

A MULTI-SCALE EVALUATION OF PYGMY RABBIT
SPACE USE IN A MANAGED LANDSCAPE

by

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ABSTRACT

A Multi-scale Evaluation of Pygmy Rabbit Space Use in a Managed Landscape

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Habitat selection has long been viewed as a multi-scale process. Observed species responses to resource gradients are influenced by variation at the scale of the individual, population, metapopulation, and geographic range. Understanding how species interact with habitat at multiple levels presents a complete picture of an organism and is necessary for conservation of endangered species. The main goal of this dissertation is to evaluate distribution, relative abundance, and habitat selection of a rare species, the pygmy rabbit *Brachylagus idahoensis*, at multiple scales in order to improve management and conservation for this species.

At the broadest scale, pygmy rabbit occurrence and relative abundance were modeled in the Duck Creek allotment of northern Utah using a hierarchical spatial model. Pygmy rabbits are not easily observable, and the model used two levels of indirect detection to make statistically rigorous spatial predictions. We found that the model predicted the general pattern of rabbit occurrence and abundance within the study area, and that there was spatial heterogeneity in the probability of pygmy rabbit

occurrence within a study domain that was known to be occupied. The resulting model framework could be used to develop a long-term monitoring program for pygmy rabbits and other species for which hierarchically nested levels of indirect observation are collected.

The mid-scale analysis evaluated pygmy rabbit home range placement and movement with respect to sagebrush removal treatments using null models based on an optimal central place foraging behavior. While placement of home-range centers did not appear to be affected by the treatments, within-home range movements were farther from treatments than expected by the null models for two rabbits (of eight), and rabbits that approached treatment edges were less likely to enter treatments than expected by chance. Rabbits are not extirpated from sites that have been treated, but the observed reluctance to enter treated patches calls for caution when conducting sagebrush removal treatments near occupied pygmy rabbit burrows.

At the finest level of resolution, the spatial ecology of pygmy rabbit use of burrows was evaluated. Both the placement of burrows in general and pygmy rabbit use of burrows were clustered. While the habitat gradients experienced by each of the rabbits evaluated affected the modeled habitat selection responses, some generalities were observed. Selection of high cover suggests that pygmy rabbit use of burrows may be linked to predator avoidance behavior. Additionally, pygmy rabbit use of clustered burrows affects management actions including: habitat modeling, monitoring, and species introduction. Explicit attention to resource distribution will improve efforts to predict species responses to management actions. (128 pages)

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CHAPTER 1

INTRODUCTION

OVERVIEW

Natural systems are structured hierarchically (Pattee 1973, Johnson 1980, Urban et al. 1987). This fundamental characteristic allows ecologists to deal with the complexity of nature by organizing processes along a spatio-temporal gradient of short and fast to broad and slow (Urban et al. 1987). Hierarchical levels are recognized by processes that operate with similar functional scales, but are not necessarily required to be distinct from one another (O'Neill 1989). Conceptually, hierarchies are universal, whether one is interested in organisms (cells → whole organisms), societies (communities → multi-national organizations), or ecological systems (individuals → ecosystems).

Similarly, there exists a natural hierarchy of species distribution that is relevant for conservation. The conceptual hierarchical model proposed by Johnson (1980) continues to be used by ecologists interested in understanding animal distribution, resource selection, and movement. At the broadest level species geographic range is of interest (Brown et al. 1996). Within this boundary, the distribution of a species is typically patchy due to resource requirements and/or habitat specialization (Brown et al. 1995). Continuing along the hierarchy, the location of metapopulation networks within suitable habitat and locations of local populations are formed by regional and local resource gradients (Kareiva 1990, Brown et al. 1995, Baguette and Meunechez 2005). The habitat selection and space use of individuals completes the hierarchy of animal

space-use (Manly et al. 2002). Throughout the hierarchy there are interrelated processes affecting metapopulations, populations and individuals that determine outcomes observed by ecologists.

It is common for ecologists to view individual levels of a hierarchical process separately. Indeed, sub-disciplines of ecology can also be classified based on hierarchical structure (eco-physiology → ecosystem science). The conceptual hierarchy of spatial ecology presented above includes the disciplines of species distribution modeling and landscape ecology at the broadest level, patch occupancy modeling and metapopulation biology in the second level, resource selection at the third level, and individual space use and resource selection at the finest level. Species respond to habitat features in a hierarchical manner; therefore, integrating these levels to the extent possible presents a more complete picture of an organism that may be necessary for conservation (Cushman and McGarigal 2002).

Sagebrush steppe

Sagebrush dominated rangelands are declining in areal extent (Knick et al. 2003). This threat is coming from the conversion of large acreages of rangelands to annual grasslands (D'antonio and Vitousek 1992, Keeley 2006), and the expansion of the human infrastructure (Knick et al. 2003). The results of this habitat loss and degradation are observed declines in avian species associated with sagebrush rangelands (Knick 1999, Dobkin and Sauder 2004), and some sagebrush-dependent mammalian species may also follow these trends (Dobkin and Sauder 2004). These observations

have led to growing awareness of the need to slow the rate of habitat loss within the sagebrush steppe.

Within remaining sagebrush communities, there is a prevailing view that sagebrush canopy cover is increasing due to a lack of natural fire (Wroblewski and Kauffman 2003; but see Baker 2006), or heavy grazing (Miller et al. 1994; but see Welch 2005). This increase in canopy cover and subsequent decline in abundance of grasses and forbs is considered by some to represent “degraded” or “decadent” community seral states. Habitat loss notwithstanding, increases in sagebrush canopy cover are perceived by some to be the biggest threat to biodiversity in sagebrush rangelands (Bunting et al. 2003). Therefore, mechanical, chemical, or prescribed fire treatments are used under the rubric of restoration to reduce the sagebrush dominance, releasing grasses and forbs from competition. Current ideas of sagebrush treatment reject the traditional, systematic type conversion over large areas in favor of smaller and more heterogeneous treatments meant to mimic natural disturbance regimes (Hemstrom et al. 2002, Davies et al. 2009). The resulting mosaic of vegetation states is thought to lead to increases in cover of grasses and forbs, which in turn benefits big game (Van Dyke and Darragh 2007) and greater sage-grouse (*Centrocercus urophasianus*; Society for Range Management 2005, Dahlgren et al. 2006; but see Schroeder et al. 2006). The effect of these treatments on many other sagebrush-dependent species, such as pygmy rabbits (*Brachylagus idahoensis*) remains unclear. Managing widespread loss of sagebrush dominated rangelands due to disturbance, paired with local degradation that

may require the same disturbances, is tricky due to the multi-level hierarchical nature of the problem.

Pygmy rabbits

The pygmy rabbit presents an excellent opportunity to use multi-scale resource use to improve management. They are small, cryptic leporids that depend on sagebrush for both food and cover (Green and Flinders 1980, Shipley et al. 2006). They are presumed to be experiencing range-wide population declines due to loss and degradation of their sagebrush habitat. However, estimation of wild pygmy rabbit populations has proved difficult, and population trend information is lacking.

Pygmy rabbits were petitioned to be listed as threatened or endangered under the Act in 2003 (Fite et al. 2003) throughout most of its range outside of the Columbia Basin. The petition was ultimately accepted and pygmy rabbits were considered for listing in 2008 (Federal Register 2008). As of this writing, there has not been a decision regarding the 12-month review that began in 2008. Additionally pygmy rabbits are considered to be “species of concern” or “sensitive” in most states where they occur. These designations allow states to enact conservation actions independent of Federal designations.

The goal of my dissertation is to evaluate space use of the pygmy rabbit at multiple nested hierarchical levels from landscape-wide distribution to individual habitat selection. The goal of Chapter 2 is to present a spatial model that predicts pygmy rabbit occurrence and relative abundance in a spatially large study domain that was known to be occupied. Chapter 3 presents a multi-scale analysis of pygmy rabbit

responses to sagebrush treatments designed to reduce canopy cover. Within home range burrow use was the focus of Chapter 4.

STUDY AREA

The study was conducted on the 9,200-ha Duck Creek allotment in Rich County, located in northern Utah, USA. The site ranged in elevation from 1800 m to 2300 m and consisted of rolling hills with small drainages, some with spring-fed perennial streams. The climate was characteristic of shrubsteppe vegetation types consisting of cold winters, warm summers, and most precipitation falling as winter snow (West and Young 2000). Land was mixed ownership (Bureau of Land Management and private) and managed as a single allotment with a four pasture grazing system. Lawson pasture aerator treatments were conducted in two of four plots within the allotment in 2004. This treatment reduced sagebrush height, cover and extent by crushing, and resulted in series of treated patches within an untreated matrix. The resulting edge is a distinct boundary between tall, dense sagebrush steppe vegetation, and a grassland with remnant small individual sagebrush plants.

The site consisted of sagebrush shrubsteppe vegetation dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), with basin big sagebrush (*A.t.* ssp. *tridentata*) and low sagebrush (*A. arbuscula*) present at much lower frequencies. Snowberry (*Symphoricarpos oreophilus*) was co-dominant with sagebrush on more mesic aspects. The under-story contained a diverse mix of small shrubs, grasses and forbs, both native and non-native. Cheat grass (*Bromus tectorum*) was present on south

facing slopes and within the treatments, but mostly absent elsewhere (Wilson, unpublished data). The site contained avian and mammalian predators, including: long-tailed weasel (*Mustela freneta*), badger (*Taxidea taxus*), golden eagle (*Aquila chrysaetos*), etc. Most of the recognized sagebrush-dependent species were present, including: greater sage-grouse, sage sparrow (*Amphispiza belli*), sagebrush vole (*Lemmiscus curtatus*), sagebrush lizard (*Sceloporus graciosus*), etc... In addition to pygmy rabbits, observed lagomorphs included: mountain cotton-tail rabbits (*Sylvilagus nuttallii*) and white-tailed jack rabbits (*Lepus townsendii*). Black-tailed jack rabbits (*Lepus californicus*) were not observed.

STYLE

My dissertation is written in multiple-paper format. Chapters 1, 4, and 5 are written according to current guidelines in use by Ecology. Chapter 2 is published in the Journal of Applied Ecology and follows the format for that journal. Chapter 3 is prepared using the guidelines of the Journal of Wildlife Management. All section headings were changed to a common format so as to appear consistent throughout the dissertation, but text and citations remain formatted as per the targeted journal of each chapter.

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CHAPTER 2

HIERARCHICAL SPATIAL MODEL FOR PREDICTING PYGMY RABBIT
DISTRIBUTION AND RELATIVE ABUNDANCE^{1,2}

SUMMARY

1. Conservationists routinely use species distribution models to plan conservation, restoration, and development actions, while ecologists use them to infer process from pattern. These models tend to work well for common or easily observable species, but are of limited utility for rare and cryptic species. This may be because honest accounting of known observation bias and spatial autocorrelation are rarely included, thereby limiting statistical inference of resulting distribution maps.
2. We specified and implemented a spatially-explicit Bayesian hierarchical model for a cryptic mammal species (pygmy rabbit *Brachylagus idahoensis*). Our approach used two levels of indirect sign that are naturally hierarchical (burrows and fecal pellets) to build a model that allows for inference on regression coefficients as well as spatially explicit model parameters. We also produced maps of rabbit distribution (occupied burrows) and relative abundance (number of burrows expected to be occupied by pygmy rabbits). The model demonstrated

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statistically rigorous spatial prediction by including spatial autocorrelation and measurement uncertainty.

3. We demonstrated flexibility of our modeling framework by depicting probabilistic distribution predictions using different assumptions of pygmy rabbit habitat requirements.
4. Spatial representations of the variance of posterior predictive distributions were obtained to evaluate heterogeneity in model fit across the spatial domain. Leave-one-out cross-validation was conducted to evaluate the overall model fit.
5. *Synthesis and Applications*. Our method draws on the strengths of previous work, thereby bridging and extending two active areas of ecological research: species distribution models and multi-state occupancy modeling. Our framework can be extended to encompass both larger extents and other species for which direct estimation of abundance is difficult.

INTRODUCTION

Ecologists, conservationists and managers often make decisions with incomplete information about the system or species of interest. The predictive spatial distribution model is one tool often used to make decisions based on incomplete information about a species (e.g. La Morgia, Bona & Badino 2008; Zarnetske, Edwards Jr. & Moisen 2007). Such models may be misleading because they can fail to account for biases in species distribution data (Carroll & Johnson 2008) due to imperfect detection (Stauffer, Ralph & Miller 2002) and autocorrelation (Cressie 1993; Hoeting 2009). Recent species

distribution models have variously addressed these problems, but only a few have capitalized on count data to produce maps of abundance that also account for both spatial autocorrelation and imperfect detection (e.g. Gorresen *et al.* 2009; Thogmartin, Sauer & Knutson 2004).

Species that are rare or secretive pose a unique set of problems for ecologists interested in using predictive species distribution models. If rarity leads to poor detection, then a high number of zero observations can lead to violations of statistical assumptions of standard generalized linear models (Cunningham & Lindenmayer 2005), and large variances in occupancy models (MacKenzie *et al.* 2009). In order to improve detection, indirect indices of presence or relative abundance such as burrows, nests, tracks, fecal material or hair samples (signs) may be used (Stanley & Royle 2005). Uncertainty is introduced to the modeling process when indirect detection indices are used to build habitat models, because it is difficult to know if the sign was produced by the organism of interest. For example, a burrow may not be a convincing indicator of presence for one of many burrowing organisms, but when combined with a species-specific observation (like fecal pellets), the burrow may become a more convincing argument for presence. Thus we observe that all burrows with fecal pellets of any species of interest (burrow utilization) are completely contained within the universe of all burrows on the landscape (burrow intensity), giving these two data levels natural hierarchical structure.

Our objective is to use an empirical Bayesian hierarchical spatial model to produce maps of ecologically important variables: distribution and relative abundance

of a small rabbit that is difficult to observe. Our model uses hierarchically related indirect detection data (counts of burrows and presence of fecal pellets) in a joint likelihood that incorporates spatial structure and measurement uncertainty. We show how inference about spatial distribution is enhanced by location-specific uncertainty estimates in unobserved variables (burrow intensity and utilization). This allows us to combine information contained in both levels of data to produce maps of distribution (burrow occupancy) and relative abundance. We then demonstrate the flexibility of our approach by presenting burrow occupancy maps using different assumptions about organismal resource use. While use of hierarchical methods to produce species distribution models is continuing to gain popularity (e.g. Gorresen *et al.* 2009; Thogmartin, Sauer & Knutson 2004), ours builds on previous efforts by using hierarchical indirect detection data as inputs. We also build on multi-level occupancy models (MacKenzie *et al.* 2009) by producing statistically rigorous spatial prediction of distribution and relative abundance.

