NEST HABITAT SELECTION OF BURROWING OWLS IN RELATION TO SOILS,

BURROW AVAILABILITY, AND BURROW TEMPERATURE

By

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NEST HABITAT SELECTION OF BURROWING OWLS IN RELATION TO SOILS, BURROW AVAILABILITY, AND BURROW TEMPERATURE

Abstract

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The availability of mammal burrows is often considered the most important habitat requirement for burrowing owls (*Athene cunicularia*), but little is known regarding factors that affect the density and distribution of fossorial mammals and their burrows, and how they ultimately influence habitat selection of burrowing owls. Soils are believed to play an important role in this relationship, particularly with respect to habitat selection at a landscape scale. In this study, I assessed whether burrowing owls in southcentral Washington prefer to nest in certain soils, and whether selection corresponds to increased burrow availability in those soils. I also evaluated whether the association between burrow temperature and soil texture may be one factor influencing nest habitat selection of burrowing owls.

Roadside surveys conducted in 2007 and 2008 indicated that the density of burrowing owl nests in the study area was quite low (0.14 nests km^{-2}). Comparisons between use and predicted burrowing owl habitat did not show an association between habitat selection and soils, although burrowing owls did nest more frequently in loamy sand and sandy loam soils. Soils influenced the distribution and abundance of badger (*Taxidae taxus*) burrows, which are the primary type of burrow used by burrowing owls

in eastern Washington. However, habitat use by nesting burrowing owls was not correlated with the availability of badger burrows in the primary soils. Owls nested in soils where burrows were both abundant and rare.

Field tests comparing temperature inside simulated nest burrows indicated that burrow temperature was significantly different among soil textures, and that burrow temperature was inversely related to the amount of coarse material (sand) in the soil. However, I failed to detect a relationship between soil texture and temperature inside burrows that had been previously occupied by burrowing owls, although sample sizes were low for this comparison. Hence, differences in burrow temperature related to soil texture alone are not likely to explain why burrowing owls may associate with certain soils. Temperature differences among previously occupied burrows may have been related to burrow characteristics that influenced convective heat exchange (e.g., entrance orientation, tunnel length, convolution), although further research is needed to test this hypothesis.

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Dedication

To my grandparents Florence and Jim,

two of the most inspiring people a person can hope to meet.

INTRODUCTION

Habitat selection is often viewed as a spatially hierarchical decision–making process in which an organism weighs the costs and benefits associated with first selecting a general place to live (a habitat), then with selecting which patches and resources within a general area it will use (Johnson 1980, Orians and Wittenberger 1991, Jones 2001). Migratory birds are thought to select their nest sites in a similar manner, such that the proximity and availability of required resources are at distances and levels that optimize reproductive success (Rozenweig 1981, Rolstad et al. 2000, Lantz et al. 2007). Hence, studies of habitat relationships of migratory birds should seek to identify not only proximate factors that may trigger a bird to settle, but also the spatial and temporal scales at which those factors are important in habitat selection. One approach to this has been to look for evidence of habitat selection at multiple scales (Orians and Wittenberger 1991, Battin and Lawler 2006). However, researchers conducting multi-scale habitat selection studies generally analyze habitat associations at each scale separately. While this approach may provide useful insight into habitat associations at different scales, it ignores the possibility that habitat variables may be correlated across the scales being analyzed (Cushman and McGarigal 2002). Cross-scale correlations have the potential to confound the interpretation of results because it is difficult to determine at which scale a particular habitat variable is influencing an animal's decisions (Battin and Lawler 2006). Also, lack of consistency in the scale at which habitat variables are evaluated across studies may lead to further confusion as to how they influence habitat selection.

These problems may explain in part some of the confusion regarding habitat selection of the western burrowing owl (*Athene cunicularia hypugaea*). The burrowing owl is a

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Neotropical migrant that breeds throughout western North America, including parts of southern Canada (se. British Columbia, s. Alberta, s. Saskatchewan, sw. Manitoba), most of the western U.S., and northern Mexico (Klute et al. 2003). Local population declines in several portions of the burrowing owl's breeding range (Wellicome and Holroyd 2001, Dechant et al. 2002, Klute et al. 2003), including in the state of Washington (Smith et al. 1997, Conway and Pardieck 2006), have prompted conservation action for burrowing owls in the United States (Bird of National Conservation Concern), Canada (Endangered), and Mexico (Klute et al. 2003). The burrowing owl is listed as either Threatened or Endangered in nine U.S. states (Klute et al. 2003), and is a State Candidate in the state of Washington. Burrowing owls have been extirpated from much of their former breeding range in Washington, which encompasses much of the shrub-steppe and grassland habitats east of the Cascades (Klute et al. 2003, Conway et al. 2005). Primary causes for population declines include habitat loss and degradation due to land development, and declines of fossorial mammal populations (Haug et al. 1993).

Burrowing owls occupy a variety of ecosystems throughout their range, including shrub-steppe, mixed- and short-grass prairie, coastal and desert scrub, and agricultural and urban lands (Klute et al. 2003). Generally, they nest in burrows excavated by fossorial mammals that are in open, sparsely vegetated, and relatively flat areas (Coulombe 1971, MacCracken et al. 1985, Rich 1986, Green and Anthony 1989, Plumption 1992, Dechant et al. 2002). But aside from these common features, there are few vegetative or structural characteristics that represent burrowing owl habitat across the specie's range (Haug et al. 1993, Klute et al. 2003, Lantz et al. 2007). Much of the information on what constitutes optimal burrowing owl habitat has come primarily from comparisons of habitat features (e.g., vegetation,

topography, burrow availability, prey availability) between the nest site and apparently

suitable unoccupied burrows located near the nest (Green and Anthony 1989, Clayton and

Schmutz 1999, Desmond and Savidge 1996, Belthoff and King 2002, Machiote et al. 2004,

Poulin et al. 2005, Smith et al. 2005, Moulton et al. 2006). While these comparisons are

useful for identifying proximate factors that influence selection of the nest burrow, they may

not be appropriate for explaining factors that influence habitat selection at larger scales.

The availability of mammal burrows is considered the most important habitat

requirement for burrowing owls because they utilize burrows in virtually all aspects of their

daily activities, including nesting, roosting, food caching, escape cover, and thermal cover

(Dechant et al. 2002, Klute et al. 2003). Yet, the influence of burrow availability on habitat

selection at the landscape scale is poorly understood because it has been examined primarily

with respect to the nest site (Plumpton 1992, Desmond et al. 1995, Desmond and Savidge

1996, Belthoff and King 2002, Poulin et al. 2005, Moulton et al. 2006, Lantz et al. 2007).

When different geographic regions are compared within the burrowing owl's range, however,

different patterns of habitat selection in relation to burrow availability begin to emerge. In

particular, these patterns appear to be linked to factors affecting the spatial distribution of the

fossorial mammal species that provide burrows for burrowing owls. In the Great Plains for

example, burrowing owls are strongly associated with black-tailed prairie dog (*Cynomys*

ludovicianus) colonies (Butts and Lewis 1982, MacCracken et al. 1985, Desmond et al. 1995,

Desmond and Savidge 1996), although the availability of burrows in active colonies appears

to be more important than the overall availability of prairie dog burrows in the landscape

(Toombs 1997, Desmond et al. 2000, Lantz et al. 2007). Outside of the Great Plains,

burrowing owls rely primarily on badgers (*Taxidae taxus*), ground squirrels (*Sciuridae*),

marmots (*Marmota spp*.), and coyotes (*Canius latrans*), to provide burrows. Several studies have suggested that burrow availability does not explain why burrowing owls associate more strongly with certain habitat types than others in these areas (Green and Anthony 1989, Moulton et al. 2006).

Environmental factors that affect the density and distribution of fossorial mammals (and consequently their burrows) have rarely been included as covariates in burrowing owl studies, although many authorities believe that soils play an important role (MacCracken et al. 1985, Toombs 1997, Holmes et al. 2003). Soil properties such as texture, depth, bulk density, and moisture, may influence the distribution of fossorial mammals, as well as the structural characteristics of their burrows (Elliot 1983, Laundre and Reynolds 1993, Shenbrot et al. 2002). Soil properties may also affect the ability of burrowing owls to modify burrows. Burrowing owls have been observed widening the burrow entrance (personal observation, G. Green, personal communication), and are believed to occasionally modify other features such as tunnel and nest chamber size as well (Butts and Lewis 1982, Haug et al. 1993). Soils may potentially influence the microclimate inside burrows (Nikol'skii 2002, Shenbrot et al. 2002), which may also have important implications for nest-site selection (Brady 2004). Many birds are believed to select nest sites that minimize thermoregulatory costs of nesting (White and Kinney 1974, Webb 1987, Reid et al. 2000), although this hypothesis has not been tested for burrowing owls. Soils may also influence other factors important to owls, such as the probability of flooding, collapse, or excavation by predators (C. Conway, personal communication).

Because soils may influence multiple habitat characteristics that may be important to burrowing owls, I chose to evaluate whether burrowing owls in a shrub-steppe environment

in southcentral Washington select for certain soils when choosing their nest habitat. In particular, I was interested in how patterns of selection corresponded to soil-related differences in burrow availability and burrow temperature. Soils have been shown to influence the distribution of fossorial mammals, therefore I expected that burrowing owls would select soils in which mammal burrows (primarily badger burrows) were more abundant. Conversely, little is known about how soils or other factors may influence the temperature of burrows, or whether burrowing owls would choose one burrow over another based on burrow temperature. Given these considerations, I characterized soil-related differences in burrow temperature to determine whether this relationship may be a biologically plausible factor in habitat selection of burrowing owls.

