZero
  output[[4]]=obs
  output[[5]]=sum(isZero)
  output[[6]]=PredDev
  output[[7]]=PredLL
  output[[8]]=PredLRE
  output[[9]]=AnscRes
  output[[10]]=DevRes
  output[[11]]=LRERes
  return(output)
}
```