MATERIALS AND METHODS

Study System

The pygmy rabbit *Brachylagus idahoensis* Merriam serves as the species of interest in the models we present. Pygmy rabbits occur only in the intermountain western United States, where they depend primarily on big sagebrush *Artemisia tridentata* Nutt. for food and cover. Pygmy rabbits are petitioned to be listed under the United States Endangered Species Act (Fite *et al.* 2003), but little is known about their

abundance or distribution. Pygmy rabbits are known to dig their own burrows, and although burrow use is little understood, occupied pygmy rabbit burrows tend to be associated with copious amounts of fecal pellets (Ulmschneider *et al.* 2004). Observing rabbits directly to estimate abundance is difficult because they are small, secretive, difficult to trap, and lack markings that would allow for the identification of individuals. As a result, monitoring distribution and relative abundance using indirect indicators of rabbit activity (burrows and fecal pellets) is an attractive alternative to direct observation. Several species distribution models have been proposed for pygmy rabbits using burrows with fecal pellets as inputs (e.g. Himes & Drohan 2007; Simons & Laundré 2004). These previous efforts were successful at delineating important habitat variables, but inference was limited because autocorrelation and detection probability were both ignored in the modeling process.

Study Area

Modeling was conducted at a 21,600-ha site in Rich County, located in northern Utah, USA. The site ranges in elevation from 1800 m to 2300 m and is predominately covered by sagebrush-steppe vegetation. Prior to the initiation of sampling, the site was known to be occupied by pygmy rabbits, but their spatial distribution within the study area was largely unknown.

We created a prediction domain consisting of systematically spaced points (300 m×200 m) that formed the centers of 6-ha rectangular polygons for the entire study area. This spacing was based on estimated maximum adult female home-range (Sanchez & Rachlow 2008). The prediction grid cell that overlapped the majority of the

area sampled by the burrow transects (described below) was selected as the point for intersecting training data with the grid.

Burrow Sampling

We used a modified systematic and stratified design to place 38 sampling locations within the study area. We used a randomly started 2500-m tessellation grid to place 28 of these points. Use of a systematic grid for sampling precludes the estimation of spatial structure that occurred at a finer scale than the tessellation grid (Wintle & Bardos 2006). To combat this problem, we randomly selected an additional ten sampling locations within soil types that could potentially harbor pygmy rabbits. It should be noted that we sampled a small area of the total domain and prediction would be improved with additional data collection.

We used distance sampling (Buckland *et al.* 2004) to conduct burrow counts at each sampling location along five parallel 200-m line transects spaced 50 m apart (1000 m of total line sampled/site). We randomly selected one of eight bearings (cardinal and inter-cardinal) as the direction the line transects were run at each of the 38 sites. A single observer documented burrows that could be seen directly from the line. Once a burrow was observed, the following were measured by additional observers: 1) distance of the burrow from the line, and 2) presence or absence of pygmy rabbit fecal pellets. We assumed 100% detection of all burrows directly on the sample transect line.

Hierarchical Model

Ecologists build statistical models using data to make inference about a process of interest. In the simplest case, a likelihood-based statistical modeling formulation seeks to maximize the probability of the data given some assumption about the process and parameters. In the case of a generalized linear model, the parameters of the process are the regression coefficients (β). This model assumes that there is only measurement uncertainty, and that it is captured by the error term. If we are aware of uncertainty in a process of interest, then we can use the natural hierarchical structure obtained by factoring the joint distribution of the data and process components to model the uncertainty affecting measurement in a data model separately from that in the process model (Cressie *et al.* 2009). An advantage of this framework for complicated models is that additional data or process levels, and information about their associated uncertainty, can be incorporated easily (Cressie *et al.* 2009).

In this study, we implemented a spatially explicit linear model using a Bayesian hierarchical framework described in detail below. Recall that we are fundamentally interested in making inference about pygmy rabbit activity at a site based on the spatial distribution of two hierarchically related levels of indirect evidence of pygmy rabbit occurrence. The first level of interest is the intensity of all burrows regardless of their use by pygmy rabbits. It was impractical to sample all burrows within our large study area, so we introduced an additional random variable at this level pertaining to the probability of detecting a burrow given it was in the 6-ha sampling area. The second level of interest is the number of burrows used by pygmy rabbits. We termed this level

utilization, where counts of burrows with pygmy rabbit fecal pellets are normalized by the total number of burrows within the domain. We assumed that if present, the probability of detecting burrows with fecal pellets was identical to those without. Utilization was therefore modeled as the probability of finding a burrow with pygmy rabbit fecal pellets given burrows. We present a joint likelihood (or data model) based on our observations of burrow counts and pygmy rabbit use inferred through fecal pellets.

We assumed that both burrow intensity and probability of utilization were related to our set of spatial covariates (Table 2.1) and potentially subject to correlated spatial error. It is impossible to know *a priori* the nature of the latent spatial structure of either process (intensity or utilization). We therefore used geostatistical methods to estimate spatial dependence parameters in an empirical Bayesian fashion (Casella 1985; see Appendix B in Supporting Information). Such empirical Bayesian approaches have proven useful in cases where fully Bayesian estimation is cumbersome in practice (Hooten, Larsen & Wikle 2003). Specifically, spatial covariance parameters have proven difficult to estimate when deeply nested in hierarchical models and only small amounts of spatial data are available (Carlin & Lewis 2009). In this case, other model parameters can help to absorb any potential uncertainty not accounted for in the empirical Bayes procedure. We also used preliminary analysis (Appendix B) to obtain the probability of detection for burrows using distance sampling (Buckland *et al.* 2004).

We implemented the hierarchical model using the Bayesian framework described as follows. Let n_i and Y_i represent observed number of burrows with fecal

pellets and burrows respectively at each location i (where $i = 1, 2, \dots, m$). The true number of burrows for each location, N_i , was not observed. We therefore considered the two binomial distributions: $n_i|Y_i, \theta_i \sim \text{Binom}(Y_i, \theta_i)$ and $Y_i|N_i, \varphi \sim \text{Binom}(N_i, \varphi)$, where θ_i is the probability of observing pygmy rabbit fecal pellets given the observed burrows at a specified location i , and φ is the probability of burrow detection. Burrow detection is defined as $\Phi^{-1}(\varphi) \sim \text{Norm}(\mu_\varphi, \sigma_\varphi^2)$, as provided by the distance sampling analysis, where $\Phi^{-1}(\varphi)$ denotes the probit transformation of burrow detectability. As part of our process stage in the hierarchical framework, we modeled the true number of burrows, N_i , with a Poisson distribution with intensity λ_i . Noting the availability of our covariates at all locations, we then specify linear models for the log transformation of λ , where $\lambda = (\lambda_1, \dots, \lambda_m)$, and probit transformation of θ , where $\theta = (\theta_1, \dots, \theta_m)$. Thus,

$$\log(\lambda) = \mathbf{X}_\lambda \boldsymbol{\beta} + \boldsymbol{\varepsilon} \quad \text{eqn 1}$$

$$\Phi^{-1}(\theta) = \mathbf{X}_\theta \boldsymbol{\alpha} + \boldsymbol{\eta} \quad \text{eqn 2}$$

where \mathbf{X}_λ is $m \times p$, \mathbf{X}_θ is $m \times q$, $\boldsymbol{\beta}$ is $p \times 1$, $\boldsymbol{\alpha}$ is $q \times 1$, $\boldsymbol{\varepsilon}$ is $m \times 1$, and $\boldsymbol{\eta}$ is $m \times 1$. The error terms, $\boldsymbol{\varepsilon}$ and $\boldsymbol{\eta}$ were assumed to have multivariate normal distributions $\boldsymbol{\varepsilon} \sim \text{Norm}(\mathbf{0}, \sigma_\varepsilon^2 \mathbf{R}_\varepsilon)$ and $\boldsymbol{\eta} \sim \text{Norm}(\mathbf{0}, \sigma_\eta^2 \mathbf{R}_\eta)$ where \mathbf{R}_ε and \mathbf{R}_η are spatial correlation matrices, the forms of which (e.g. exponential, Gaussian, or spherical) are dictated by the residual spatial structure in our preliminary data analysis (Appendix B). The hierarchical model is summarized as follows:

$$n_i|Y_i, \theta_i \sim \text{Binom}(Y_i, \theta_i), \quad i = 1, 2, \dots, m \quad \text{eqn 3}$$

$$Y_i|N_i, \varphi \sim \text{Binom}(N_i, \varphi), \quad i = 1, 2, \dots, m \quad \text{eqn 4}$$

$$N_i|\lambda_i \sim \text{Pois}(\lambda_i), \quad i = 1, 2, \dots, m \quad \text{eqn 5}$$

$$\log(\lambda) | \boldsymbol{\beta}, \sigma_{\varepsilon}^2 \mathbf{R}_{\varepsilon} \sim \text{Norm}(\mathbf{X}_{\lambda} \boldsymbol{\beta}, \sigma_{\varepsilon}^2 \mathbf{R}_{\varepsilon}) \quad \text{eqn 6}$$

$$\Phi^{-1}(\boldsymbol{\theta}) | \boldsymbol{\alpha}, \sigma_{\eta}^2 \mathbf{R}_{\eta} \sim \text{Norm}(\mathbf{X}_{\theta} \boldsymbol{\alpha}, \sigma_{\eta}^2 \mathbf{R}_{\eta}) \quad \text{eqn 7}$$

where eqns 3 and 4 form the data model and eqns 5–7 make up the process model. In order to make our priors on the regression parameters vague, we specified multivariate normal distributions with mean vectors equal to zero and variance components equal to 1000 for $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$. For the variance component σ_{ε}^2 , we specified a conjugate Jeffreys prior since it is difficult to estimate the scale parameter using geostatistics without observing λ . We then obtain the posterior distribution given the number of burrows with fecal pellets (n_i) and burrows (Y_i) as proportional to the product of the likelihood of the data given the latent process models and parameter models shown below.

$$\begin{aligned} [\{N_i\}, \{ \theta_i \}, \{ \lambda_i \}, \boldsymbol{\beta}, \boldsymbol{\alpha}, \sigma_{\varepsilon}^2 | \{Y_i\}, \{n_i\}] &\propto \prod_{i=1}^m [n_i | Y_i, \theta_i] \times \prod_{i=1}^m [Y_i | N_i, \varphi] \times \prod_{i=1}^m [N_i | \lambda_i] \\ &\times [\lambda | \boldsymbol{\beta}] \times [\boldsymbol{\theta} | \boldsymbol{\alpha}] \times [\boldsymbol{\beta}] \times [\boldsymbol{\alpha}] \times [\sigma_{\varepsilon}^2] \end{aligned} \quad \text{eqn 8}$$

The posterior in eqn 8 is not analytically tractable. Thus, given empirical estimates of spatial dependence parameters ($v_{\varepsilon}, v_{\eta}$) and burrow detection probability (φ), the model was then implemented using a hybrid Metropolis-Hastings and Gibbs Markov Chain Monte Carlo (MCMC) algorithm using program R (R Development Core Team 2009). The MCMC algorithm was run for 10,000 iterations after a burn-in period of 2,000 iterations. Convergence occurred rapidly and was assessed visually to ensure a stationary posterior distribution was well characterized. MCMC samples from the posterior distribution were used to calculate summary statistics for all latent processes and model parameters. Using composition sampling, posterior predictive distributions

were obtained for the latent parameters θ (burrow utilization), and λ (burrow intensity) for the entire spatial domain. The details of the MCMC algorithm are beyond the scope of this paper, and interested readers are referred one of many texts on the subject (e.g. Banerjee, Carlin & Gelfand 2003; Carlin & Lewis 2009).

Model Validation

We evaluated the spatial precision of the posterior expectations of our latent processes (burrow intensity and burrow utilization) by finding the standard deviations of the predicted posterior distributions. We mapped the standard deviations to assess the heterogeneity of predictive precision throughout the site. Maps of posterior predictive standard deviations do not evaluate overall model performance. We therefore performed a leave-one-out cross-validation procedure to formally evaluate overall model fit. We omitted the data for one of the 38 sites, and then re-ran the model obtaining posterior predictions of the expected data (n_i and Y_i) for the omitted site. It was only possible to evaluate the counts (n_i and Y_i) using cross validation because all other processes were unobserved.

RESULTS

The predictive map of burrow intensity (λ) shows high burrow intensity in the valley bottoms of the study area (Fig. 2.1A). Recall that burrow intensity represents all burrows, regardless of origin, expected to occur within each 6 ha grid cell. High burrow intensity was predicted for slopes near drainages of perennial streams within the study area. Covariate relationships were considered statistically significant if 95% credible

intervals did not overlap zero (Table 2.2). Burrow intensity was positively associated with northing (Y), slope (SLOPE), and soil moisture (ASPVAL), and negatively associated with easting (X), near infrared reflectance (NIR), and distance to water (WATER)(Table 2.2).

We modeled utilization (θ) as the proportion of the burrows that were expected to contain evidence of pygmy rabbit. High utilization was observed along the slopes and ridge tops within the central portion of the spatial domain (Fig. 2.1B). Given burrows, utilization was positively related to soil and snow deposition (ASPWEST) and red band reflectance (RED), and negatively related to easting (X), near infrared reflectance (NIR), and distance to water (WATER)(Table 2.2). Slope (SLOPE) and soil moisture (ASPVAL) were not shown to be statistically significant because regression coefficient 95% credible intervals overlapped zero.

While burrow utilization (θ) and intensity (λ) were processes leading to our observations, those processes can also be used to learn about the total number of burrows expected to have pygmy rabbit fecal pellets. If we let Z represent the true number of burrows with fecal pellets, then conditioned on the true number of burrows (N_i) and probability of utilization (θ_i), Z_i comes from a binomial distribution: $Z_i \sim Binom(N_i, \theta_i)$. We can thus obtain predictions for pygmy rabbit burrow abundance over the entire spatial domain. If we assume that the pygmy rabbit burrow abundance (Z) is proportional to the number of pygmy rabbits, then Z becomes a metric of relative pygmy rabbit abundance. Maps of relative abundance (Fig. 2.1C) shows the expectation of pygmy rabbit burrow abundance attributable to spatial covariates and spatial

autocorrelation formally included in our model. Pygmy rabbit burrow abundance is predicted to be higher in both valleys and slopes in the center of the domain. An unsampled region in the western edge of the domain is also expected to have high pygmy rabbit abundance.