STUDY AREA

I conducted this study on the U.S. Department of Energy Hanford Site near Richland, Washington, which encompasses approximately 1500 km^2 of shrub-steppe environment in the Interior Columbia River Basin (Figure 1). The Hanford Site has been free of grazing and agriculture since it was established in 1943, and has been largely retained in an unmanaged condition with no residential use. Shrub-steppe plant communities in the study area are typically characterized by a shrub overstory (*Artemisia tridentata*, *Purshia tridentata*, *Ericameria nauseosa*, *Chrysothamnus viscidiflorus*, *Grayia spinosa*), perennial bunchgrasses (*Poa secunda*, *Pseudoroegnaria spicatum*, *Hesperostipa comata*, *Achnatherum hymenoides*), and a number of forbs. However, shrub cover has been significantly reduced throughout the by wildfire. Non-native plants such as cheatgrass (*Bromus tectorum*), tumblemustard (*Sisymbrium altissimum*), Russian thistle (*Salsola kali*), and diffuse knapweed (*Centaurea*

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repens) have become dominant components of the understory in many areas due to disturbance from fire and past agricultural and grazing practices. Average annual precipitation is 17 cm, with most precipitation occurring between the months of November and February (Neitzel 2005). Average monthly temperatures range from -0.7° C in January to 24.7° C in July (Neitzel 2005). Topography generally ranges from flat to less than 10% slope, and is characterized by channeled scablands, stabilized and active dunes, kettle-and-basin hills, river bluffs, and several mountains. Elevation ranges from 79 – 1066 m above sea level.

Soils vary from deep accumulations of loess-derived loams to shallow lithosols in areas where glacial floods and wind erosion scoured the loess from underlying basalt (Wildlung and Garland 1988). Sandy soils cover an extensive portion of the study area, which are the result of glacial outwash and alluvial and wind-blown deposition (Wildlung and Garland 1988). Fifteen unique soil types have been described for the portion of the Hanford Site south of the Columbia River (Hajek 1966), and 130 unique soil types have been described for the portion north of the Columbia River (Soil Survey Staff, NRCS). However, when grouped by primary textural classification, approximately 98% of the soils in the study area can be described as sandy loam (14%), loamy sand (58%), or silt loam (26%) associations (Figure 1). Soil disturbance is generally low in most portions of the study area, except in the immediate vicinity of industrial areas and where farming or grazing historically took place. Disturbance to plant and soil communities in the areas surrounding the Hanford Site has been considerably greater due to conversion to agricultural and urban land uses.

METHODS

Nest habitat selection, burrow availability, and burrow temperature were assessed in relation to the primary soils found in the study area (silt loam, sandy loam, loamy sand). Because the methods and level of detail used to classify individual soil types were considerably different for the north and south portions of the study area, I categorized soils by their primary textural classification. I assessed nest habitat selection of burrowing owls at a population level by comparing estimates of habitat availability and use (defined by nest locations) in the three primary soils. I classified habitat as *selective* if burrowing owls nested in a given soil more frequently than would be expected based on the availability of that soil within the landscape (Johnson 1980).

Habitat Use

Habitat use was measured by conducting standardized roadside surveys during the breeding season (March – August) in 2007 and 2008 to estimate burrowing owl nest density in each of the three primary soils. Prior to this study, there was little available information regarding burrowing owl distribution in the study area. In 2007, I conducted driving surveys because they are more effective at locating nesting owls per unit time (Conway and Simon 2003). However, the detection rate of nests was low in 2007, so I switched to conducting call-broadcast point-counts in 2008 because they are more effective at locating owls per unit distance (Conway and Simon 2003). I also spaced survey routes farther apart in 2008 to cover a broader extent within the study area.

I chose to maximize search effort rather than optimize sampling design because burrowing owls were thought to be rare in the study area (Conway et al. 2005, C. J. Conway, personal communication) and because the number of drivable roads was limited.

Consequently, I did not restrict individual driving routes or call-broadcast stations to soils that were of the same texture (i.e., driving routes and search areas at broadcast stations often overlapped soils of more than one soil texture). I conducted surveys along all road types including paved, gravel, and dirt roads, utility rights-of-way, and abandoned railroads. Most roads used for surveys in the study area are traveled infrequently; therefore, I did not attempt to evaluate potential differences in nest density or detection associated with different road types.

Total effective search area was estimated using maximum effective search distances recommended by Conway and Simon (2003): 200 m on either side of the road for driving surveys, and 400 m in all directions for call-broadcast surveys. A total of 10 driving routes and 111 point-count locations were surveyed during the 2007 and 2008 breeding seasons (Figure 2). Each driving route was surveyed twice between 5 – 17 May and 15 June – 5 July, 2007, and each point-count (with the exception of 26 locations that were added after the first round) was surveyed three times between 4 – 28 April, 17 May – 18 June, and 8 July – 23 August, 2008.

Upon completion of each survey, I returned to areas where I had detected a burrowing owl and conducted a thorough ground search to look for a burrow with signs of occupancy (e.g., regurgitated pellets, "whitewash" or fecal splays, tracks, feathers, prey remains, dung). Occupied burrows were monitored weekly by scanning the site with binoculars from approximately 100 m away, and then slowly approaching on foot (Conway et al. 2006). Burrows in which an owl was detected on two or more visits were classified as nest. Hence, burrows occupied by an unpaired male that failed to attract a mate (or I failed to detect a mate) were included as nests in this study. This definition has been shown to provide better

estimates of demographic parameters for burrowing owls because it better represents the true

proportion of nesting attempts by burrowing owls in a given area (Garcia and Conway 2009).

Detection Trials

Call-broadcast detection trials were conducted at active nest sites throughout the breeding

season in 2008 to determine whether detection probability differed among soils due perhaps

to soil-related differences in topography, plant composition or structure, background color, or

other features. Trials were conducted from an arbitrary location on the shoulder of the road

approximately 100 m from the nest burrow when possible, except in cases where nests were

>100 m from the road. During the trials, I focused my attention in the direction of the focal

nest because I was interested in the extent to which an extrinsic factor (soil) influenced

detection probability. If an owl was not detected during the trial, I then checked the nest site

to determine whether an owl was present or not.

Habitat Availability

The relative amount of burrowing owl habitat in each primary soil was estimated using a

Geographic Information Systems (GIS) model that incorporated 5–m resolution shrub canopy

and 10–m resolution slope data (Figure 3). I defined habitat in my model as areas with ≤10%

shrub canopy and ≤10% slope. This definition was based both on the range of estimated

shrub canopy and slope within 50 m of previously known nest sites within the study area, and

information from previous studies (Rich 1986, Green and Anthony 1989, Conway et al.

2005).

Shrub canopy data were derived from high resolution (0.29–m) natural-color aerial

photos taken in May 2002 (J. D. Tagestad, unpublished data) using an analysis of image

texture (coarseness or smoothness caused by the variability or uniformity of image tone or

color; Tagestad and Downs 2007). Slope data were derived from a 1–arc second (30–m resolution) digital elevation model (U.S. Geological Survey, National Elevation Dataset). Preliminary accuracy assessments indicate that this method may slightly overestimate shrub canopy in areas with <10% shrub canopy (J. D. Tagestad, unpublished data). Thus, available burrowing owl habitat may have been underestimated to some degree, however, this potential bias likely was similar among the different soils (J. D. Tagestad, personal communication).

Burrow Availability

Burrow availability in the three primary soils was estimated by counting burrows that appeared suitable to burrowing owls within 10–m wide variable-direction belt transects. An suitable burrow was defined as a burrow having an entrance ≥8 cm in diameter (Belthoff and King 2002) and no obstructions blocking the tunnel passage that would prevent a burrowing owl from entering. Shallow (<0.5 m) vertical digs created by badgers or coyotes were not included as suitable burrows.

Belt transects were conducted within 400–m radius of point-count stations to provide a valid comparison between habitat use and burrow availability. I chose this distance because it represents the maximum effective search distance for locating burrowing owls via call-broadcast surveys (Conway and Simon 2003). Transects were restricted to point-count stations surrounded by one soil texture only because each belt transect was considered one sampling unit. One belt transect was conducted at each of these point-count stations, representing a total of 16, 21, and 24 belt transects in silt loam, sandy loam, and loamy sand respectively. I started each transect at a random location and trajectory within the 400 m search area, and ended either when I counted five suitable burrows or walked a total distance of 1000 m. If I encountered the outer boundary of the 400-m search area or a barrier that

prevented me from continuing on my current trajectory, I randomly selected a new direction within the search area and continued walking.

A GeoXM™ (Trimble, Sunnyvale, CA) handheld Global Positioning System was used to navigate and record the transect path and locations of suitable burrows. For each suitable burrow, I recorded cardinal aspect of the burrow entrance (true N, S, E, W), maximum height and width of the tunnel entrance to the nearest 0.1 cm, and relative tunnel length (≤0.5, 0.5 – 1.0, >1.0 m). Relative tunnel length was recorded using a flexible measuring rod made out of a 0.635–cm pipe snake. In addition, I also recorded the species that likely created each burrow (i.e., badger, coyote, marmot, ground squirrel, unknown). I was confident in my determination of which species created the burrow for several reasons: (1) marmots have rarely been observed in the study area, and observations have been restricted primarily to basalt outcroppings in areas outside of where I conducted surveys; (2) the two known species of ground squirrels that occur in the study area (*Spermophilus townsendii*, *S. washingtonii*) are colonial and typically do not make burrows larger than 8 cm; (3) coyote dens can be distinguished from badger burrows by their shape (coyote dens tend to be larger and vertically oval whereas badger burrows tend to be smaller and horizontally oval) and the presence of tracks.