We gain insight about pygmy rabbit occupancy within the spatial domain if we assume that a site with at least one burrow with pygmy rabbit fecal pellets is occupied by pygmy rabbits. Thus, we compute the posterior probability that a site has at least one burrow with evidence of pygmy rabbits given expected count data: $p(\mathbf{Z}>0|\mathbf{n},\mathbf{Y})$. Maps of pygmy rabbit burrow occupancy (Fig. 2.2A) show that burrows with evidence of pygmy rabbits are expected to be found throughout the spatial domain. However, there are areas where the probability of pygmy rabbit burrow occupancy is expected to be reduced, indicating within site heterogeneity in pygmy rabbit distribution of a spatial domain that is known to be occupied. In particular, the agricultural fields on the east side of the domain are expected to have low probabilities of pygmy rabbit occupancy.

We also demonstrated how different assumptions about the number of burrows required to indicate animal presence affect the maps of pygmy rabbit distribution. If the number of burrows with fecal pellets required to indicate pygmy rabbit presence was changed from one to five, $p(\mathbf{Z}\geq 5|\mathbf{n},\mathbf{Y})$, then the total area expected to be used by pygmy rabbits was reduced (Fig. 2.2B). If this occupancy criterion was further increased to ten, $p(\mathbf{Z}\geq 10|\mathbf{n},\mathbf{Y})$, the total area expected to be occupied was again reduced, and the number of occupied polygons connected by $p>0.5$ was changed from one to two (Fig. 2.2C).

Maps of standard deviations were produced from the marginal predictive distributions for the intensity and utilization processes (Fig. 2.3). As expected, maps of burrow intensity show that prediction precision was best in regions of the map where data collection points were close together, and less precise in areas of the map with sparse data and in areas of extrapolation. Recall that burrow intensity (λ) was modeled with a log-linear model, where the mean and variance are expected to have a one-to-one relationship as an artifact of the Poisson distribution. This can be seen in the similarity of appearance of the prediction maps of standard deviation (Fig. 2.3) and mean (Fig. 2.1). The appearance of the mean (Fig. 2.1) and standard deviation (Fig. 2.3) prediction maps for the utilization parameter (θ) are also quite similar. This is because the maximum proportion of all burrows that are expected to have pygmy rabbit fecal pellets was just over 50%. The variance of the binomial distribution is maximum at $\theta = 0.50$ and falls as the probability of the event of interest occurring (or not) is more certain. Leave-one-out cross validation revealed that predictions for burrows and burrows with fecal pellets missed the observed values at some of the sites. However, the predictions followed the general pattern of the omitted observations (solid line in Fig. 2.4), suggesting that the model captured the overall behavior well.

DISCUSSION

We used our hierarchical model to successfully incorporate two sources of indirect data in a coupled likelihood and create posterior predictive distributions for the processes of interest over the spatial domain. This framework allowed us to present

maps of ecologically important variables such as relative abundance and occupancy. Our model is similar to previous hierarchical Bayesian species distribution models that incorporate spatial structure (e.g. Carroll & Johnson 2008; Hooten, Larsen & Wikle 2003; Howell, Peterson & Conroy 2008; Latimer *et al.* 2006), except that, these used presence-absence data and were limited to making inferences on distribution. The use of count data allows for the estimation of relative abundance represented over space while accounting for both observation bias and spatial structure (e.g. Gorresen *et al.* 2009; Thogmartin, Sauer & Knutson 2004). Our approach is similar to the above studies, except that we use counts of indirect detection indices and a geostatistical approach to estimate the spatial covariance structure. The use of geostatistics rather than Markov random field models allowed us to treat the landscape as a continuous gradient of habitat, rather than a series of classified habitat polygons, which may be conceptually more desirable (Manning, Lindenmayer & Nix 2004). The resulting posterior predictive distribution maps account for both process and observation uncertainty, and provide a framework for improving ecological inference while informing conservation and management decisions.

Our approach also draws on the strengths of multi-state occupancy models (e.g. MacKenzie *et al.* 2009; Nichols *et al.* 2007), but with two important distinctions. First, our model uses signs that persist in the environment, and we can not assume that burrows with fecal pellets are currently occupied. However, a burrow with fecal pellets does indicate use by our species of interest at some point in the recent past, and can safely be considered important for habitat modeling. Secondly, our model explicitly

accounts for spatial autocorrelation, where multi-state occupancy models as presented in MacKenzie *et al.* (2009) do not. This allowed us to use geostatistics to produce statistically rigorous prediction maps of our unobserved processes of interest. While MacKenzie *et al.* (2009) argue that careful study design and the use of model averaging precludes the need to account for spatial structure in occupancy models, our approach follows that of Hoeting (2009) who argues that even in well-designed studies of a spatial process, misspecification is likely if autocorrelation is ignored during model selection. Our model therefore provides a useful extension of multi-state occupancy models by formally accounting for spatial structure.

The relative abundance map presented in Fig. 2.1C takes advantage of the number of burrows estimated using the intensity parameter, and the number expected to have sign of pygmy rabbit activity as estimated by the utilization parameter. Although a similar, but ad hoc, metric would have been easily calculated by multiplying the burrow density obtained from program DISTANCE by the ratio of the number of burrows observed to have fecal pellets, our metric provides a statistically rigorous estimate of relative abundance over the entire spatial domain. The autecology of the species of interest could then be used to link relative abundance to actual abundance. For example, if the number of burrows used by a single pygmy rabbit were known, then we could use that information to produce maps of actual abundance.

Our methods produced probabilistic maps pygmy rabbit burrow distribution (Fig. 2.2A). This map is based on the assumption that a single burrow showing fecal pellets is occupied. This assumption may not be valid if pygmy rabbits use more than

one burrow (Sanchez & Rachlow 2008). We therefore demonstrate the flexibility of our approach by presenting two additional maps (Fig. 2.2B and C) of pygmy rabbit occupancy using different criteria for determining site occupancy. We do not know which of the maps are “correct” because the minimum number of burrows showing sign in a currently occupied pygmy rabbit home range is not known. However, we demonstrate how the autecology of the focal species could be used to inform the choice of an occupancy criterion used for determining presence in the distribution maps.

We were primarily interested in optimal spatial prediction, but examination of covariates gives some information about the habitat variables important to burrowing animals and pygmy rabbits within our study domain. Inferences about habitat variables made from our model are specific to our study domain, although comparison with previous studies may highlight useful general habitat requirements. Additionally, inferences about pygmy rabbit/habitat relationships are limited to the spatial covariates that were available for each grid location within the spatial domain. Therefore, direct resource selection of variables that may relate to fitness (food and cover) cannot be made at this level. We therefore use surrogates such as aspect, distance to water and spectral reflectance, which may not be directly linked to the biology of the organism in question. A benefit of our approach is that we are able to evaluate the factors influencing burrow intensity separately from those affecting use by pygmy rabbits. These factors are likely to be confounded in studies which model burrows and scat simultaneously.

In the case of our study, interpretation of the regression parameters reveals that both burrow intensity and utilization were negatively associated with near infrared reflectance and distance to water. This indicates that burrowing animals in general and pygmy rabbits specifically select habitat near perennial water sources, but do not occur in riparian habitat or in agricultural fields (types that absorb near infrared radiation). Burrow intensity was also positively associated with slope and aspects related to soil moisture. Given the presence of burrows, pygmy rabbits were positively associated with increased red reflectance, which is consistent with their reliance on sagebrush (sagebrush is the least red-band absorbent of all major plants present at the site). Further they were associated with potential snow and soil deposition (easterly aspects), possibly reflecting microsite preferences of pygmy rabbits that are separate from burrowing animals in general. Previous models using untransformed aspect values show inconsistent results, prompting Rachlow & Svancara (2006) to recommend that aspect not be used in large-scale predictive models of pygmy rabbits. This lack of consistency could indeed be related to differences between study areas, or could illustrate confusion resulting from the confounding of burrow intensity and utilization of traditional species distribution models.

Evaluation of model performance is a vital part of any modeling effort. The many methods available for the evaluation of spatial distribution model performance include a number of cross-validation techniques. However, model fit within the prediction surface is assumed to be homogenous for all traditional model-fit metrics. A benefit of the Bayesian approach is that inference is made based on the posterior

distribution, and the standard deviation of the posterior distribution can be used to assess spatial precision of modeled expectations. Evaluating the map of standard deviations can be used to construct optimal sampling designs for spatio-temporal monitoring (Hooten *et al.* 2009). For example, our processes of interest were modeled from the Poisson distribution where variance has a one-to-one relationship with the mean. An optimal design could be one where sites with expected higher abundance were sampled more intensively than those with lower expected abundance.

SYNTHESIS AND APPLICATION

The modeling framework we presented here is applicable to any species for which multiple levels of indirect detection are available. For example, models of cavity-nesting birds based on snag-density (e.g. Ohmann, McComb & Zumrawi 1994) or actual cavities (e.g. Lawler & Edwards Jr. 2002) can benefit from this approach. Our method is also scaleable to different spatial grains and extents through collection of additional data.

For species where indirect observations have natural hierarchical structure and where direct species detection is low, our method is attractive for surveying large spatial extents. This is because variance of occupancy model parameters increases as detection decreases (MacKenzie & Royle 2005). In order to combat this problem MacKenzie & Royle (2005) suggest adding additional visits to a site before increasing the number of sites sampled, thereby increasing the precision of occupancy estimates. If the goal of the study is to make spatial prediction of species occurrences, then there is a trade-off

between increasing detection, which increases precision, and increasing the number of sites, which improves prediction. Our method allows us to estimate both distribution and relative abundance efficiently while still accounting for imperfect detection, thereby bridging and extending two active areas of ecological research: species distribution models and occupancy modeling.

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Table 2.1. Spatial covariates used in burrow intensity and burrow utilization models.

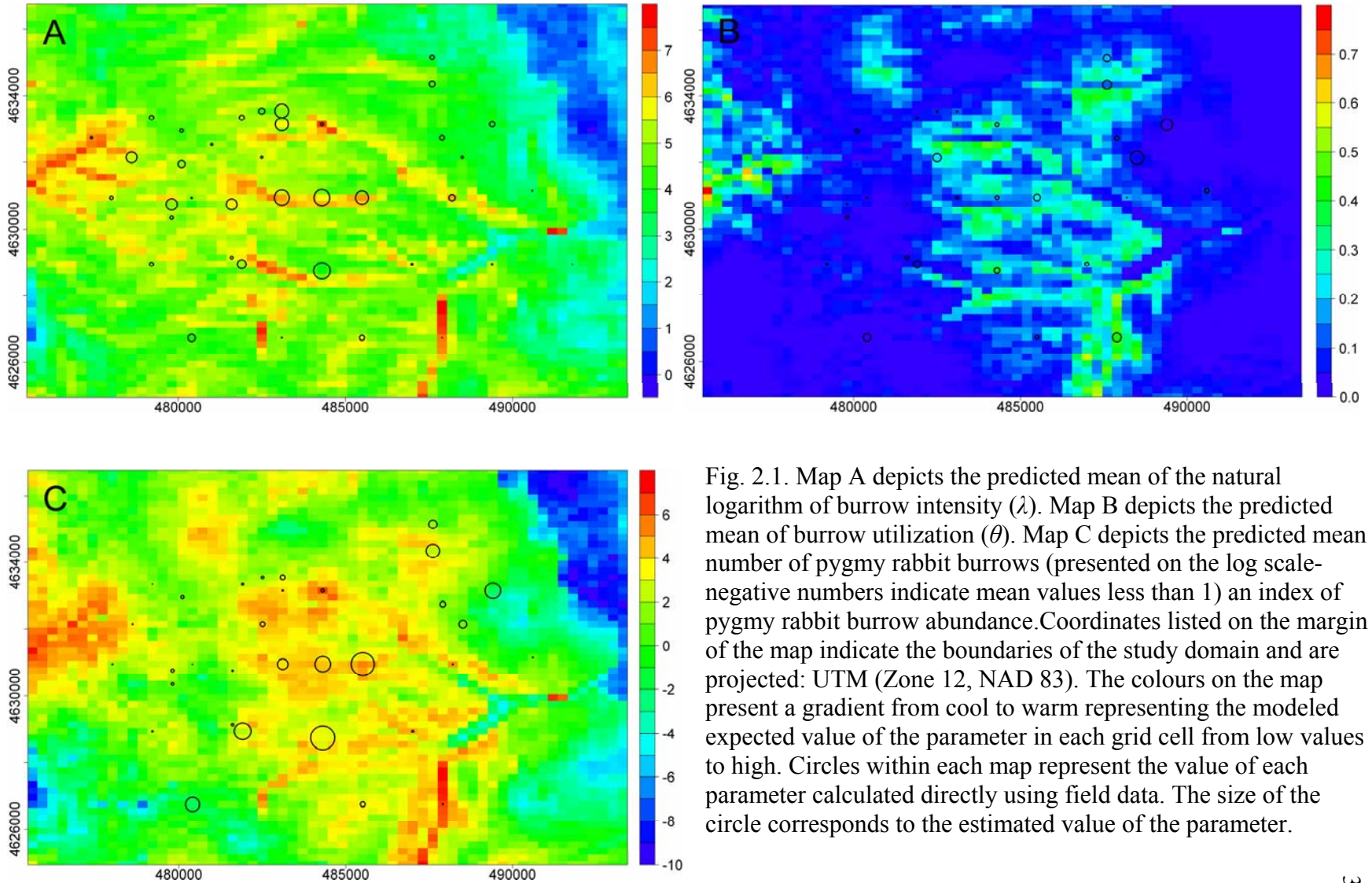
Variable	Description	Source
SLOPE	Per cent slope	NED
ASPVAL	Aspect transformed to create an index ranging from 0 to 1 where 0 is minimum soil moisture and 1 is maximum soil moisture	NED
ASPWEST	Aspect transformed to create an index ranging from 0 to 1 where 0 is maximum scouring and 1 is maximum deposition	NED
NIR	Near Infrared band reflectance	NAIP
RED	Red band reflectance	NAIP
WATER	Euclidian distance to nearest water source (stream or spring)	DLG
X	Easting in Universal Transverse Mercator, zone 12, NAD83	Prediction grid
Y	Northing in Universal Transverse Mercator, zone 12, NAD83	Prediction grid

Raster data were summarized for each 6ha grid cell and the mean value was used for modeling. Data sources include: National elevation dataset (NED; 10m raster), National Agriculture Imagery Program (NAIP; 2 m raster), and Digital Line Graph (vector DLG; ground-truthed with NAIP).