Burrow Temperature

The relationship between soil texture and burrow air temperature (hereafter referred to as "temperature") was assessed by monitoring the temperature inside artificial simulated burrows, and burrows previously occupied by burrowing owls during the latter half of the 2008 breeding season (late June to mid-August). Two types of simulated burrows were used in this assessment: randomly located simulated burrows and simulated burrows paired with

previously occupied burrows (hereafter referred to as "control" and "paired" burrows, respectively). For control simulated burrows, I generated 120 random locations (40 in each of three primary soils) using a GIS random point generator (IMAGINE v. 9.2, Leica Geosystems Geospatial Imaging, LLC). All random locations were restricted to within 400 m of roads (paved, gravel, two-track, rights-of-way) so that field personnel could more easily access sites. However, approximately half of the locations were still too difficult to access (many roads were overgrown or simply did not exist anymore), or were in culturally or ecologically sensitive areas in which I could not dig. Of the locations I did access, 16 were too rocky to bore a simulated burrow (particularly in areas mapped as sandy loam), resulting in a total of 42 control simulated burrows.

A total of 61 previously occupied burrow locations were obtained from driving surveys and incidental observations during the pilot phases of this study (2006 – 2007), as well as from historic records (2005 – 2007) kept by the U.S. Fish and Wildlife Service. However, I was interested in burrows that were most likely to have been used by burrowing owls as a nest, therefore I only selected previously occupied burrows where a burrowing owl had been seen ≥1 breeding season. I did not include burrows where only burrowing owl sign (i.e., pellets, bones, feathers, whitewash) had been observed. Of the 61 previously occupied burrow locations, only 10 were still intact and fit the criteria for this study.

The vertical depth, tunnel diameter, tunnel slope, and tunnel length of simulated burrows was similar to that reported for burrows used by burrowing owls in other areas: ~ 1 m vertical depth, ~ 15 cm diameter, ~ 25° tunnel slope (Butts and Lewis 1982, Belthoff and King 2002), and ~ 2.5 m long (Lantz et al. 2007). Simulated burrows were created by boring a straight circular hole into the ground at a 25° angle (relative to horizontal) using a custom–

made 15-cm diameter bucket auger. No artificial structures (pipes, buckets) were used in the construction of simulated burrows because I wanted to simulate the direct soil-to-air interface of a real burrow. Simulated burrows were bored to 2.4 m in length in order to achieve a vertical depth of 1 m at the end of the burrow. However, I was not able to bore to 2.4 m at 11 of the control burrow sites due to high rock content in the soil. All control simulated burrows were constructed on flat ground and oriented to face the same direction as the most common burrow aspect (south) observed during burrow availability surveys. Paired simulated burrows were placed within 5 m of previously occupied burrows, and constructed on the same slope and aspect as the previously occupied burrow at each site. All paired simulated burrows were bored to 2.4 m in length at a 25° angle relative to horizontal.

Burrow temperature was recorded from 27 June – 12 August 2008 in all control simulated burrows, and from 17 July – 12 August 2008 in all paired burrows, using DST milli™ archival temperature tags (Star-Oddi Ltd., Reykjavik, Iceland). These tags are designed for aquatic applications, however, their small size (38-mm long, 12-mm diameter, 9.2 g) makes them ideal for deploying in burrows or other small cavities. Prior to deployment, I compared their performance in ambient air to an ambient air temperature probe (CS500, Campbell Scientific, Inc., Logan, UT) to assess their accuracy.

Temperature tags were synced to the same time prior to deployment, and programmed to record temperature every 15 minutes. Tags were housed inside 6.35–cm diameter stainless steel mesh tea infusers (G&H Tea Services, Toronto, Canada) to keep them from direct contact with the soil (i.e., to prevent recording soil temperature rather than air temperature of the burrow). A rubber washer was placed around the tag to keep the thermocouple–end upright inside the housing, and the top and bottom of the housing was flattened to keep the

housing from rolling over. Tags were placed inside burrows using a home-made cable release tool made out of a 0.635–cm pipe snake. A home-made infrared video probe was used to ensure tags were placed upright inside the burrows. For simulated burrows, I deployed the tags at the end of the hole. For previously occupied burrows, I attempted to deploy tags at the same depth as the paired simulated burrow (2.4 m) at each site. However, I was rarely able to feed the video probe the necessary depth inside the previously occupied burrow due to the convolution of the burrow and amount of loose soil on the floor.

Upon recovery of the tags, I discovered that many (69% of control simulated burrows and 50% of paired simulated burrows) had become buried to some degree due to natural erosion or backfilling caused by surface winds or small mammal excavation. I visually estimated whether the tag was unburied (0 – 25%), partially buried (25 – 50%), mostly buried (50 – 99%), or completely buried (100%) using either the video probe or by shining a flashlight down the burrow. I only classified burial level for tags that were buried by less than a couple of inches of soil (i.e., for burrows that were almost entirely intact) and excluded data from burrows that became completely filled in because I was only interested in measuring air temperature inside burrows.

Soil samples were collected to determine the primary soil texture (i.e., percent of sand, silt, and clay) at locations where I monitored burrow temperature. Three sub-samples were collected at each site 1 m below the surface using a 7.62–cm diameter bucket auger, although some samples were obtained from <1 m deep due to high rock content in the soil. All samples were collected within 5 m of the burrow.

I classified the soil texture at each site based on the mean percentage of sand and combined percentage of silt and clay in the three sub-samples. Sand and silt/clay fractions

were measured using standard dry-sieving practices (Soil Survey Division Staff 1993). I did

not quantify individual silt and clay fractions because most soils in the study area contain

little (0-5%) clay, and doing so likely would not have resulted in different textural

classifications. I also did not quantify the proportions of different-sized rock fragments (>2.0

mm) because the auger used to collect soil samples was too small to obtain a representative

sample in rocky soils.

Statistical Analyses

Habitat Selection

The number of nests detected during roadside surveys was too low to compare habitat

selection separately for both years. I did not detect any of the same nests initially detected in

2007 during call-broadcast surveys in 2008, therefore I pooled data for both years and used a

Chi-square goodness-of-fit test to determine whether burrowing owls nested in a given soil

more frequently than would be expected based on the amount of burrowing owl habitat in

that soil. I used the estimated number of nests found in both years, rather than actual number

observed, to account for differences in detection probability between years. I assumed the

same detection probabilities as those estimated by Conway and Simon (2003) for driving

(37.5%) and call-broadcast surveys (64.3%) of burrowing owl nests in calculating the

estimated number of nests each year. This was appropriate because I was concerned with

potential differences in detection probability associated with soils, rather than overall

accuracy. In addition to the roadside survey analysis, I compared the number of all

burrowing owl nests found in each primary soil between 2006 – 2008 (both during roadside

surveys and incidentally) to the amount of burrowing owl habitat in each primary soil using a

Chi-square goodness-of-fit test. However, it should be noted that some (26%) of these nests

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were located in artificial structures (old irrigation pipes). Thus, to ensure that I did not bias the comparison of use vs. availability by including nests that may have been in areas that would otherwise be unavailable to burrowing owls due to a lack of burrows, I performed the same analysis without nests in artificial structures.

Burrow Availability

For the purposes of this study, I was more concerned with differences in the relative abundance of burrows rather than differences in the actual number or density of burrows among soils. In addition, the distribution of the number of burrows per transect and burrow density were highly skewed even after numerous quantitative transformations, preventing a more rigorous analysis. Therefore, I compared burrow availability among soils using burrow presence/absence for each transect, and the cumulative probability of observing a burrow based on search effort (distance walked). Unlike the presence/absence approach, 'zero' observations were not accounted for in the cumulative probability analysis. For this approach, I assumed that the relationship between the cumulative probability of finding a burrow and search effort remained constant in any given soil (i.e., the slope of a fit line to cumulative probability would be the same had I continued walking until I observed a burrow).

Chi-square goodness-of-fit was used to assess differences in burrow presence/absence, burrow orientation, and burrow length among soils. Burrow presence/absence was first compared for all three soils, and then for each unique pair of soils. Least squares linear regression and Tukey's Honest Significant Difference (HSD) were used to compare the cumulative probabilities of finding a suitable burrow (hereafter referred to as "location probability") based on search effort among the primary soils. I assumed that burrow

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abundance was inversely related to search effort, and that the relationship between search effort and location probability did not change between soils (i.e., slope did not differ among soils).

Based on field observations, I suspected that burrows may be aggregated. I evaluated this suspicion by comparing the mean distance between consecutive burrows encountered on transects using analysis of variance (ANOVA) in hopes of better explaining differences in burrow availability. Burrows distances were natural log-transformed to improve normality and independence of means and variances.

Burrow Temperature

I used repeated measures multivariate analysis of variance (MANOVA) to assess differences in daily minimum temperature (T_{MIN}), daily maximum temperature (T_{MAX}), and daily temperature range ($T_{RANGE} = T_{MAX} - T_{MIN}$) in control burrows and paired burrows. For the MANOVA based on data collected in control burrows, I included variables for the following factors: primary soil texture (*SOIL*), tunnel length (*LENGTH*), level of tag burial (*BURIAL*), and date of measurement (*DATE*) as a within-subjects factor. For the paired burrow analysis, I included *SOIL*, *BURIAL*, *DATE*, and burrow type (*BURROW*) to test for temperature differences between paired simulated and previously occupied burrows. *LENGTH* was not included in the paired burrow analysis because I was able to bore all paired simulated burrows to 2.4 m. Post hoc univariate analysis of variance (ANOVA) and least squares linear regression were used to assess differences between specific variable levels. "Sand" was included as a fourth soil texture in the temperature analyses because soil texture analyses indicated that some burrows (both control and paired burrows) were in soil classified as sand (i.e., >85% sand, <15% silt/clay). The final sample size of control and

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paired burrows was 13, 7, 7, and 15, and 2, 1, 6, and 1 in silt loam, sandy loam, loamy sand, and sand respectively.