Table 2.2. Regression coefficients (β, α) for the burrow intensity [$\log(\lambda)$] and pygmy rabbit utilization [$\Phi^{-1}(\theta)$].

	Mean	Standard Deviation	Lower 95% Credible Interval	Upper 95% Credible Interval
Burrow intensity				
$\log(\lambda)$				
X	-1.52×10^{-04}	2.92×10^{-06}	-1.57×10^{-04}	-1.46×10^{-04}
Y	6.64×10^{-05}	4.52×10^{-06}	5.77×10^{-05}	7.54×10^{-05}
SLOPE	6.12×10^{-02}	2.20×10^{-03}	5.69×10^{-02}	6.56×10^{-02}
ASPVAL	6.02×10^{-01}	3.52×10^{-02}	4.33×10^{-01}	6.70×10^{-01}
NIR	-4.22×10^{-02}	1.23×10^{-03}	-4.46×10^{-02}	-3.97×10^{-02}
WATER	-6.89×10^{-04}	1.81×10^{-05}	-7.25×10^{-04}	-6.56×10^{-04}
Utilization				
$\Phi^{-1}(\theta)$				
X	-1.66×10^{-04}	5.17×10^{-05}	-2.67×10^{-04}	-6.66×10^{-05}
SLOPE	3.02×10^{-02}	2.54×10^{-02}	-1.93×10^{-02}	8.05×10^{-02}
ASPVAL	-7.14×10^{-01}	4.92×10^{-01}	-1.68×10^{-00}	2.38×10^{-01}
ASPWEST	1.74×10^{-00}	7.75×10^{-01}	2.16×10^{-01}	3.38×10^{-00}
NIR	-7.35×10^{-01}	2.85×10^{-02}	-1.30×10^{-01}	-1.95×10^{-02}
RED	6.39×10^{-02}	1.70×10^{-02}	3.13×10^{-02}	9.78×10^{-02}
WATER	-6.77×10^{-04}	1.80×10^{-04}	-1.03×10^{-03}	-3.27×10^{-04}

Regression coefficients where the 95% credible interval does not overlap 0 are highlighted with bold text.



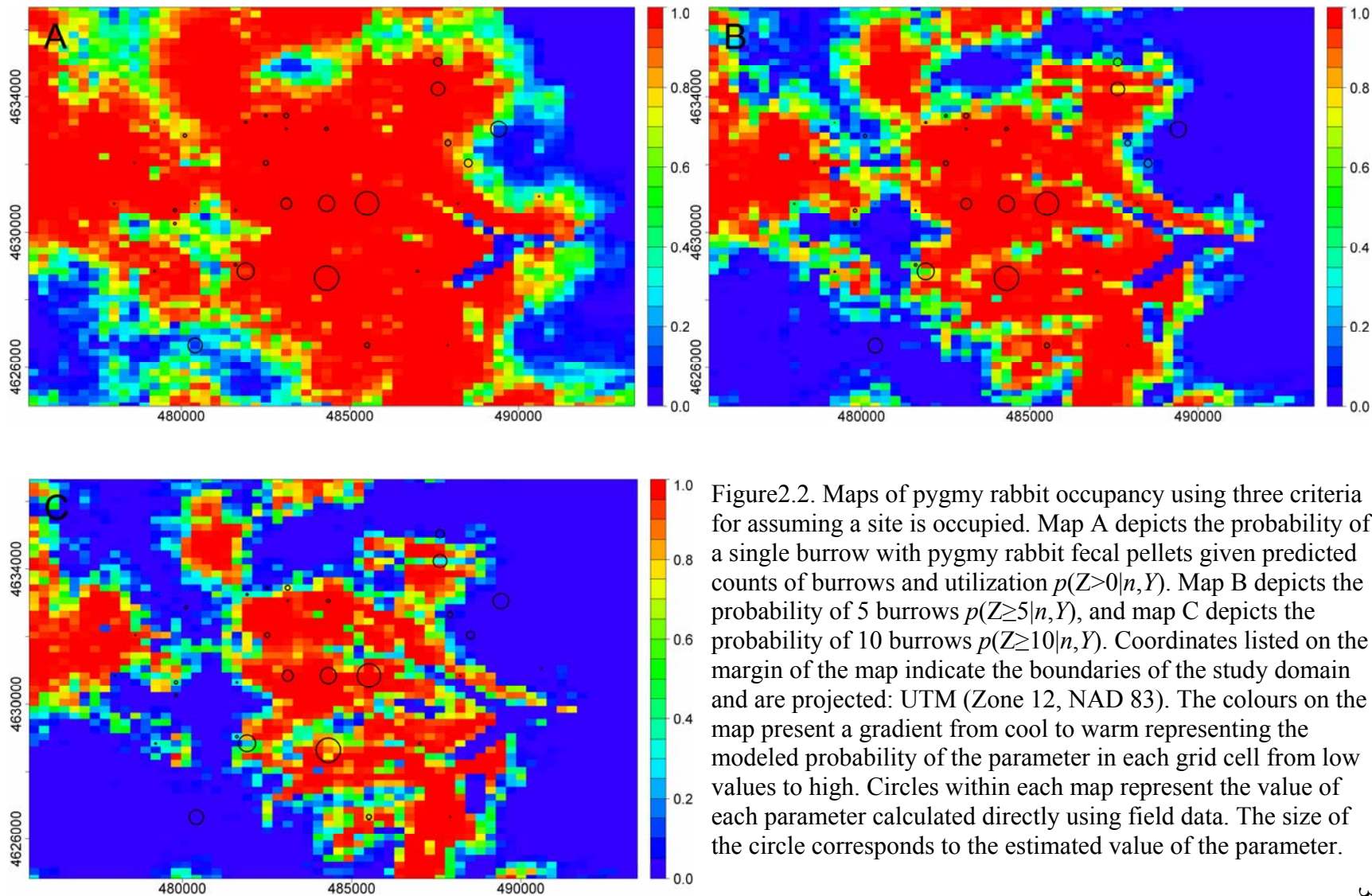


Figure 2.2. Maps of pygmy rabbit occupancy using three criteria for assuming a site is occupied. Map A depicts the probability of a single burrow with pygmy rabbit fecal pellets given predicted counts of burrows and utilization $p(Z > 0 | n, Y)$. Map B depicts the probability of 5 burrows $p(Z \geq 5 | n, Y)$, and map C depicts the probability of 10 burrows $p(Z \geq 10 | n, Y)$. Coordinates listed on the margin of the map indicate the boundaries of the study domain and are projected: UTM (Zone 12, NAD 83). The colours on the map present a gradient from cool to warm representing the modeled probability of the parameter in each grid cell from low values to high. Circles within each map represent the value of each parameter calculated directly using field data. The size of the circle corresponds to the estimated value of the parameter.

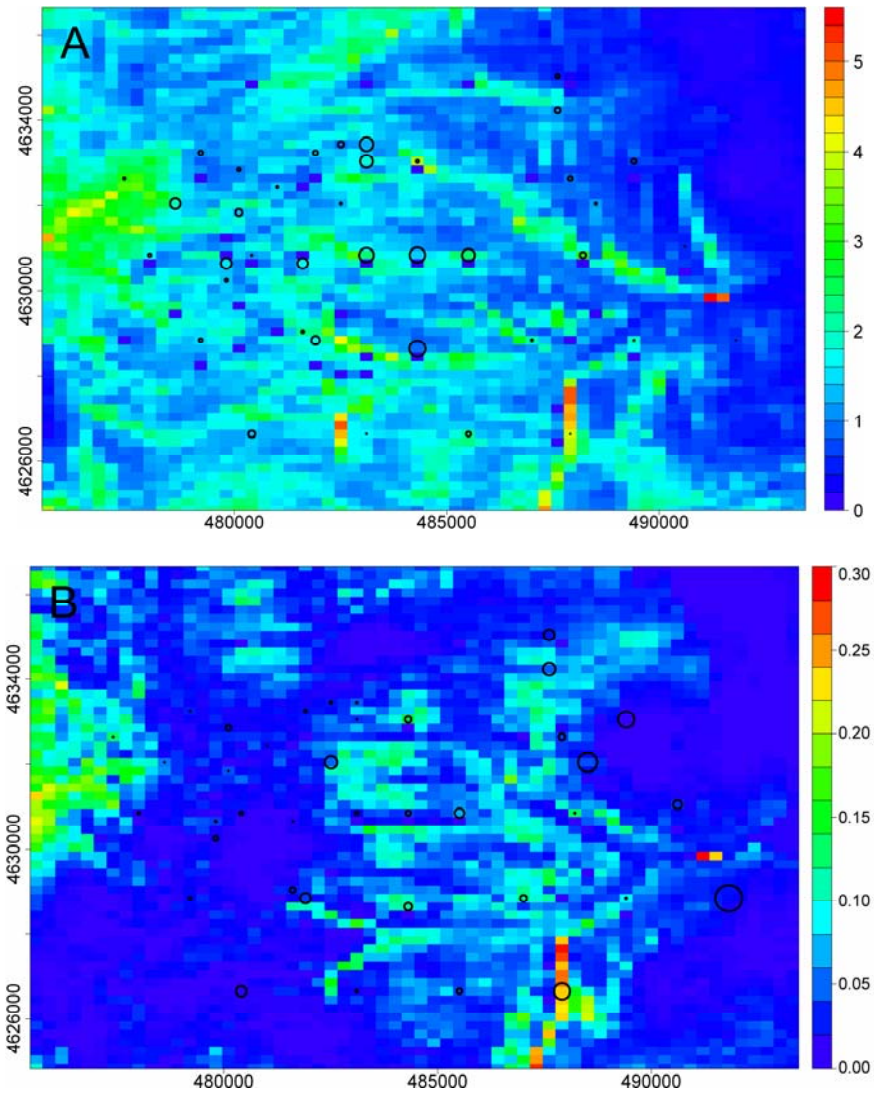


Fig.2.3. Standard deviation of predictive distributions for burrow intensity (A; presented on the log scale) and burrow utilization (B). The colours on the map present a gradient from cool to warm representing the modeled standard deviation of the parameter in each grid cell from low values to high. Circles within each map represent the value of each parameter calculated directly using field data. The size of the circle corresponds to the estimated standard deviation of the parameter.

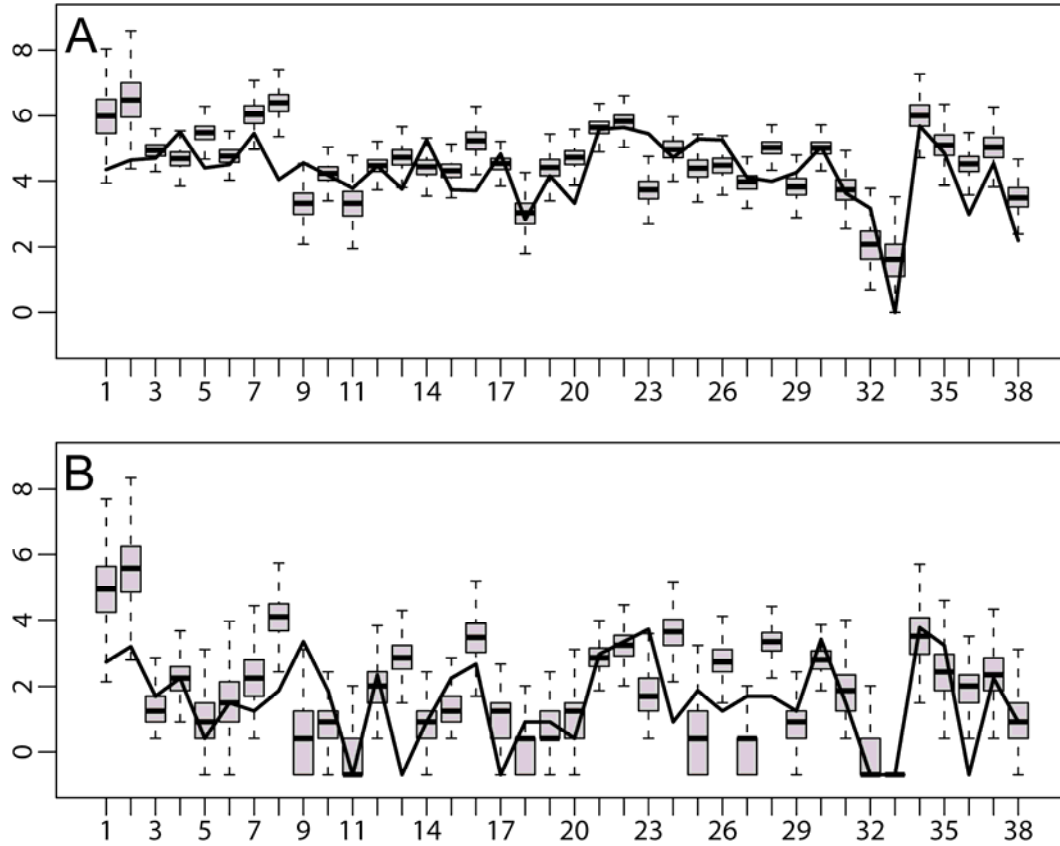


Fig.2.4. Leave-one-out cross validation results for the observed counts of burrows (A) and burrows with sign (B). The boxplots indicate the median, 1st and 3rd quartiles, and a rough estimate of the 95% credible intervals of the posterior predictive distribution. The solid line connects the actual observations.