Daily T_{RANGE} was natural log transformed [Ln(T_{RANGE}*100)] in all analyses to improve model fit. For the control burrow MANOVA, I only included temperature data collected during the first 34 days (28 June – 31 July 2008) because that was the maximum number of days I could include in the analysis without complete loss of degrees of freedom. Similarly, I could only include a maximum of eight days in the paired burrow analysis. However, rather than use the first eight consecutive days, I randomly selected dates (17, 21, 26, 28 July, and 4, 5, 7, 10 August) for the paired burrow analysis to try to improve independence of measurements.

RESULTS

Habitat Selection

The GIS habitat model indicated that there was approximately 248.1, 139.1, and 624.3 km^2 of burrowing owl habitat in silt loam, sandy loam, and loamy sand soils in the study area (Table 1). The model appeared to represent burrowing owl habitat well, as all 61 previously occupied burrow locations either fell within or ≤50 m of predicted habitat. In addition, the proportion of total area in each primary soil that was classified as burrowing owl habitat was relatively similar among soils (i.e., 65, 68, and 72% of the total area in silt loam, sandy loam, and loamy sand soils was classified as burrowing owl habitat).

In 2007 and 2008, I surveyed a cumulative effective area of approximately 21.0, 27.2, and 68.2 km^2 in silt loam, sandy loam, and loamy sand respectively, and detected a total of 11 burrowing owl nests (Table 1). Of these 11 nests, four (36%) were located in sandy loam

and seven (64%) were located in loamy sand soils. I did not detect any burrowing owl nests

in silt loam, therefore I excluded silt loam from the roadside survey analysis.   Results of the

roadside analysis indicated that burrowing owls nested in sandy loam habitat more than

would be expected based on availability (Table 2), although this result was not statistically

significant ($\chi^2 = 3.692$, $df = 1$, $P = 0.0547$).

Between 2006 – 2008, a total of 34 burrowing owl nests were discovered within the study

area (either incidentally or during roadside surveys) that had been occupied by burrowing

owls ≥1 breeding season. Of these 34 burrows, 4 (12%), 7 (21%), and 23 (68%) were

located in silt loam, sandy loam, or loamy sand habitat (Table 2), and 24 (71%) were located

in abandoned badger burrows (nine were in old irrigation pipes and one was in an abandoned

coyote den). Results of the chi-square analysis based on all nests indicated that burrowing

owls nested in sandy loam and loamy sand more than would be expected based on

availability (Table 2), although this result was not significant ($\chi^2 = 2.990$, $df = 2$, $P = 0.2242$).

Similarly, when I excluded nests in artificial structures from the analysis, there was no

indication that burrowing owls selected any given soil more than would be expected based on

availability ($\chi^2 = 0.93$, $df = 2$, $P = 0.6271$).

Detection Trials

I detected ≥1 burrowing owl during 19 of 21 call-broadcast detection trials (90.5 %)

which were conducted at 9 individual nest sites in 2008. Most detections were visual (three

were detected aurally and then visually). Visual detection distance ranged from 67 – 319 m,

and aural detection distance ranged from 67 – 110 m. Burrowing owls were initially detected

during the broadcast segment (last 3-min) at 8 of 19 (42%) detection trials. However, most

owls initially detected during the passive segment often became more visible during the broadcast segment by flying to a perch or standing upright on the burrow mound.

Burrow Availability

Presence/absence of suitable burrows within 1000-m variable-direction belt transects was significantly different among soils (Table 3). At least one suitable burrow was present at 71, 43, and 81% of belt transects in loamy sand, sandy loam, and silt loam respectively. I was more likely to find burrows in silt loam than sandy loam, and in loamy sand than sandy loam, although this difference was not statistically significant (Table 3). I failed to detect a difference in the proportion of transects with burrows present between silt loam and loamy sand (Table 3).

Comparison of location probabilities (the cumulative probability of finding a burrow) suggested that burrow availability was significantly different among soils ($F = 4.7143$, $df = 2$, $P = 0.0154$), although post-hoc comparisons among individual soils conflicted with presence/absence results. Location probability was 11.2% greater in silt loam than loamy sand ($F = 9.271$, $df = 35$, $P = 0.0044$), 4.8% greater in silt loam than sandy loam ($F = 1.277$, $df = 35$, $P = 0.2661$), and 6.4% greater in sandy loam than loamy sand ($F = 2.474$, $df = 35$, $P = 0.1247$). Mean search effort to locate a burrow (i.e., search effort corresponding to 50% cumulative probability) was 265, 318, and 389 m in silt loam, sandy loam, and loamy sand respectively (Table 4). These results should be interpreted with caution though, because they are based on fewer transects (i.e., only those in which burrows were encountered) than presence/absence results. Also, the relationship between location probability and search effort was not linear for silt loam and sandy loam, indicating that the assumption that location probability did not change based on search effort may not have been valid in those soils.

This may also indicate that burrows were more aggregated along the call-broadcast routes where I measured burrow availability. Distance between adjacent burrows was somewhat closer in silt loam than the other soils, although this difference was not statistically significant ($F = 2.381$, $df = 2$, $P = 0.0988$). Mean distance between adjacent burrows in all three primary soils was 54 m (Table 4).

A total of 124 suitable burrows were located within the 10-m belt transects. Of these burrows, 120 (97%) were created by badgers and 4 (3%) were created by an unknown species. I failed to detect any significant difference in either the entrance aspect ($\chi^2 = 10.08$, $df = 6$, $P = 0.1215$) or relative tunnel length of suitable burrows among soils ($\chi^2 = 3.57$, $df = 4$, $P = 0.4676$). However, suitable burrows tended to face south ($\chi^2 = 10.80$, $df = 3$, $P = 0.0128$) and had relative tunnel lengths of <0.5 m ($\chi^2 = 50.13$, $df = 2$, $P < 0.0001$) more so than would be expected based on chance.

Burrow Temperature

Tag Accuracy

Comparison of temperature tags to an ambient air temperature sensor indicated they were accurate within ± 0.2° C. Tags responded almost immediately to rapid changes in temperature, although they took ~ 15 minutes to fully equilibrate. Given that air temperature generally does not fluctuate rapidly in a burrow (Nikol'skii 2002), I decided the tags were sufficient for obtaining measurements of maximum and minimum daily temperature inside simulated and previously occupied burrows.

Control Simulated Burrows

Daily T_{MIN} in control burrows was not significantly different ($\alpha = 0.05$) between primary soils, tunnel lengths, levels of tag burial, or dates of measurement in the multivariate

(MANOVA) model (Table 5). Although *SOIL* was not statistically significant, the model did

indicate that it was an important variable. Therefore, I conducted pairwise univariate

comparisons of daily T_{MIN} among soils and found that daily T_{MIN} was significantly less in silt

loam than the other three soils ($F = 6.79$, $df_N = 1$, $df_D = 34$, $P = 0.0135$). Mean daily T_{MIN} in

control burrows ranged from 23.3, 23.5, 22.6, and 21.8° C in sand, loamy sand, sandy loam,

and silt loam respectively.

   Daily T_{MAX} in control burrows was significantly different between primary soils, tunnel

lengths, and dates of measurement (Table 6). However, the effect of soil and tunnel length

did not change throughout the study. Univariate tests revealed that daily T_{MAX} was

significantly less in silt loam than the other three soils ($F = 11.74$, $df_N = 1$, $df_D = 34$, $P = $

0.0016), and decreased 1.4° C per meter tunnel length in control burrows ranging from 0.9 –

2.4 m in length ($F = 201.15$, $df = 1$, $P <0.0001$). Mean daily T_{MAX} ranged from 25.1, 25.7,

24.0, and 22.6° C in sand, loamy sand, sandy loam, and silt loam respectively.

   Daily T_{RANGE} in control burrows was significantly different between primary soils, tunnel

lengths, and levels of tag burial (Table 7). In addition, daily T_{RANGE} changed little

throughout the study (Table 7). Univariate tests suggested that daily T_{RANGE} was

significantly less in silt loam than the other three soils ($F = 13.49$, $df_N = 1$, $df_D = 33$, $P = $

0.0008). Mean daily T_{RANGE} ranged from 1.2, 1.5, 1.1, and 0.7° C in sand, loamy sand, sandy

loam, and silt loam respectively. Daily T_{RANGE} did not differ between control burrows with

unburied or partially buried tags ($F = 0.002$, $df_N = 1$, $df_D = 33$, $P = 0.9636$), or between

burrows with mostly or completely buried tags ($F = 0.33$, $df_N = 1$, $df_D = 33$, $P = 0.5721$).

Therefore, I compared control burrows with unburied and partially buried tags to those with

mostly and completely buried tags. Mean daily T_{RANGE} in burrows unburied and partially

buried tags ($\bar{x} = 1.5°$ C) was significantly greater than burrows with mostly or completely buried tags ($\bar{x} = 0.8°$ C, $F = 12.98$, $df_N = 1$, $df_D = 33$, $P = 0.0010$). Daily T_{RANGE} decreased $1.25°$ C per meter tunnel length in control burrows ranging from $0.9 - 2.4$ m in length ($F = 430.53$, $df = 1$, $P < 0.0001$), although this value decreased rapidly with increasing tunnel length.