CHAPTER 3

EFFECTS OF SAGEBRUSH RESTORATION TREATMENTS ON MULTI-SCALE
RESOURCE SELECTION BY PYGMY RABBITS³

ABSTRACT

The effects of widespread sagebrush removal treatments on pygmy rabbits (*Brachylagus idahoensis*) are not well understood. Due to reliance on sagebrush, pygmy rabbits are among the species for which these treatments may be detrimental. Our objectives were to evaluate the effects of experimental sagebrush treatment on eight radio-collared pygmy rabbits between and within home range habitat selection using Monte Carlo simulation from null models. Pygmy rabbits were not extirpated from plots containing habitat treatments. However, we found evidence of within home range selection against treatments from two of eight rabbits located very close to the treatments. We also used snow tracking to show that pygmy rabbits entered treatments less often than expected by chance. Conservatively, sagebrush removal treatments should not be conducted on active or recently active pygmy rabbit burrows. Elsewhere in the vicinity of known pygmy rabbit sites, the treated patches should be small and connected by untreated corridors to prevent potentially limiting movement of rabbits among the untreated habitat.

³ This chapter is co-authored by Tammy L. Wilson, Frank P. Howe and Thomas C. Edwards Jr.

INTRODUCTION

There is growing awareness of the need for habitat restoration in sagebrush rangelands due to both observed and assumed population declines of species that depend on sagebrush for some portion of their life-history (Knick and Rotenberry 1995, Dobkin and Sauder 2004). In addition to widespread habitat loss and fragmentation (Knick and Rotenberry 1995), sagebrush rangelands are perceived to be in a degraded condition throughout much of the western United States (Winward 1991). This degradation is typified by higher shrub cover and lower herbaceous vegetation cover than ideal for many species (Bunting et al. 2003). This has led to widespread implementation of management actions meant to either reduce shrub dominance (Winward 1991, Bunting et al. 2003), or to reduce fire fuels (Bunting et al. 2003, Davies et al. 2009b). To accomplish this, sagebrush reduction by fire, chemical, or mechanical means is a common management practice in sagebrush rangelands throughout the Intermountain West of the United States.

Current approaches towards sagebrush treatment reject the traditional, systematic type conversion over large areas in favor of smaller and more heterogeneous treatments meant to mimic natural disturbance regimes (Hemstrom et al. 2002, Davies et al. 2009a). We refer to these as modern treatments. The resulting mosaic of vegetation states in modern treatments is thought to lead to increases in cover of grasses and forbs, which in turn benefits big game (Van Dyke and Darragh 2007) and greater sage-grouse (*Centrocercus urophasianus*; Society for Range Management 2005, Dahlgren et al. 2006; but see Connelly et al. 2000, Schroeder et al. 2006). However,

reductions of sagebrush cover and volume caused by mowing treatments may take up to 20 years to recover (Davies et al. 2009a). This suggests that increases in sagebrush forage quality may be counteracted by decreases in winter browse quantity when some animals are most dependent on sagebrush for food and thermal cover (Connelly et al. 2000, Davies et al. 2009a). The effects of these manipulations on space use of many sagebrush-dependent species remains unclear.

For example, the pygmy rabbit (*Brachylagus idahoensis*; a species petitioned to be listed under the United States Endangered Species Act) uses sagebrush as a primary food source for much of the year (Green and Flinders 1980, Shipley 2006). Pygmy rabbit burrow density is highest in areas with the tallest and densest sagebrush stands available (Green and Flinders 1980, Katzner and Parker 1997) and movement is rarely recorded outside of dense cover (Lee 2008). Similarly to the pygmy rabbit, brush rabbits (*Sylvilagus bachmani*) and Lower Keys marsh rabbits (*Sylvilagus palustris hefneri*) have been shown to select habitat based on dense shrub cover (Chapman 1971, Forsy and Humphrey 1996). These rabbits are able to cross open habitat for dispersal (Forsy and Humphrey 1996) or homing (Chapman 1971), but do not venture too far from cover during regular movements. This suggests that habitat treatments designed to reduce shrub cover may be detrimental to pygmy rabbits.

Pygmy rabbit burrow use is not well understood, but researchers agree that their activities center on burrows or burrow complexes (e.g. Heady and Laundré 2005, Rachlow et al. 2005, Sanchez and Rachlow 2008). Rather than indicating limited movement ability, observations of relatively short movements near burrows, such as are

exhibited by pygmy rabbits (Wilde 1978, Katzner and Parker 1997, Heady and Laundré 2005), may reflect optimal behavior of a central-place forager (Pyke 1984, Rosenberg and McKelvey 1999). Indeed, placement of burrows in tall and dense cover combined with short foraging movements could maximize access to food and protection from predation concurrently (Bakker et al. 2005).

Resource selection (or avoidance) can be observed at several different levels which are hierarchical in nature (Johnson 1980, Chalfoun and Martin 2007). The broadest level of selection that could be affected by sagebrush treatments is termed second order selection (Johnson 1980), which describes the location of home ranges in space. Second-order selection is a population level response potentially reflecting differences in resource quality caused by, for example, application of management treatments to a landscape. A subordinate level of selection is termed third order selection (Johnson 1980), where individuals choose where to conduct activities within their home range. At this level, individuals could select or avoid the treatments when moving about their home range.

Our objective was to evaluate the effects of sagebrush restoration treatments on second and third order habitat selection of pygmy rabbits using radio collared animals and snow tracking on an experimentally altered landscape. The study was conducted on a landscape that was divided into 4 plots, with two plots receiving modern sagebrush restoration treatments and two left untreated. To measure between home range selection we compare the centers of pygmy rabbit home ranges within the treated plot with a complete spatial randomness (CSR) null model. We use resource selection statistics

(Manly et al. 2002) and bootstrapping of random samples to evaluate if the placement of the centers of activity for all rabbits differs from what one would expect from random placement. Similarly, a null model was used to test third order selection by comparing observed rabbit locations with the random locations expected of a central-place forager. We used snow tracking to gain a better understanding of how the treatments affected pygmy rabbit movement. We evaluated the fine-scale behavior of pygmy rabbits at treatment edges, with the null expectation that a rabbit encountering an edge will go into the treatment or turn to avoid the treatment with equal likelihood.

STUDY AREA

The study was conducted on the 9,200-ha Duck Creek allotment in Rich County, located in northern Utah, USA. The site ranged in elevation from 1800 m to 2300 m and consisted of rolling hills with small drainages, some with spring-fed perennial streams. The climate is characteristic of shrubsteppe vegetation types consisting of cold winters, warm summers, and most precipitation falling as winter snow (West and Young 2000). The average maximum temperature was 4.8°C in winter and 23.4°C in summer. Total precipitation was 20.6 cm in winter and 11.5 cm in summer (data from Utah Climate Center, Laketown Station). Land was mixed ownership (Bureau of Land Management and private) and managed as a single allotment with a four pasture grazing system. Pastures were between 1290 and 3110 ha size ($\bar{x} = 2300$, $SD = 750$, $n = 4$). Lawson pasture aerator (Lawson Manufacturing Inc., Kissimmee, FL) treatments were conducted in two of the four pastures within the allotment in 2004. The treatments reduced sagebrush height, cover and extent by crushing, and resulted in series of treated

patches within an untreated matrix (Fig. 3.1). The treated patches were between 5 and 56 ha size ($\bar{x} = 22$, $SD = 15$, $n = 12$). The resulting edge is a distinct boundary between tall, dense sagebrush steppe vegetation and a grassland with remnant small individual sagebrush plants.

The site consisted of sagebrush shrubsteppe vegetation dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), with basin big sagebrush (*A.t.* ssp. *tridentata*) and low sagebrush (*A. arbuscula*) present at much lower frequencies. Snowberry (*Symphoricarpos oreophilus*) was co-dominant with sagebrush on more mesic aspects. The under-story contained a diverse mix of small shrubs, grasses and forbs, both native and non-native. Cheat grass (*Bromus tectorum*) was present on south facing slopes and within the treatments, but mostly absent elsewhere (Wilson, unpublished data). The site contained avian and mammalian predators, including among others, the long-tailed weasel (*Mustela freneta*), badger (*Taxidea taxus*), and golden eagle (*Aquila chrysaetos*). Most of the recognized sagebrush-dependent species were present, including the greater sage-grouse, sage sparrow (*Amphispiza belli*), sagebrush vole (*Lemmiscus curtatus*), and sagebrush lizard (*Sceloporus graciosus*). In addition to pygmy rabbits, observed lagomorphs included mountain cotton-tail rabbits (*Sylvilagus nutallii*) and white-tailed jack rabbits (*Lepus townsendii*). Black-tailed jack rabbits (*Lepus californicus*) were not observed.

METHODS

We evaluated responses of pygmy rabbits to treated patches using snow tracking during winter of 2006 to 2007, and with radio telemetry from May 2008 until April

2009). In spring 2008, we captured 16 adult pygmy rabbits (11 Females and 5 males) at burrow sites in the Duck Creek allotment (Fig. 3.1); 8 of these rabbits (5 females and 3 males) were captured within 1.5 maximum summer home range radii (~400 m; Sanchez and Rachlow 2008, Estes-Zumpf and Rachlow 2009) of a treatment edge (treatment group), while 8 (6 females and 2 males) were captured in areas occurring more than 400 m from a treatment (control group, used for null model parameter estimation). All rabbits were fitted with 5-g radio transmitters (model PD-2DC[®], Holohil Systems Ltd., Carp, Ontario, Canada) using collars made from plastic zip ties and rubber tubing. We visually located collared rabbits every 7-10 days using homing techniques. We used long treatment edges to evaluate rabbit location relative to the treatment (in or out) before the rabbit was approached closely enough to potentially affect behavior. We were careful not to disturb the rabbit upon final approach. If we did not flush the rabbit, the location was recorded by adjusting the GPS position (~3-m accuracy) of the observer by the distance (estimated) and bearing (measured) of the rabbit, otherwise we recorded the location at the site where the rabbit was originally observed without adjustment. The Utah State University Institutional Animal Care and Use Committee approved all pygmy rabbit capture, handling, and monitoring techniques (Protocol #1258).

Between Home Range Selection

At the coarsest level of resolution, we evaluated placement of pygmy rabbit home ranges of the eight rabbits from the treatment group. This scale of resolution is comparable to second order selection (Johnson 1980) using design II (Manly et al.

2002). Adopting an approach similar to Larsen et al. (2010), we used a null model to test for selection or avoidance of sagebrush removal treatments. We defined the home range centers as the median value of all locations (Range = 17-27 locations per rabbit) collected via homing telemetry during the season of interest for each of the eight rabbits within the treatment group. We used summer home ranges (15 May – 15 October) for females and non-breeding seasonal home ranges (15 July – 15 Feb) for males. Home range centers rather than isopleth polygons were used for comparison to the null model for four reasons: (1) polygon distances are typically measured from the centroid; (2) unless it is affected by influential outliers, the centroid of a core isopleth (50%, say) of a central place forager should theoretically occur at the area of the highest point intensity (as measured by the kernel), which should also be the central place; (3) the center of the area of highest point intensity, and thus the central place, is also well defined by the median X and Y coordinates of all measured locations; and (4) modeling the centers of null circular polygons is more parsimonious than modeling the polygons themselves. Indeed, it has been noted that certain estimators of the smoothing parameter necessary for calculating kernel home ranges perform poorly with small numbers of locations (e.g. <50; Horne and Garton 2006). We avoid this problem by modeling home range based on the median X and Y coordinates, which are not sensitive to outliers.

We assumed that pygmy rabbits not engaging in habitat selection would have home-range centers that were arranged in spatially random point process. We used Monte Carlo simulations to generate repeated experiments, drawing random home range centers from a complete spatial randomness (CSR) point process. To do this, we

first generated X random home-range centers ($X = 5000$) within a 400 m edge buffer (~1.5 home range diameters; Sanchez and Rachlow 2008, Estes-Zumpf and Rachlow 2009) of all treatment edges. We then drew eight random home range centers (from the original 5000) to generate a single iteration of the null model. Eight points were repeatedly drawn to create 999 samples of the null home range centers.

We digitized sagebrush treatments using 2006 National Agriculture Imagery Program (NAIP) high resolution imagery, and treatment edge buffers (400 m) were created in ArcGIS (ESRI, Redlands, CA). We found the nearest perpendicular distance of all simulated points from the treatment edge for each point (d). We then applied a nearest-treatment distance metric for each point by multiplying the perpendicular distance from edge by an indicator function: $d \times I(x)$, where x is 1 if the point is outside of a treatment, and -1 if inside.

We used a log likelihood ratio analysis to test the null hypothesis of no habitat selection (Manly et al. 2002), where the expected proportions of home range centers occurring in either of two habitat types (in the treatments or outside of them) was defined by the number of random points falling into either class. We also evaluated the distance by which pygmy rabbits avoided treated edges (or not) when placing home ranges by comparing mean nearest-treatment distances with the means of each of the bootstrap trials. We used 95% simulation envelopes to test deviations of the mean nearest-treatment distance expected from repeated draws from the the null model.

Within Home Range Selection

To evaluate within home range habitat selection (third order) we compared weekly telemetry locations (Range = 17-27 locations per rabbit) of each rabbit in the treatment group (8 rabbits) to simulated locations sampled to repeated draws of null locations from a null model. For this level of the analysis, the null model was based on the expected behavior of a central-place forager that is not engaging in habitat selection. We used a distance-based null model that assumed that the probability of finding a central-place foraging animal at any given distance (d) becomes smaller as distance from the central place increases (Rosenberg and McKelvey 1999). Similar to Rosenberg and McKelvey, we chose a null model based on the exponential distribution, but our model differs because we did not apply a maximum distance. There is evidence that some pygmy rabbits may use multiple burrow systems even within a single season (Sanchez and Rachlow 2008), and so a single locus exponential model may not be appropriate in some cases. However, the cause and frequency of burrow switching by pygmy rabbits is currently not understood well enough to parameterize a multi-locus model. Thus, we decided that the more parsimonious, single-locus exponential null model was more appropriate in our case.