Paired Simulated and Previously Occupied Burrows

Daily T_{MIN} and in paired burrows was not significantly different among soil textures, burrow types, or levels of tag burial (Table 8). However, the model did indicate that daily T_{MIN} was significantly different among soil textures on certain days (Table 8). This result should be interpreted with caution, however, given the low sample size of paired burrows in each soil. In addition, daily T_{MIN} was not correlated with soil texture, as seen in the control burrows (i.e., daily T_{MIN} was not lowest in silt loam and higher in sandy soils). Daily T_{MIN} in simulated burrows was ~$0.8°$ C cooler on average than in previously occupied burrows, although this difference was not statistically significant.

Similarly, daily T_{MAX} in paired burrows was not significantly different among soil textures, burrow types, or levels of tag burial, but did differ significantly among soil textures on certain days (Table 9). Again, these differences were not correlated with soil texture as seen in the control burrows. Daily T_{MAX} inside simulated burrows did tend to be ~$1.0°$ C cooler on average than previously occupied burrows, although this difference was not statistically significant.

Daily T_{RANGE} in paired burrows was not significantly different between soil textures, burrow types, or levels of tag burial (Table 10). Daily T_{RANGE} did vary depending on the date of measurement, although there was no significant interaction between *DATE* and any of the

main factors (Table 10). Daily T_{RANGE} in simulated burrows was ~0.4° C greater on average than previously occupied burrows, but this difference was not significant.

DISCUSSION

Habitat Selection

Results of roadside surveys indicated that burrowing owls may select nest habitat in sandy loam more frequently than would be expected based on availability. However, these results may be misleading because are based on a low number of nest detections. In addition, the roadside survey results do not account for habitat use in silt loam, given that I failed to detect any nests in silt loam. Burrowing owls did nest in silt loam habitat during the study (although infrequently), thus, the analysis based on the total number of nests located in each soil from 2006 – 2008 was probably more appropriate. However, when I included all nests in the analysis I failed to detect an association between habitat selection and soils. The same was also true when I excluded nests that were located in artificial structures.

Small sample sizes of nests during this study may have been due in part to restricting burrowing owl surveys to roadside habitats. However, there was no indication that burrowing owls avoided roadside habitats, as most nests (including those not found during surveys) were within ~400 m of a road. Similar observations have been noted for burrowing owls in eastern Washington (Conway et al. 2005), as well as by others that have attempted locating burrowing owl nests away from roadsides (Conway and Simon 2003). Hence, burrowing owls may be positively associated with roadside habitat on the Hanford Site, as well as in other areas. This hypothesis is further supported by extrapolating population size based on the estimated nest density for the entire study area. For example, one could expect

a total 142 burrowing owl nests on the Hanford Site, assuming nest density is 0.14 nests km^{-2} and there is a total of 1011.5 km^2 of burrowing owl habitat. However, this estimate would appear to be highly inaccurate, given that I only located a total of 16 nests in 2007 and 17 nests in 2008. As such, the estimates of nest density reported in this study probably should not be extrapolated to large contiguous areas away from roads.

Despite the potential bias toward roadside habitat, the results of roadside surveys in this study did not appear to misrepresent population size (i.e., the estimated number of nests found was almost identical to the total number of nests found in 2007 and 2008). Results of call-broadcast detection trials suggested that detection probability of call-broadcast surveys may have been higher than that used to estimate the number of nests. Thus, it is possible that I may have actually underestimated the number of nests in the study area. However, the detection probability of call-broadcasts used in this study (64.3%) is within the range of detection probabilities reported for call-broadcasts to locate burrowing owl nests in eastern Washington (52.4 – 65%; Conway et al. 2008). Even so, it is likely that the density of burrowing owl nests on the Hanford Site is too low to assess habitat selection at a population level.

The apparent decline of burrowing owl populations in many portions of their range presents a problem for identifying landscape-scale factors that affect burrowing owl habitat selection, and consequently population dynamics. As populations decrease, the amount of area and effort required to locate enough individuals to derive adequate sample sizes for statistical analyses must be increased. Thus, researchers should seek to understand how inherent changes in the spatial variability of habitat variables may affect their perception of habitat selection (Cushman and McGarigal 2002). Soils are presumed to primarily have

bottom-up effects on proximate factors affecting burrowing owl nest habitat selection at larger scales (e.g., vegetation, burrow availability, prey availability, topography). For example, soil texture indirectly influences burrowing owl distribution in a 1700 km^2 area in southeastern Colorado by influencing black-tailed prairie dog distribution (Toombs 1997). Soils may be important in habitat selection at finer scales as well, by influencing factors such as burrow depth, the ability to modify burrows, topography, and burrow microclimate. Ultimately though, the scale at which soils affect these factors will depend on the spatial heterogeneity of factors such as soil texture, depth, and chemical composition, which vary with regional changes in soil-parent relationships.

In this study, burrowing owls were not abundant enough to accurately assess habitat selection at a landscape scale (~1500 km^2). However, patterns of habitat selection in relation soils or other landscape factors may be more evident at a regional scale for burrowing owls in eastern Washington. In eastern Washington, burrowing owls are more abundant in agricultural and urban-interface areas in the central and south-central portions of the state (Conway et al. 2006), although it should be noted that population data outside these areas is limited (Conway and Pardieck 2006). Burrowing owls are thought to associate with agricultural habitats in other shrub-steppe regions due to increased prey availability (Rich 1986, Moulton et al. 2006). However, this seems unlikely with respect to core occupied areas in Washington due to an abundance of similar agricultural habitat in both areas. Previous studies in eastern Washington (Conway et al. 2004) indicate that burrowing owls may utilize certain soils more frequently than others in each core occupied area, although this relationship has yet to be assessed quantitatively.

Burrow Availability

Previous studies have suggested burrowing owls may select for nest sites that have a greater availability of burrows nearby (Poulin et al. 2005, Smith et al. 2005, Lantz et al. 2007). However, this relationship appears to vary depending on the scale and location in which burrow availability is measured (e.g., Green and Anthony 1989, Plumpton 1992, Desmond et al. 1995, Belthoff and King 2002, Moulton et al. 2006). One reason for this may be that burrow availability influences habitat selection at multiple scales. For example, the availability of burrows surrounding the nest site may not appear important to burrowing owls if burrows are randomly distributed around the nest site. However, burrow availability may be important in habitat selection at larger scales if burrows are not randomly distributed within the landscape. Results of this study indicate that burrows (primarily abandoned badger burrows) are not randomly distributed across the landscape on the Hanford Site in southcentral Washington. In particular, suitable burrows were more abundant in silt loam and loamy sand soils compared to sandy loam, although this difference is probably due to high rock content in sandy loam soils which likely discourages burrowing activity by badgers.

Despite these differences, there was no clear indication that burrowing owls prefer to nest in soils that offer greater burrow availability. For example, the proportion of burrowing owl nests found in soils with both high (loamy sand) and low (sandy loam) burrow availability was slightly higher than expected based on the availability of habitat in those soils, although this difference was not statistically significant. This, as well other findings of this study, may suggest that burrowing owls choose to nest in loamy sand and sandy loam soils more often due to reasons other than burrow availability (e.g., vegetation, topography, prey availability).

One finding that may support this is that burrowing owls nested in artificial structures (usually old irrigation pipes) more frequently in sandy loam than in the other soils (i.e., 43, 26, and 0% of nests in sandy loam, loamy sand, and silt loam were in artificial structures). Generally, burrowing owls prefer to nest in abandoned mammal burrows. Most (71%) burrowing owl nests located during this study were found in abandoned badger burrows. Similarly, burrowing owls in other parts of eastern Washington utilize mammal burrows (badger, marmot, and ground squirrel) more frequently than artificial structures (Conway et al. 2004). Hence, burrowing owls may have used artificial structures in sandy loam due to the presence of other desirable habitat features besides mammal burrows. However, this may also suggest that burrows are limited in habitat types preferred by burrowing owls. Other studies of burrowing owls in the northwest U.S. have found similar evidence, indicating that habitat use by nesting burrowing owls was not correlated to burrow availability in those habitats (Green and Anthony 1989, Moulton et al. 2006). Others have also noted that reuse of burrows by burrowing owls is higher in sandier soils, despite lower availability and longevity of burrows in those soils (Holmes et al. 2003).

It is important to note however, that the definition of an "available" burrow used in these studies, as well as this study, may affect our perception on the importance of burrow availability in habitat selection. Most definitions of what constitutes an suitable burrow to a burrowing owl are based on known ranges for aboveground characteristics of burrows used by burrowing owls (e.g., entrance diameter, tunnel slope, absence of obstructions), presumably because it is difficult to measure belowground features. In addition, it is not known what constitutes a suitable burrow to burrowing owls because they are capable of digging and have been known to modify features such as entrance diameter and mound

height (Haug et al. 1993). However, belowground features such as tunnel length and nest chamber size may also be important in habitat selection. For example, Lantz et al. (2007) examined nest site selection of burrowing owls in northeastern Wyoming in relation to habitat parameters at four spatial scales, and found that tunnel length was the most influential factor affecting nest site selection. Mean tunnel length of occupied burrows in their study was 3.0 m, whereas mean length of unoccupied burrows was 1.7 m. Similarly, the tunnel length of burrowing owl nests in eastern Washington is generally about 3.0 m (Conway et al. 2005, personal observation). It should be noted, however, that it is possible that owls may have modified tunnel length to some extent prior to measurement in these studies. In contrast, less than 9% of all apparently suitable burrows observed in this study were >1 m long. Consequently, a large percentage of the burrows I classified as suitable may not have been suitable to burrowing owls. I tried to assess whether this affected my interpretation of burrow availability among soils by comparing burrow presence/absence on belt transects using only burrows that were >0.5 m long (sample size of burrows >1 m long was too small). The availability of burrows >0.5 m long was still greater in silt loam and loamy sand ($\chi^2 =$ 8.34, $df = 2$, $P = 0.0151$), but not significantly different between those two soils ($\chi^2 = 0.86$, $df = 1$, $P = 0.3532$). However, the proportion of transects at which a burrow (>0.5 m long) was present decreased by 12, 19, and 17% in silt loam, sandy loam, and loamy sand respectively. Hence, the definition of an suitable burrow used in this study (≥ 8 cm diameter and no apparent obstructions) may have been appropriate for comparing burrow availability among soils, but it may also underestimate true availability. Even so, it is suggested that further investigation be conducted to assess what constitutes a suitable "start" for burrowing owls in order to improve estimates of burrow availability.