The exponential distribution has a rate parameter (λ) describing the decrease in probability of occurrence with distance (d). The maximum likelihood of the rate parameter is defined as follows $\hat{\lambda} = 1/\bar{d}$. The estimated variance for $\hat{\lambda}$ from eight control rabbits in the Duck Creek allotment ($\bar{x} = 0.022$, $SD = 0.010$) was too large to be useful as a baseline for the Monte Carlo simulations because they generated

impossible $\hat{\lambda}$ values (included zero). To solve this problem we modeled $\hat{\lambda}$ by assuming that the maximum diameter of known pygmy rabbit home ranges approximates the 95% quantile of observed locations, and use the quantile formula of the exponential distribution to approximate $\hat{\lambda}$ as $-\hat{\lambda} = \ln(0.05)/d^*$ (see Appendix C for the derivation of this equation), where d^* is treated as a random variable defined using maximum diameter of 95% isopleths of 31 adult female pygmy rabbit minimum convex polygon home ranges from Idaho (Sanchez and Rachlow 2008, as reported by Estes-Zumpf and Rachlow 2009), such that $d^* \sim \text{Norm}(\mu = 276.3/2\text{m}, \sigma = 37.5/2)$. The mean modeled estimate of $\hat{\lambda}$ ($\bar{x} = 0.022$, $\text{SD} = 0.003$) was similar to the mean $\hat{\lambda}$ of eight observed rabbits ($\bar{x} = 0.022$, $\text{SD} = 0.010$).

For purposes of the null model and similar to above, we defined the central place as the median of all measured telemetry locations for each rabbit in the treatment group (8 rabbits). We used program R to generate x null locations ($x \sim 10000$) around the central places of each pygmy rabbit ($n = 8$; Fig. 3.2). For each simulation set, we drew l random null locations ($l = \text{total number of locations for each rabbit}$; Range = 17-27). Simulations of the null model were completed 500 times. Using the same method as for the home range centers, we calculated location to treatment edge distance for each of the random points and observed rabbit locations. We found the mean location to treatment edge distance for each of the 500 simulation sets to generate the expected distribution of means from repeated null experiments. We calculated 95% simulation envelopes from the 500 simulation means. Treatments were avoided, and the null

hypothesis of no effect was rejected, if the mean nearest-treatment distance of the observed locations was greater than the upper simulation envelope value.

Responses to Treatment Edge

We used tracks left in fresh snow to evaluate daily pygmy rabbit behavior at or near a treatment edge. We observed tracks by skiing the perimeter of accessible treatments the first morning after fresh snow during the winters of 2006 and 2007. The treatment edges were visible after most snow events because pre-treatment brush height was typically more than 60 cm. We considered tracks to be from the same individual if the distance between tracks encountered along the edge was less than 50 m, otherwise they were considered independent. We recorded whether or not the rabbit ever crossed the treatment edge, and used log likelihood ratio analysis to evaluate relative frequencies of the two behaviors.

RESULTS

There was no evidence of second order selection (treatment avoidance) by pygmy rabbits in our study area. The home range centers of radio collared pygmy rabbits ($n = 8$) occurred in the landscape as expected compared to a CSR null model ($X = 5000$). Although only one of seven home range midpoints was located in a treatment polygon, the selection ratios for home range mid-points falling in treated or untreated areas were not significantly different from that expected by the CSR point process ($G^2 = 0.429$, $P = 0.512$). There was also no evidence that pygmy rabbits avoided treatment edges when placing home ranges. The mean nearest-treatment distance (112m, $n=8$) for

the sampled home ranges did not fall outside of the simulation envelopes of expected distances based on 999 random draws of 8 locations from 5000 CSR points (Fig. 3.3).

Two rabbits (of 8 for which the center of activity was less than an expected home range diameter from a treatment) showed evidence of third order habitat selection compared to expectations generated from an exponential null model (Fig. 3.4). Two rabbits (F3 and M1) displayed treatment avoidance because the mean nearest-treatment distance of all of weekly locations was larger than the upper simulation envelope expected from 500 simulations of the exponential model in both cases (Fig. 3.4). Both rabbits had expected movements that were closer to the treatments than any of the other 4 rabbits evaluated. If these 2 rabbits were behaving as expected by the exponential model, then they would have been expected to have locations within the treatments as indicated by the histograms overlapping zero (Fig. 3.4); however, they were not observed within the treatments (minimum distance from edge = 5 m for F3 and 11 m for M1). The remaining four rabbits (F1, F2, and F4 and M2) were only rarely expected to use the treatments as indicated by the histograms not overlapping zero (Fig. 3.4), and their movements matched expectations of the null model. The only rabbit (F4) that was ever observed in the treatments (minimum distance from edge = -13 m) did not show statistically significant treatment avoidance or selection because the mean nearest-treatment distance of all locations fell within the simulation envelopes of the null model.

Rabbits generally avoided entering the treatments by more than 1m during winter tracking surveys. Of 21 total observations, the rabbits only entered the treatments

4 times. This was less than expected if entering the treatment were treated as independent Bernoulli trials ($G^2 = 8.662$, $P = 0.003$).

DISCUSSION

Due to their reliance on sagebrush for food and cover (Green and Flinders 1980, Shipley et al. 2006), it is generally assumed that any sagebrush restoration treatments that remove sagebrush cover are detrimental to pygmy rabbits. Treatments can affect pygmy rabbits through population-level placement of home ranges or movement of individuals within them (second and third order habitat selection, respectively; Johnson 1980). We evaluated pygmy rabbit responses to sagebrush treatments designed specifically to create a mosaic of treated patches in an untreated matrix within an experimentally manipulated landscape. Within this landscape, we conducted a multi-scale habitat selection study that evaluated both home range placement and within home range movements.

Home range placement as measured by the center of activity of radio-collared pygmy rabbits did not differ from a random point process. This was evident in both the number of points expected to fall within or outside of treatments and by measured distance to the treatment edge. This means that pygmy rabbits are not extirpated from plots with treated sagebrush. The lack of an observed treatment effect at this level means that if treatment avoidance were to occur, it would be seen in a subordinate level of resource selection.

Pygmy rabbits are believed to be reluctant to use open habitats and thus sensitive to habitat and population fragmentation (Weiss and Verts 1984). However,

pygmy rabbits have been observed to cross large expanses of open habitat during dispersal (Katzner and Parker 1998), suggesting that coarse scale movements may not be affected by treatments. In contrast, a test of fine scale treatment effects found that use of open areas as evidenced by fecal pellets was less than that in untreated habitats (Lee 2008). We evaluated within home range habitat selection for 8 rabbits living near treatment patches. Six of 8 rabbits showed no evidence of third order habitat selection. However, these rabbits lived far enough away from treatments that they were rarely expected to use them; as a result, their use matched null model expectations. Evidence of third order habitat selection was found for the 2 rabbits of 8 tested with centers of activity that fell closest to the habitat treatments. These rabbits were expected to have locations within the treatments, but were never actually observed there. Our results show that on a weekly basis pygmy rabbits occurring very near the treatment avoid using the treatment as expected by the null model. Both second and third order observations indicate that pygmy rabbits are not responding to the presence of nearby treatments, but are responding to the treatments by limiting their movements at the treatment edge. This is further corroborated by snow tracking surveys where tracks indicated that rabbits recognized and reacted to the treatment edges.

During snow tracking, we found that pygmy rabbits do occasionally cross more than 1m into treatments, but the rate is less than expected (also see Lee 2008). This does not contradict observations of Katzner and Parker (1998), but serves to explain the effects of treatments on the daily movement of pygmy rabbits rather than on permanent dispersal movements. We show that pygmy rabbits altered their behavior at the

treatment edge, suggesting that they are perhaps reacting to the abrupt reduction in cover caused by the treatments.

European rabbits alter use of open areas based on predation risk (Palomares and Delibes 1997). Therefore, it is possible that pygmy rabbits may be reluctant to enter treatments because reduced shrub cover exposes them to unacceptable risk of predation, especially from avian predators (Gahr 1993). Tests of treatment effects on eastern cottontail rabbits (*Silvilagus floridanus*), desert cottontail (*Silvilagus audubonii*) and black-tailed jack rabbits (*Lepus californicus*), however, show higher than expected use in treatments (Howard et al. 1987, Lochmiller et al. 1991). These studies are not necessarily contrary to our results, because the treatments in them were done in forested systems, where dense tree canopy may reduce understory cover needed by rabbit. If trees limit shrub and herbaceous cover, then one would expect that removing trees would have a positive effect on rabbit space use if cover near the ground is increased as a result. Furthermore, Howard et al. (1987) noted that lagomorphs used cover provided by upturned trees in the pinyon-juniper chaining.

The exponential model is appropriate to evaluate third order habitat selection for pygmy rabbits to the extent that they use a single burrow system as a central place. There is evidence that pygmy rabbits may use many different burrow systems even within a single season (Sanchez and Rachlow 2008), and so a single locus exponential model may not be appropriate in some cases. The cause and frequency of burrow switching by pygmy rabbits is currently unknown, but it is reasonable to hypothesize that burrow switching may be affected by resource selection. Thus, we decided that the

exponential null model was the most appropriate and parsimonious model that would enable us to evaluate the expected behavior of our rabbits in the absence of any resource selection behavior.

The exponential null model provides an excellent alternative to the kernel density estimated home range (KDE) for evaluation of third order habitat selection for two reasons. First, the KDE optimally fits observed animal locations, which are actual realizations of the habitat selection process; therefore, using the KDE to infer availability in habitat selection algorithms confounds second and third order selection making habitat inferences suspect (White and Garrott 1990; Mitchell and Powell 2008). Second, the KDE prevents the generation of random points coming from any distribution other than CSR within a fixed contour interval (say 95%), which essentially assumes equal availability of all habitat types within a given contour interval of all points. This assumption may be violated for central-place foragers who are more likely to use habitat close to their central place (Rosenberg and McKelvey 1999).

MANAGEMENT IMPLICATIONS

Our study indicates that modern sagebrush restoration treatments designed to create mosaics of treated patches in an untreated matrix may not be as detrimental for pygmy rabbits as traditional, systematic sagebrush removal over large areas. However, our results suggest that treatment patches are used less frequently than adjacent untreated sagebrush, and may limit the ability of pygmy rabbits to move about the landscape freely. Additionally, losses of sagebrush forage and cover may take decades to recover (Davies et al. 2009a). We therefore do not refute conservative

recommendations of Roberts (2003) and Lee (2008) that sagebrush removal treatments of any type should be avoided in areas with current pygmy rabbit activity. We find no evidence, however, that treatments affected the general placement of pygmy rabbit home ranges within treated plots; therefore, further limiting the placement of treatments by creating large no-treatment buffers around active rabbit burrows may be unnecessary. We suggest that when the treatment of occupied pygmy rabbit habitat cannot be avoided, the treated patches should be small, narrow and widely spaced relative to the maximum pygmy rabbit home range (~13 ha, Sanchez and Rachlow 2008). We further recommend that in lieu of islands (*sensu* Longland and Bateman 2002), treatments mosaics should include strips of undisturbed habitat which would connect untreated areas and act as corridors for daily pygmy rabbit movement.

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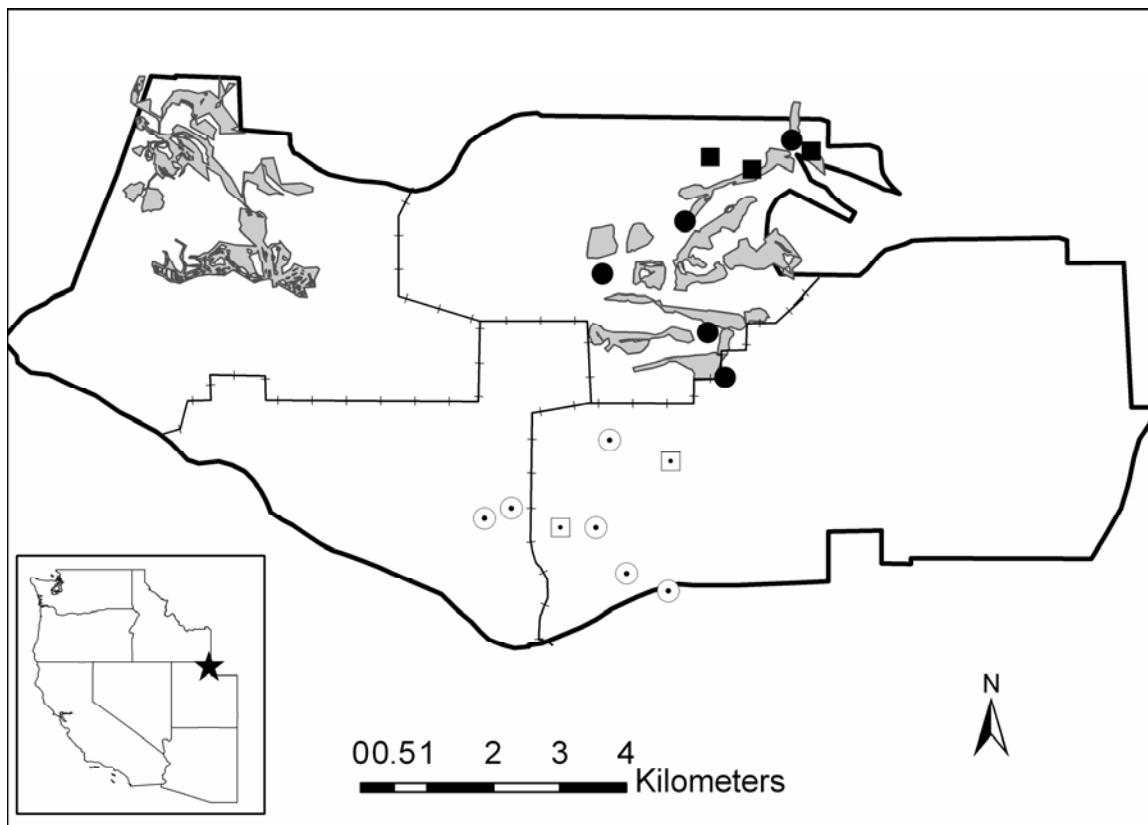


Fig. 3.1. The Duck Creek Allotment in northern Utah, USA

The study area is divided into 4 plots marked by the cross-hatched lines. The shaded areas indicate sagebrush removal treatments. Median locations of 16 pygmy rabbits are shown by symbols. The treatment group (8 rabbits) is marked by solid symbols and the control group (8 rabbits) is marked by open symbols. Females (11 rabbits) are marked by circles and males (5 rabbits) are marked by squares. The black star in the inset shows the study area location in the western United States.