Aside from these considerations, the results of this study further support previous findings that badgers are an important component of burrowing owl ecology in the northwest portion of their breeding range (Rich 1986, Green and Anthony 1989, Holmes et al. 2003, Conway et al. 2005, Moulton et al. 2006). Yet, little is known about factors that influence badger distribution and abundance, or how they may ultimately affect habitat selection of burrowing owls. Existing information regarding habitat selection of burrowing owls at a landscape scale has come almost entirely from areas where burrowing owls are associated with black-tailed prairie dogs (Toombs 1997, Desmond et al. 2000, Orth and Kennedy 2001, Lantz et al. 2007, Restani et al. 2008). Results of this study suggest that soils influence badger distribution in southcentral Washington, as indicated by the presence of their burrows. Others have also noted an association between badger distribution, habitat use, and soils (Messick and Hornocker 1981, Apps et al. 2002). For example, badgers in southeastern British Columbia occur primarily in fine-textured glaciolacustrine and glaciofluvial sediment deposits at both a landscape scale (23.8 km^2) and fine scale (14.5 ha). Badgers exhibited a similar association in this study, preferring deeper glacial and wind-blown loess deposits and avoiding areas of high rock content.

Burrow Temperature

There is little agreement among studies of cavity-nesting birds concerning the importance of nest microclimate in nest-site selection. Perhaps one reason for this confusion is that much of the debate has centered on microclimatic variation associated with the compass orientation of the nest entrance. Although the microclimatic consequences of differing nest orientations are relatively well known for non-cavity nests (reviewed by Walsberg 1985), microclimates in cavity nests may be dependent on multiple environmental influences in

addition to orientation (Dobkin et al. 1995). However, these additional influences have been examined primarily with respect to species that nest in tree cavities (Facemire et al. 1990, Rendell and Robertson 1994, Dobkin et al. 1995, Arsenault 1999, Hooge et al. 1999). Hence, relatively little is known about factors that influence microclimate in ground cavities.

The results of this study suggest that under controlled conditions, soil texture may have a significant effect on daily temperature variation inside burrows. Daily T_{MIN}, T_{MAX}, and T_{RANGE} inside randomly located simulated burrows were higher on average in sandy soils (sand, loamy sand, sandy loam) than in fine-textured silt loams. In general, these observations are consistent with the thermodynamics of near-surface soils, in that thermal conductivity (the ability to absorb and transfer heat) tends to be greater in soils with a high proportion of sand (Campbell 1977). However, it should be noted that this relationship is based on soil temperature, whereas I measured air temperature inside burrows. Hence, the temperature inside simulated burrows was probably influenced primarily by heat conduction from the surrounding soil. Nikol'skii (2002) reached this same conclusion, noting that burrow temperature was either identical to or slightly higher ($+1.5°$ C) than soil temperature, and that both burrow and soil temperature were considerably lower than surface air temperature and experienced little to no diel fluctuation.

In contrast, I failed to detect a positive association between soil texture and temperature inside paired simulated and previously occupied burrowing owl nests. However, this may have been due in part to a low sample size of nests. Consequently, I was not able to examine the influence of other environmental factors that may also have influenced burrow temperature, such as vegetation cover and soil moisture (Campbell 1977), entrance aspect and slope, and burrow depth and convolution. Of these factors, entrance aspect, slope,

burrow depth, and convolution, are believed to have played an important role in determining temperature differences between sites. Previous studies have indicated that these factors can affect convective heat exchange in burrows (Nikol'skii and Khurtorskoi 2001, Nikol'skii and Savchenko 2002). For example, in European badger (*Meles meles*) setts, the orientation of the entrance of relative to wind direction can affect the speed of air currents in the sett (Roper and Moore 2003). In addition, this effect may be mitigated to some extent by the height of the soil mound at the entrance. Prairie dogs (*Cynomys ludovicianus*), for example, may achieve passive ventilation of their burrows by increasing the height of the entrance mound at one end, which effectively increases the gradient of the boundary layer, creating viscosity suction in the burrow (Vogel and Bretz 1972, Vogel et al. 1973).

Another important factor that may have affected heat exchange in burrows was convective turnover. In arid environments, the surface temperature at night will often drop below that in the burrow, resulting in rapid cooling of the burrow due to convective turnover (Nikol'skii and Khurtorskoi 2001, Nikol'skii and Savchenko 2002). This phenomenon usually takes place when surface temperature approaches 5° C below that of the burrow, which often coincides around 1-2 hours before sunrise (Nikol'skii and Savchenko 2002). Both simulated and previously occupied burrows often underwent rapid cooling about an hour before sunrise as well, presumably due to convective turnover. However, simulated burrows generally remained ~ 1° C cooler than previously occupied burrows. One reason for this may be due to the lack of convolution in simulated burrows. Previous studies have indicated that the convolution (shape and complexity) of the tunnel may affect the depth in which convective exchange between burrow and surface air influences temperature in the burrow. For example, the temperature in the upper (slanting) zone of steppe marmot

(*Marmota bobak*) burrows tends to be more similar to the surface and fluctuate more than in the lower (gently slanting) portion of the burrow (Nikol'skii and Khurtorskoi 2001, Nikol'skii and Savchenko 2002). Hence, convective turnover may have taken place deeper inside simulated burrows due to the lack of convolution, although further testing is required to test this hypothesis. Another reason simulated burrows may have appeared slightly cooler than previously occupied burrows may be because I often was unable to deploy tags in previously occupied burrows at the same length as simulated burrows. In addition, it is unclear how continuation of previously occupied burrows beyond the tag may have affected temperature. However, I believe these explanations are unlikely given that tunnel length did not influence daily minimum temperature in the control simulated burrows. Another possible explanation may be differences in the shape or diameter of the tunnel between simulated and previously occupied burrows. Although the diameter of simulated burrows (15 cm) was similar to that of previously occupied burrows, the shape of the tunnel differed between the two burrow types (simulated burrows were circular whereas previously occupied burrows were horizontally oval).   Given that temperature tags were deployed so that the thermocouple-end of the tag was facing up, it is possible that tags in previously occupied burrows were influenced to a larger degree by the surrounding soil. However, this effect likely would have resulted in lower temperatures in previously occupied burrows because soil temperature tends to be slightly cooler than air temperature in burrows (Nikol'skii 2002).

    In summary, there was little evidence to suggest that soil texture was an important determinant of temperature variation among burrows that had been previously occupied by burrowing owls. As such, soil-related differences in burrow temperature are not likely to explain why burrowing owls may or may not select for certain soils. This does not preclude,

however, that burrowing owls may select for other factors that mitigate microclimatic variation, such as entrance aspect, slope, and burrow depth and convolution. Results of this study, as well as previous works (Vogel and Bretz 1972, Vogel et al. 1973, Nikol'skii and Khurtorskoi 2001, Nikol'skii and Savchenko 2002, Roper and Moore 2003), suggest that these factors may play an important role in convective heat exchange in burrows. Few studies have examined whether burrowing owls exhibit a preference for burrow characteristics that mitigate microclimatic variation. Some studies have indicated that owls may select burrows facing a certain aspect (Rich 1986, Conway et al. 2004), whereas other studies have failed to detect a preference for burrows of a particular aspect (Butts and Lewis 1982, Belthoff and King 2002). Others have indicated that owls may select for burrows with longer tunnels (Lantz et al. 2007) or shallower tunnel slopes (Belthoff and King 2002). However, the relationship between these characteristics and burrow temperature was not assessed in any of these studies, thus it is not certain whether selection was related to microclimatic preference. Furthermore, these factors likely interact to affect burrow temperature differently depending on geographic location and local climate.

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APPENDIX

Table 1. Summary of driving and call-broadcast surveys conducted on the Hanford Site in southcentral Washington between 2007 –

2008.

	Silt loam	*Sandy loam*	*Loamy sand*	*Total*
Total burrowing owl habitat (km^2)	248.1	139.1	624.3	1011.5
Total no. of driving routes [1]	-	-	-	10
Total no. of point-counts	29	42	40	111
Cumulative area surveyed (km^2) [2]	21.0	27.2	68.2	116.4
Total no. of burrowing owl nests detected	0	4	7	11
Estimated no. of burrowing owl nests [3]	0	6	10	16
Estimated no. of burrowing owl nests km^{-2} [4]	0.00	0.23	0.15	0.14

[1] Number of driving routes in each primary soil not shown because routes traversed multiple soils.

[2] Represents cumulative area surveyed in 2007 and 2008

[3] Estimated number of nests found during driving surveys and call-broadcast point-counts were calculated using separate detection probabilities and then added together.

[4] Calculated by dividing the estimated number of burrowing owl nests by the cumulative area surveyed

Table 2. Occurrence of burrowing owl nests located during roadside surveys and throughout the study (2006 – 2008), in relation to estimated burrowing owl habitat in silt loam, sandy loam, and loamy sand soils on the Hanford Site in southcentral Washington.