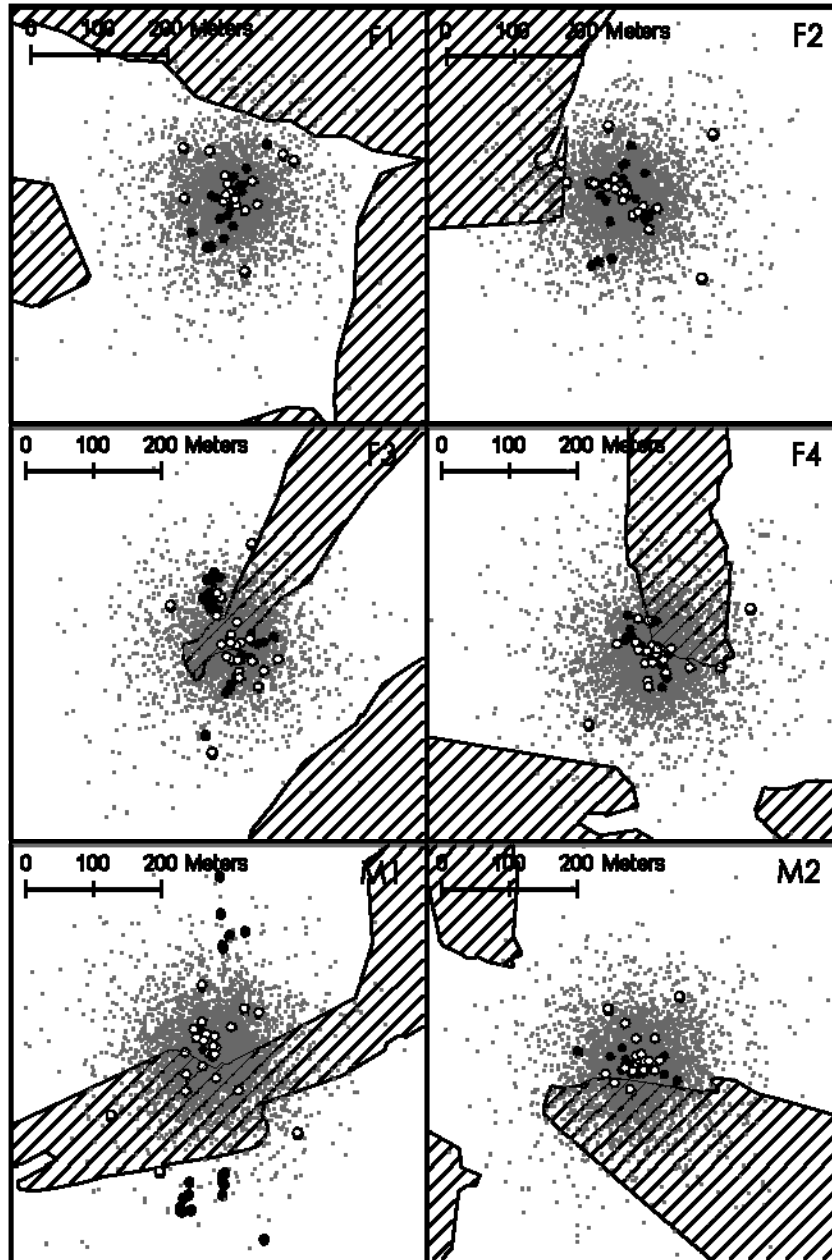


Fig. 3.2. Maps of the exponential model simulations for six of eight pygmy rabbits in northern Utah, USA.

The observed rabbit locations are represented by black circles. The simulated points are represented by open circles (single simulation set) and gray tick marks (all simulated points). The treatments are represented by the hatched polygons. Two rabbits (F3 and M1) show observed departures from model expectations. Given the placement of their home ranges they were expected to use the treated polygons extensively, but were not observed there.

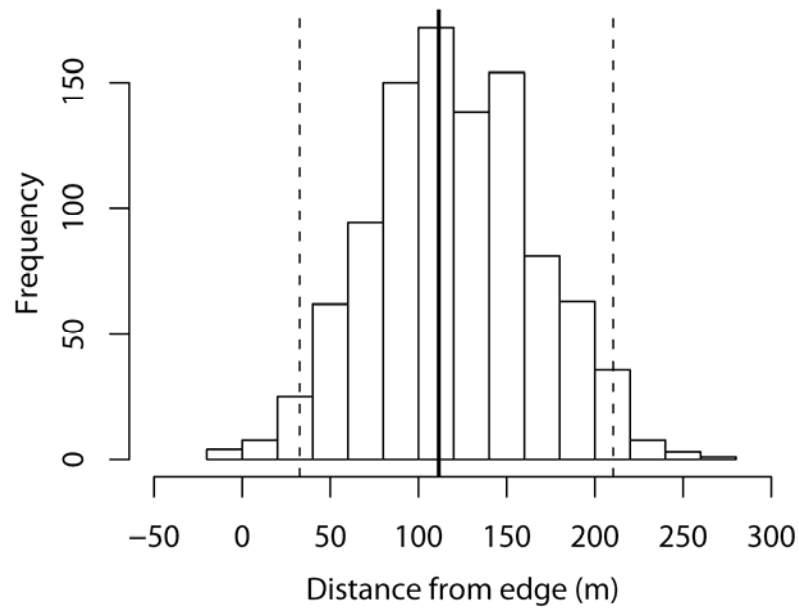


Fig. 3.3. The histogram presents results of between home range (2nd order) habitat selection null model simulation trials for pygmy rabbits in northern Utah, USA. The histogram represents 999 simulated mean nearest-treatment distances (n=8 random points/simulation). Nearest treatment distance is a metric describing the nearest perpendicular distance from a treatment edge of any home range center multiplied by $I(x)$, where $x = 1$ if the point is outside of the treatment, and -1 if inside. The solid line represents the measured mean nearest-treatment distance of eight radio-collared pygmy rabbits with home range centers within a 400m edge-buffer of all treatments. The dashed lines represent 95% simulation envelopes of the null model. Statistically significant treatment avoidance would be shown by a measured mean value (solid line) to the right of the upper simulation envelope (dashed line).

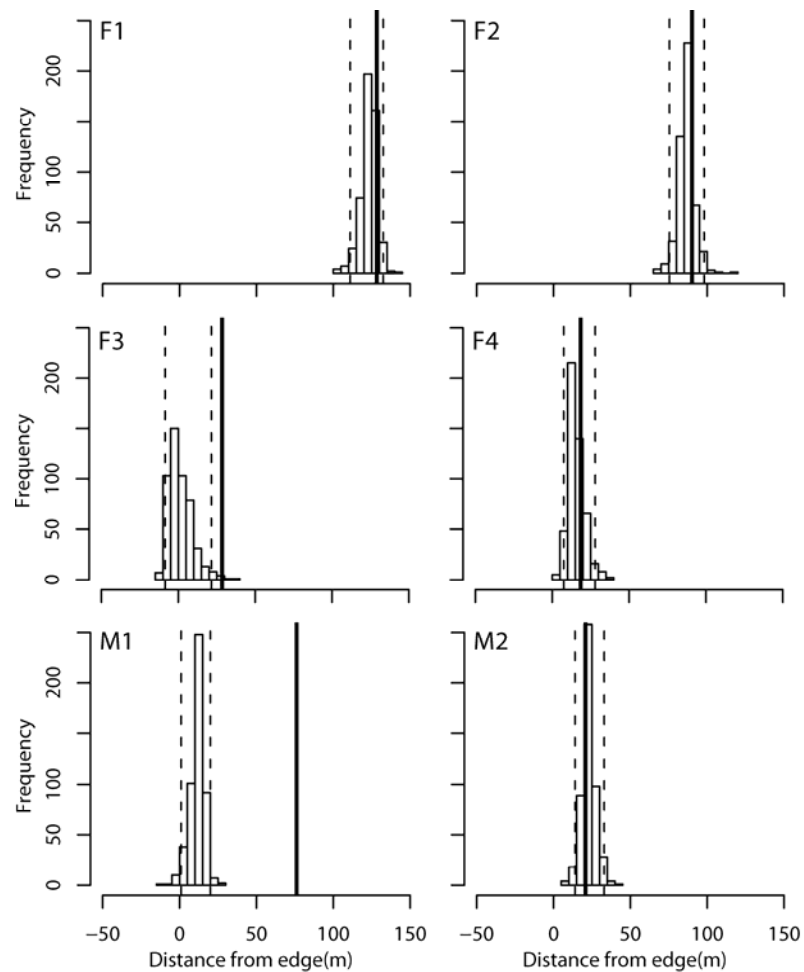


Fig. 3.4. The histograms present results from within home range habitat selection (3rd order) null model simulation trials for pygmy rabbits in northern Utah, USA. The histograms represent 500 mean rabbit to treatment edge distances ($n=17-27$ random points/simulation) for each of 6 rabbits with home ranges closer than 1 average home range diameter from the treatments. Rabbit to treatment distance is a metric describing the nearest perpendicular distance from a treatment edge of any rabbit location multiplied by $I(x)$, where $x = 1$ if the point is outside of the treatment, and -1 if inside. The solid lines represents the measured mean rabbit to treatment edge distance of all locations for a single pygmy rabbit. The dashed lines represent the 95% simulation envelopes of the exponential models for each rabbit. Statistically significant treatment avoidance is shown by a measured mean value (solid line) to the right of the upper simulation envelope (dashed line) for each rabbit.

CHAPTER 4

SPATIAL ECOLOGY OF BURROW USE BY PYGMY RABBITS⁴

ABSTRACT

Conservation of species is improved by multi-scale understanding of resource selection processes. In particular, fine-scale distribution of resources may be a large driver for habitat selection of individuals. For pygmy rabbits (*Brachylagus idahoensis*) some habitat requirements, such as a strong association with sagebrush (*Artemisia* sp.) and the need for burrows are well established. However, little is known about how the distribution of resources affects individual space use. We used a census of burrows within the home ranges of radio-collared pygmy rabbits to evaluate within-home range burrow use. We show that burrows are clustered, and that use of burrows is non-random within burrow clusters. As expected, we found a positive correlation between the rabbit utilization distribution and burrow intensity. Burrow intensity, above ground plant cover, and topography were all useful in predicting whether or not pygmy rabbit burrows showed evidence of use by pygmy rabbits. We discuss how explicit accounting of the spatial arrangement of burrows may improve conservation strategies for pygmy rabbits.

INTRODUCTION

Resource selection is viewed as a multi-scale process (Johnson 1980, Manly et al. 2002). However, within home range distribution of resources is not often explicitly

⁴ This chapter is co-authored by Tammy L. Wilson and Thomas C. Edwards Jr.

accounted for in resource selection studies, which often use maps of vegetation classes as surrogates for resource patches (e.g. Rettie and Messier 2000, Beasley et al. 2009). These maps assume that resources are uniformly distributed within a vegetation class (Manning et al. 2004), so evaluating animal behavior in relation to the spatial distribution of actual resources, not surrogates, is necessary for complete understanding of resource selection (Fernandez et al. 2003, Buskirk and Millspaugh 2006, Millspaugh et al. 2006).

Burrowing animals are common in arid environments where other forms of shelter are rare (Kinlaw 1999). The burrow is thought to provide many benefits for an animal occupant, including protection from predation, thermal regulation, protection from dehydration, protection from fire, and food storage (Kinlaw 1999). Studies of burrowing rodents have shown that burrows are costly to excavate (Vleck 1979), and clustering is expected due to the physical limitations of moving through soil (Whitford and Day 1999). For example, pocket gopher (*Geomys*) mounds are known to be generally clustered and more so in areas with high forage availability (Reichman and Seabloom 2002). Additionally, The European rabbit (*Oryctolagus cuniculus*) is known to use highly clustered burrow systems called warrens. Warrens are used to whelp young and may be shared by many breeding groups depending on the degree of clustering and site limitation experienced by the population (Cowan 1987). Soil disturbances caused by burrowing are long lasting, if not permanent (Whitford and Day 1999), and once the initial burrow system has been established it will continue to be used by many types of burrowing organisms, some of which are themselves incapable

of digging. Therefore, it is possible that historical burrow sites affect current use by burrowing organisms.

Pygmy rabbits (*Brachylagus idahoensis*) are a burrow-dependent species with recent conservation interest in the United States. This interest arises in part due to the Federal listing of a distinct population segment (Columbia Basin pygmy rabbit) as endangered in Washington (Federal Register 2003), and a recent ruling to consider the pygmy rabbit for listing in the remainder of the range (Federal Register 2008). Pygmy rabbits are known to be capable of digging their own burrows (Green and Flinders 1980a), and burrows are a central part of pygmy rabbit habitat (Green and Flinders 1980b, Heady and Laundré 2005). Many researchers have studied habitat selection based on burrows (e.g. Gabler et al. 2001, Horne and Garton 2006, Himes and Drohan 2007), but none of these have adequately addressed within home range habitat selection in a manner that accounts for the spatial arrangement of burrows. Pygmy rabbits are known to construct shallow, single-chamber natal burrows for whelping young some distance away from the more complex, so-called residential burrow systems used daily by adult rabbits (Rachlow et al. 2005). It is not known, however, what function “residential” burrow systems serve for pygmy rabbits. Therefore, despite the perceived importance and active monitoring of these easily observable features, burrow use by pygmy rabbits remains poorly understood.

In this paper, we focus on three basic questions about distribution of the burrows on the landscape and pygmy rabbit responses to them: 1) are burrows and pygmy rabbit use in relation to burrows spatially clustered; 2) if so, are home ranges oriented in

relation to the spatial arrangement of burrows (burrow intensity); and 3) what habitat characteristics determine burrow selection (used versus unused)? We used burrow censuses conducted within pygmy rabbit home ranges to address these questions. We expected that pygmy rabbits would use many burrows and that burrows would be clustered. We expected that the utilization distribution (estimated spatial intensity of rabbit locations) would be positively correlated with burrow intensity (a continuous measure of burrow distribution). We hypothesized that pygmy rabbits would behave like central place foragers with activity centered on burrows, and therefore expected the correlation of probability of use and burrow intensity to be stronger in the interior portion of the utilization distribution than the exterior. Finally, we expected that burrow neighborhood characteristics would contribute to the probability burrows had pygmy rabbit pellets, but that habitat features related to food and protection from predation would also influence rabbit use of burrows.

We interpret these results in the context of conservation strategies being considered for the rabbit. For example, understanding the spatial ecology of burrows may improve heretofore unsuccessful reintroduction efforts (Zeoli et al. 2008), by providing guidance on choosing adequate reintroduction sites. This information may also improve the ability of managers to monitor pygmy rabbits based on burrow observations.