	Silt loam	Sandy loam	Loamy sand	Total
Total burrowing owl habitat (km^2)	248.1	139.1	624.3	1011.5
Roadside surveys [1]				
Proportion of burrowing owl habitat [2]		0.182	0.818	1.0
Estimated no. of nests [3]		6	10	16
Expected no. of nests [4]		3	13	16
All nests (2006 – 2008) [5]				
Proportion of burrowing owl habitat	0.245	0.138	0.617	1.0
Total no. of nests [6]	4	7	23	34
No. of nests in mammal burrows	4	4	15	25
Expected no. of nests [4]	8	5	21	34
Expected no. of nests in mammal burrows [4]	6	4	15	25

[1] Silt loam excluded due to lack of detections.

[2] Based on the proportion of each soil with respect to the total burrowing owl habitat in sandy loam and loamy sand only.

[3] Estimated number of burrowing owl nests found during driving surveys and call-broadcast point-counts were calculated using separate detection probabilities and then added together.

[4] Calculated by multiplying the observed/estimated number of burrowing owl nests by the proportion of burrowing owl habitat in each soil.

[5] Based on all burrowing owl nests located between 2006 – 2008 either during roadside surveys or incidentally.

Table 3.   Presence-absence of suitable burrows in silt loam, sandy loam, and loamy sand soils on the Hanford Site in southcentral Washington.

	Silt loam	Sandy loam	Loamy sand	χ^2	df	P
Total no. of transects	16	21	24			
No. of transects ≥1 burrow present	13	9	17			
Proportion of transects ≥1 burrow present	81.3	42.9	70.8			
Expected no. of transects ≥1 burrow present						
Silt loam/Sandy loam/Loamy sand	10	13	15	6.664	2	0.0357
Silt loam/Sandy loam	10	13	-	5.836	1	0.0157
Silt loam/Loamy sand	12	-	18	0.570	1	0.4504
Sandy loam/Loamy sand	-	12	14	3.633	1	0.0566

Table 4. Mean distance searched and probability to locate a suitable burrow, and mean distance between burrows in silt loam, sandy loam, and loamy sand soils on the Hanford Site in southcentral Washington.

	Silt loam	Sandy loam	Loamy sand	All soils
No. of transects with ≥1 burrow	13	9	17	39
Mean distance searched to locate a burrow (m)	265	318	389	332
95% CI for mean search distance (m)	89, 441	89, 548	244, 535	238, 425
Mean probability of locating a burrow (± SE) [1]	0.56 ± 0.03	0.512 ± 0.03	0.448 ± 0.02	-
No. of transects with ≥2 burrows	13	9	17	39
No. of burrows [2]	39	15	31	85
Mean distance between burrows (m)	34.7	76.0	80.1	54.1
95% CI for distance between burrows (m)	20.0, 60.2	31.3, 184.4	43.2, 148.4	37.1, 78.9

[1] Least squares mean cumulative probability of finding a burrow based on search distance
[2] Based only on transects in which ≥2 burrows were located

Table 5. Repeated measures multivariate analysis of variance results for daily minimum (T_{MIN})

temperature in control simulated burrows on the Hanford Site in southcentral

Washington.

Variable	F	df_N	df_D	P
Between-subjects				
Whole model	2.02	7	34	0.0814
Tag Burial	0.75	3	34	0.5321
Tunnel length	0.02	1	34	0.8788
Soil Texture	2.81	3	34	0.0539
Within-subjects				
Whole model [1]	1.34	231	26.2	0.1907
Date	6.00	33	2	0.1527
*Date*Tag Burial* [1]	0.59	99	6.9	0.8833
*Date*Tunnel length*	2.79	33	2	0.2985
*Date*Soil texture* [1]	0.76	99	6.9	0.7523

[1]   Results based on Wilks Lambda *F* statistic

Table 6.   Repeated measures multivariate analysis of variance results for daily maximum (T_{MAX}) temperature in control simulated burrows on the Hanford Site in southcentral Washington.

Variable	F	df_N	df_D	P
Between-subjects				
Whole model	6.46	7	34	<0.0001
Tag Burial	0.97	3	34	0.4198
Tunnel length	6.89	1	34	0.0130
Soil Texture	5.67	3	34	0.0029
Within-subjects				
Whole model [1]	1.20	231	26.2	0.3019
Date	108.15	33	2	0.0092
*Date*Tag Burial* [1]	0.81	99	6.9	0.7077
*Date*Tunnel length*	8.48	33	2	0.1108
*Date*Soil texture* [1]	0.95	99	6.9	0.5974

[1]   Results based on Wilks Lambda *F* statistic

Table 7.   Repeated measures multivariate analysis of variance results for daily temperature range (T_{RANGE}) in control simulated burrows on the Hanford Site in southcentral Washington.

Variable	F	df_N	df_D	P
Between-subjects				
Whole model	9.31	7	33	<0.0001
Tag Burial	5.28	3	33	0.0044
Tunnel length	8.23	1	33	0.0071
Soil Texture	4.92	3	33	0.0062
Within-subjects				
Whole model [1]	1.00	238	19.3	0.5372
Date	1.03	33	1	0.6681
Date*Tag Burial [1]	0.48	99	3.9	0.9121
Date*Tunnel length	2.76	33	1	0.4488
Date*Soil texture [1]	0.83	99	3.9	0.6861

[1]   Results based on Wilks Lambda *F* statistic

Table 8.   Repeated measures multivariate analysis of variance results for daily minimum (T_{MIN}) temperature in paired simulated and previously occupied burrows on the Hanford Site in southcentral Washington.

Variable	F	df_N	df_D	P
Between-subjects				
Whole model	1.95	6	13	0.1471
Soil	1.47	3	13	0.2676
Burrow type	2.24	1	13	0.1580
Tag burial	0.70	2	13	0.5123
Within-subjects				
Whole model [1]	2.30	42	36.3	0.0061
Date	30.26	7	7	0.0001
*Date*Soil* [1]	3.15	21	20.7	0.0060
*Date*Burrow type*	0.51	7	7	0.8037
*Date*Tag burial* [1]	2.46	14	14	0.0519

[1]   Results based on Wilks Lambda *F* statistic

Table 9.   Repeated measures multivariate analysis of variance results for daily minimum (T_{MAX}) temperature in paired simulated and previously occupied burrows on the Hanford Site in southcentral Washington.

Variable	*F*	*df$_N$*	*df$_D$*	*P*
Between-subjects				
Whole model	2.49	6	13	0.0795
Soil	2.44	3	13	0.1109
Burrow type	1.64	1	13	0.2229
Tag burial	0.46	2	13	0.6433
Within-subjects				
Whole model [1]	1.88	42	36.3	0.0273
Date	9.16	7	7	0.0046
*Date*Soil* [1]	2.09	21	20.7	0.0499
*Date*Burrow type*	1.47	7	7	0.3132
*Date*Tag burial* [1]	1.50	14	14	0.2306

[1]   Results based on Wilks Lambda *F* statistic

Table 10. Repeated measures multivariate analysis of variance results for daily minimum

(T_{RANGE}) temperature in paired simulated and previously occupied burrows on the

Hanford Site in southcentral Washington.

Variable	F	df_N	df_D	P
Between-subjects				
Whole model	1.60	6	13	0.2238
Soil	1.15	3	13	0.3675
Burrow type	0.70	1	13	0.4184
Tag burial	1.36	2	13	0.2899
Within-subjects				
Whole model [1]	1.14	42	36.3	0.3441
Date	5.22	7	7	0.0223
Date*Soil [1]	1.37	21	20.7	0.2376
Date*Burrow type	0.35	7	7	0.9075
Date*Tag burial [1]	1.13	14	14	0.4129

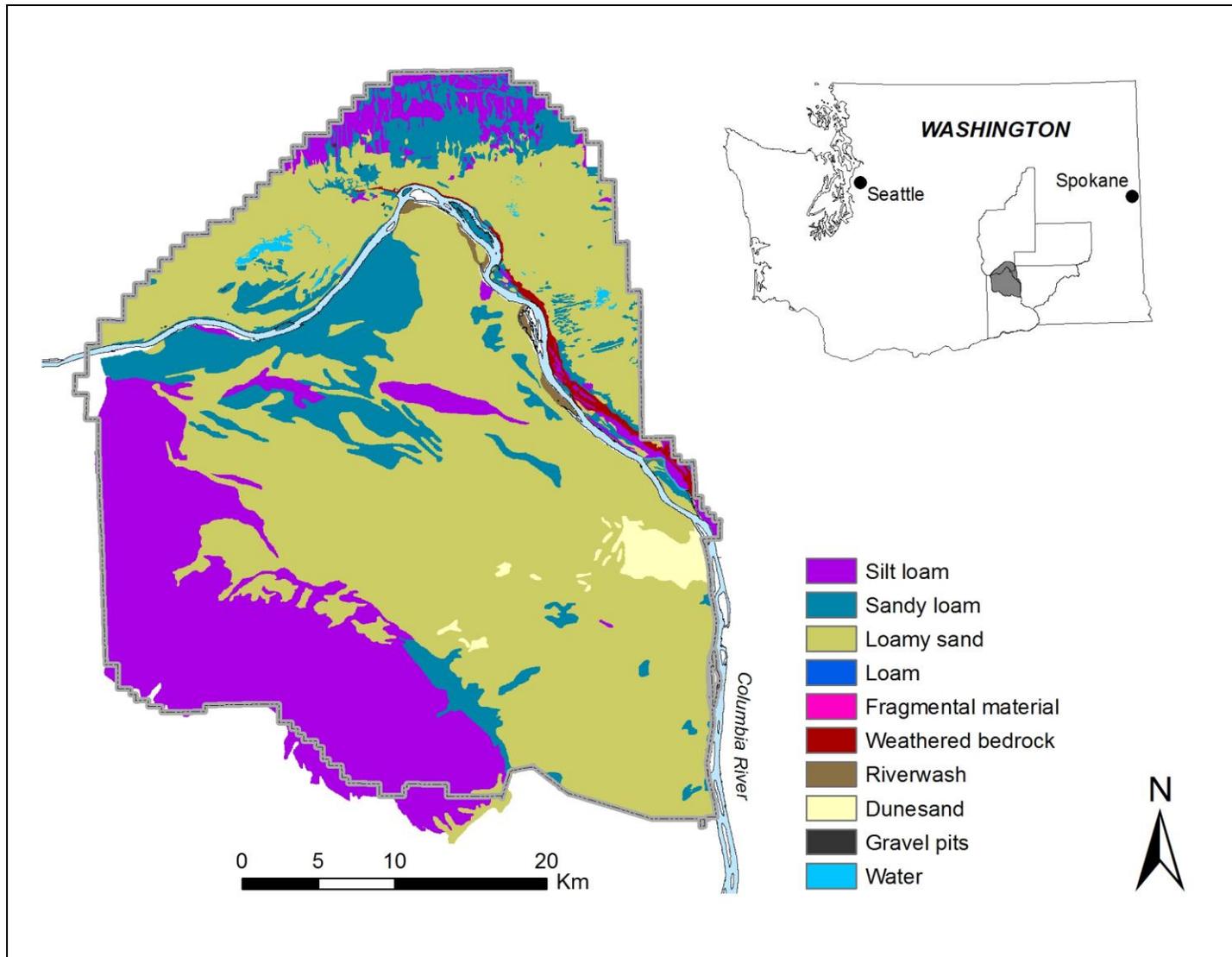[1] Results based on Wilks Lambda *F* statistic

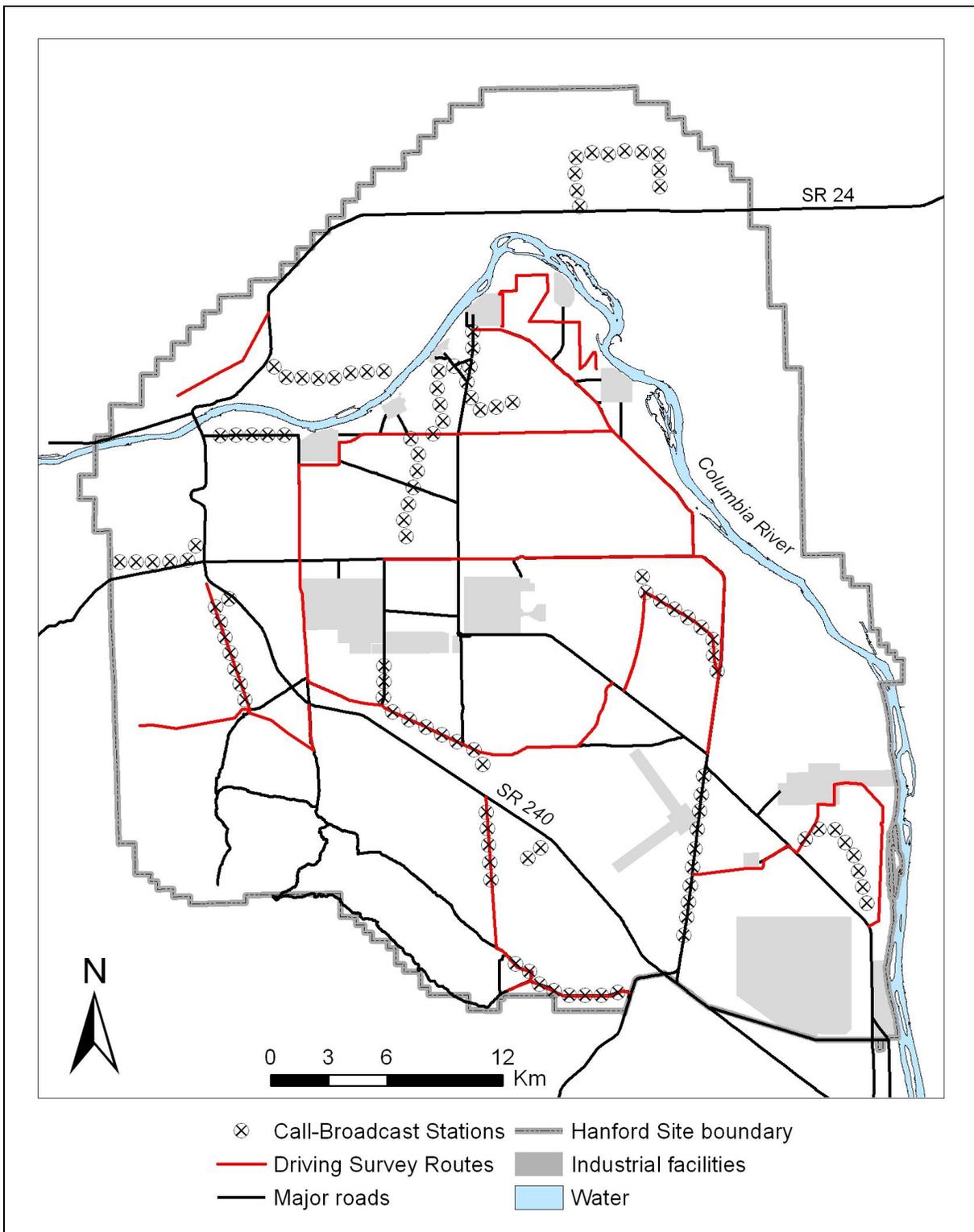Figure 1.   Map of primary soils found on Hanford Site in southcentral Washington.

Figure 2.   Location of driving surveys conducted in 2007 and call-broadcast point-counts

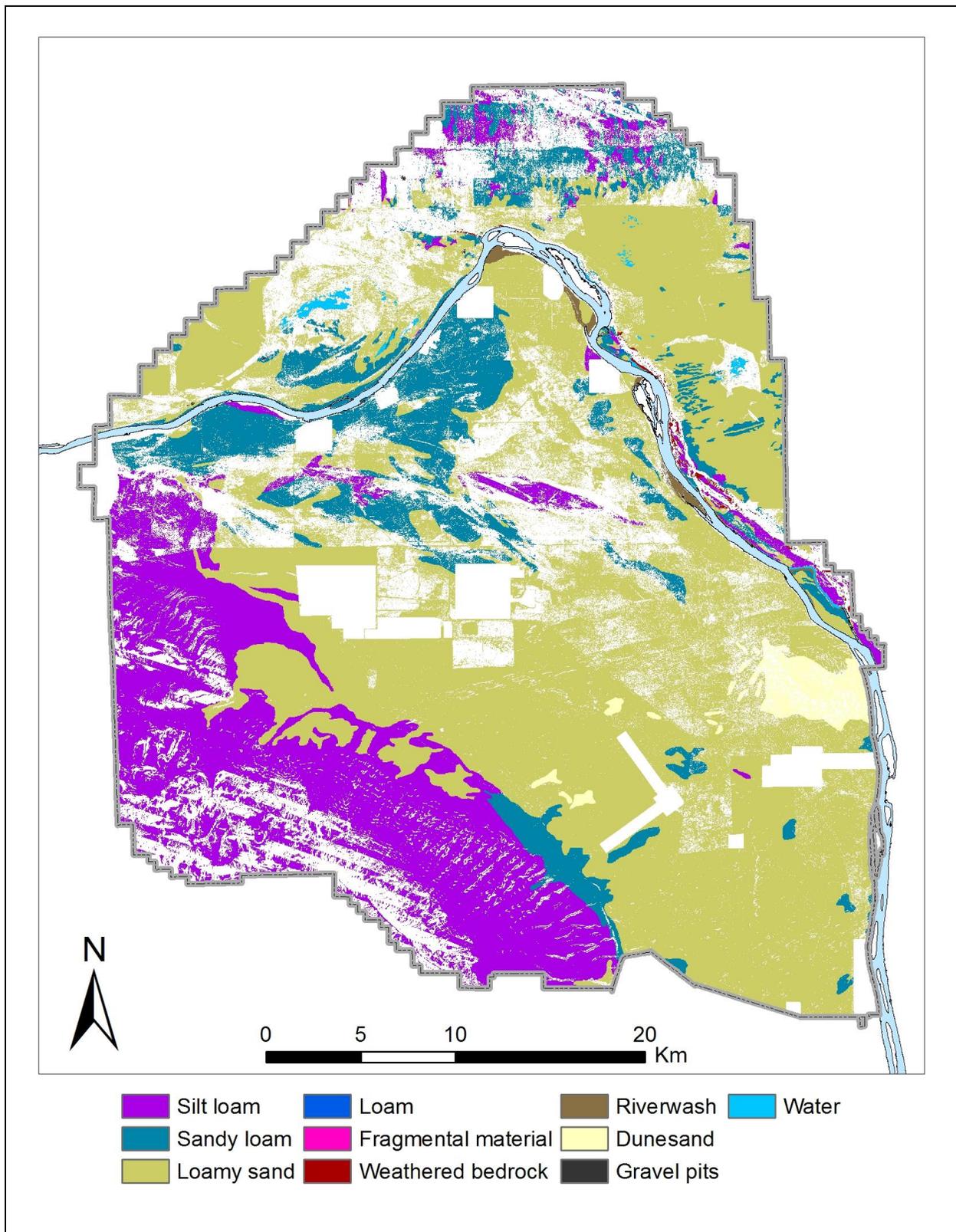conducted in 2008 on the Hanford Site in southcentral Washington.

Figure 3. Map of GIS model output of burrowing owl habitat in each of the primary soils found on the Hanford Site in southcentral Washington.