METHODS

Study Area

The study was conducted on the Duck Creek allotment in Rich County, located in northern Utah, USA. The site was dominated by sagebrush shrubsteppe vegetation, and known to be occupied by pygmy rabbits. Broad-scale pygmy rabbit burrow studies that were recently conducted on the site (Wilson et al. 2010b) found areas of high burrow intensity throughout the study domain. Pygmy rabbit occurrence given the presence of burrows was predicted to be concentrated in the central portion of the study domain. While some mounding was observed near pygmy rabbit burrows, Duck Creek lacked the “mima mound” micro-topography characteristic of well-studied pygmy rabbit sites in Idaho (Tullis 1995). Additionally, sagebrush cover in our study area was relatively continuous with variation caused by treatments meant to reduce sagebrush cover, and by broad scale topographic effects.

The site harbored Uinta ground squirrels (*Spermophilus armatus*) and American badger (*Taxidea taxus*), which are also primary burrowers. In addition, pocket gophers (*Thomomys talpoides*) created extensive burrow systems in the study area, but their burrows were not often open to the surface and were generally too small for pygmy rabbits. Mammalian meso-predators of the area such as the long-tailed weasel (*Mustela freneta*) and badger were present, and known to pursue prey in burrow systems. Defenses against these predators included use of burrows with multiple entrances and chambers. Burrows were also an effective refuge from commonly observed avian predators, such as golden eagle (*Aquila chrysaetos*), and larger mammalian predators,

such as coyote (*Canis latrans*). Sympatric lagomorphs included mountain cotton-tail rabbits (*Sylvilagus nutallii*) and white-tailed jack rabbits (*Lepus townsendii*).

Field techniques

We sampled burrows within the use areas of four adult female pygmy rabbits using a model-based nested design. The rabbits chosen for sampling were located more than 1 home range radius (~140m; Sanchez and Rachlow 2008) away from each other, and thus can be considered independent sample units. We conducted censuses of burrows within a 6-ha circle centered on the median locations for each of the four rabbits. To conduct the censuses, two or three observers systematically searched for all burrows >8 cm in any dimension (height or width) within the circle. The lower threshold of 8 cm was set in order to distinguish pygmy rabbit burrows from those of ground squirrels, which construct burrows that are typically < 8 cm in both height and width (Laundré 1989). Burrow locations were measured using a ProMark™ 3 survey grade GPS (Magellan Professional GPS, Carquefou, Cedex, France). We post-processed burrow locations with GNSS Solutions® (v. 3.10.01, Magellan Navigation, 2007) using one local and at least two regional base-stations. The resulting precision of burrow locations was under 3 cm for most burrows.

We found and recorded over 3000 burrow entrances during the burrow census. While we made every attempt to find all burrows within the 6-ha area, some burrows were inevitably missed due to observer error or not recorded due to equipment malfunction. However, we are confident that almost all of the burrows were found and recorded. In addition to location, we marked pygmy rabbit use by recording the

presence or absence of scat near the burrow entrance. Greater than five pygmy rabbit pellets within 25 cm of the burrow entrance were required for a burrow to be considered used. It has been noted that pygmy rabbit scat overlaps in size with juvenile cottontail rabbits, making false positive burrow identification possible (J. L. Rachlow personal communication, Moscow, ID). To minimize this problem, determination of pygmy rabbit scat was made by the first author, who had five years of experience conducting burrow censuses. This combined with the telemetry evidence of past occupancy, the observation of several pygmy rabbits during surveys, and the lack of observation of juvenile cottontail rabbits, gave us confidence in our identification of burrow use by pygmy rabbits. Procedures were approved by the Utah State University Animal Care and Use Committee (Protocol #1258).

We collected habitat covariates for a random sample of the mapped burrows. Roughly one in every 20 burrows was randomly selected and sampled for covariates. We measured the height of the tallest shrub located within a 0.25-m² square Daubenmire frame placed over the burrow. Other vegetation measurements included percent cover of grasses, forbs and shrubs, overstory, and understory, using the square sampling frame. Topographic covariates came from 10-m National Elevation Dataset (NED; <http://ned.usgs.gov/>).

Analyses

Habitat selection at the burrow level was evaluated using individual logistic regression models for each rabbit (four models), with pygmy rabbit pellets as the bivariate indicator of occurrence. Tests for normality and multicollinearity were

performed prior to fitting regression models. Non-normal variables were transformed to meet assumptions, and variables that were highly correlated were not included in the same models. We used Akaike Information Criterion (AIC) model selection to evaluate relative support for 20 biologically relevant *a priori* models (Table 4.1), and Akaike weights normalized by the number of models containing the variable to rank variable importance.

Burrow clustering was measured using Ripley's K-function (Ripley 1981, Diggle 1983). To test for clustering, we constructed 95% Monte Carlo envelopes created from simulated completely spatially random (CSR) point processes generated within the 6-ha circle surrounding the centroid of each rabbit ($N_{\text{sim}} = 99$). The K-function was converted to an L-function, which creates an index where negative values are regularly distributed, and positive values are clustered. Significant clustering was noted if the L-functions measured for each rabbit was greater than the upper 95% Monte Carlo envelope generated from the simulated CSR point processes. To visualize clusters and generate spatial estimates of burrow intensity, kernel density estimation was used for the recorded burrow points using the bandwidth $h = 3$. The value of the bandwidth parameter was based on the mean LSCV bandwidth for each rabbit (mean = 2.732, SD = 0.645) rounded to the nearest integer to be consistent with other studies on clustering in burrowing animals (Hayes et al. 2007).

We created summary statistics related to burrow counts for each rabbit using utilization distributions (Worton 1989, Millspaugh et al. 2006). We created a utilization distribution for each pygmy rabbit using kernel density estimation in ArcGIS® (v. 9.2,

ESRI, 2006), and the *HRT tools* extension (Blue Sky Telemetry, Aberfeldy, Scotland). We used a bivariate normal kernel, with the bandwidth parameter (h) estimated using least squares cross validation (LSCV; Seaman and Powell 1996). We used the 95% and 50% isopleths to define the home range and core area boundaries of the utilization distribution respectively. Peripheral and interior areas of the utilization distribution were defined by the 75% isopleth. We recognize the arbitrary nature of selecting isopleths to define specific areas of a utilization distribution (Wilson et al. 2010a), but found that bandwidth affected these definitions as much or more than isopleths selection, and do not see this as a major impediment to comparative inference as long as consistent procedures are applied.

We evaluated the relationship between rabbit utilization and burrow intensity at 100 random locations using Spearman's correlation. Both burrow intensity and rabbit utilization were log-transformed prior to analysis. We then split the utilization distribution into 2 roughly equally sized portions based on the 75% home range isopleths to evaluate differences in the relationship between the periphery of the utilization distribution relative to the interior.

RESULTS

All logistic models converged, but one rabbit (F588) did not have a model with adequate explanatory power ($R^2_{adj} < 0.1$; $P > 0.1$). Of the remaining rabbits, burrow intensity was always included in the most likely model selected by AIC model selection (Table 4.2). Topography variables such as slope and aspect (transformed to a 0-1 index reflecting soil moisture), and total plant cover were also included in the best models of

rabbits F577 and F561, respectively. Excluding the rabbit for which no good model was found, burrow intensity was always among the top three most important variables for discriminating between used and unused burrows (Table 4.3). Overstory cover was also among the top three most important variables for two of the rabbits.

There were between 197 and 342 (mean = 252, SD = 61.65) burrows in a pygmy rabbit utilization distribution. Of these, roughly 65% showed evidence of pygmy rabbit use (mean = 163, SD = 59.41). Between 75% and 84% of the burrows located within the core areas of the utilization distributions showed evidence of pygmy rabbit use. All burrows and burrows with pygmy rabbit fecal pellets were clustered beginning at about 2 m (Fig. 4.1, column 1). Additionally, pygmy rabbits showed non-random use of burrows, with evidence of use being clustered relative to all burrows (Fig. 4.1, column 2) for all but one rabbit. For rabbit 577 there was a distinct change in overall burrow intensity caused by an intermittent drainage located in the center of its use area. This represents a violation of the assumptions of the random labeling procedure, and could have caused the observed regularity (negative $k_{\text{sign-none}}$; Fig. 4.1, column 2).

Pygmy rabbit utilization distributions contained between two and three cores. The probability of use based on the utilization distributions for the four rabbits was positively related to burrow intensity ($r_{\text{Spearman}} < 0.4$, Table 4.4). The relationship was improved slightly if the intensity of only burrows with pygmy rabbit pellets was considered. The positive relationship was stronger in the utilization distribution interior versus the periphery for all but one rabbit (Table 4.4).

DISCUSSION

We used high precision GPS to evaluate the spatial ecology of burrows within known pygmy rabbit home ranges. We found that habitat selection varied between individuals, but that burrow arrangement was an important predictor of pygmy rabbit use for all individuals where model-fit was adequate. We also found that there were many burrows in a pygmy rabbit home range, that burrows were clustered, and that pygmy rabbit use tended to be clustered within all burrows. That burrows would be clustered is not surprising because many burrowing animals, including Columbia ground squirrels (*Spermophilus Columbianus*; Weddell 1989), degus (*Octodon degus*; Hayes et al. 2007), and European rabbits (Cowan 1987) construct burrow systems with more than one entrance, and there are limits to how far a small animal can travel through soil (Vleck 1979). Non-random use of burrows within burrow clusters suggests that rabbits use habitat, social cues, or both when selecting burrows.

We found that potentially different cues affect within-home range habitat selection behavior than were used to select the placement of home ranges at a landscape scale. For example, our landscape level model showed that surrogates for sagebrush cover and soil deposition were important for predicting the occurrence of burrows with pygmy rabbit pellets (Wilson et al. 2010b). These same variables were again useful for predicting burrow use, but the variables important for selection depended on the specific gradients of covariates within the home range for each rabbit. This suggests that while landscape level habitat selection may be possible with global models, habitat selection at the local level may vary by individual. Individual variation is under-

appreciated in habitat selection studies (Addicott et al. 1987), and can lead to large variation in global model parameters (Millspaugh et al. 2006). One rabbit, in particular, did not appear to be engaged in habitat selection based on any of the variables that we measured. This means that either we failed to account for all processes affecting within-home range resource selection in our data collection efforts, or that the home range did not vary in quality enough for selection behavior to be observed. There are precedents for leporids to change burrow use behavior based on local vegetation cover. For example, European rabbits use burrows (or warrens) more intensely if the amount of local above-ground cover is low (Kolb 1994, Palomares, 2003).

Contrary to European rabbits overhead vegetative cover was positively correlated with placement of burrows by degus, and is thought to be reduce their risk of predation (Hayes et al. 2007). Similarly, risk of predation was thought to influence the timing of burrow use by European rabbits (Palomares 2003). We observed that over-story cover was important for predicting burrow placement for some of the rabbits. Similar to the European rabbit and degas, risk of predation may be an important mechanism behind this observation. Indeed, other studies of pygmy rabbits have found that increasing sagebrush cover leads to increases in the probability of pygmy rabbit occurrence (e.g. Green and Flinders 1980b, Simons and Laundré 2004, Larrucea and Brussard 2008). However, burrow intensity was positively related to the probability that a pygmy rabbit used a burrow in the selected model for three of the four rabbits. This strongly suggests that the spatial arrangement of burrows cannot be ignored as an important factor in habitat suitability models.

We found weak positive correlations between the probability of rabbit use, based on utilization distribution, and burrow intensity. As expected, the correlation was stronger in the home range interior than in the exterior for most rabbits, suggesting that movement is consistent with a central place forager dependent on a burrow network for refugia. The observation that a higher proportion of burrow entrances showed evidence of use within the home range core also supports this view. The presence of several cores within the home ranges (2-3), and frequent observations of burrow switching for rabbits in Idaho (Sanchez and Rachlow 2008, Price 2009), suggests that some rabbits use multiple foci as central places. The weak relationship between burrow intensity and utilization suggests that resources other than burrows (e.g. food, above ground cover, conspecifics, intraspecific competitors, and predators) likely influence habitat use by pygmy rabbits.

The number of burrows present at a site is known to be correlated with both the probability of pygmy rabbit occurrence (Wilson et al. 2010b) and the number of pygmy rabbits occupying a site (Price 2009). Therefore, monitoring of burrows or burrow clusters is attractive because of the simplicity of observing burrows. If clusters are used for monitoring, the definition of a burrow cluster must either be made by observers in the field, by using a map of all burrows in a geographic information system (buffer), or through spatial statistics (Kernel Density Estimator). The latter two methods involve a subjective choice of buffer radius, or smoothing parameter, respectively. We used established methods to choose values for these parameters, but attention to this matter is crucial for burrow counts to be a useful predictor of rabbit abundance.

Explicit attention to burrow arrangement could be used to choose and prepare sites for pygmy rabbit reintroduction. Multiple observations, including: the presence of many burrows per rabbit, clustering of use, and use of multiple burrows, suggest that the idea that an individual rabbit excavates and maintains a single burrow system (*sensu* Heady and Laundré 2005) may not be accurate. Therefore, constructing a single artificial burrow for each rabbit prior to release most likely does not provide adequate refugia for reintroduced pygmy rabbits. Reintroduction sites should be located where existing burrow networks provide rabbits with access to many burrow refuges. Burrow use and social organization are known to be closely linked in European rabbits (Cowan 1987), but knowledge of the social structure of free ranging pygmy rabbit is lacking. Therefore additional studies of social cues affecting burrow use should be conducted prior to reintroduction so that success can be maximized.

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Table 4.1. *a priori* candidate models for logistic regression on burrow utilization of pygmy rabbits in the Duck Creek allotment in Rich County, Utah, USA.

Model	# Var	Model Description
Model 1	1	Measured- Percent cover of all plants less than 20cm tall): Understory
Model 2	1	Measured- Percent cover of all grasses: Grass
Model 3	1	10-m DEM- Aspect transformed to reflect soil moisture (index 0-1): Moisture
Model 4	1	10-m DEM- Slope in degrees: Slope
Model 5	1	Modeled- Burrow intensity (n/m ²): Intensity
Model 6	1	Measured- Shrub height (cm): Height
Model 7	1	Measured- Percent cover of all shrubs): Shurb
Model 8	1	Measured- Percent cover of all plants greater than 20cm tall): Overstory
Model 9	2	Hheight + Shrub
Model 10	2	Overstory + Understory
Model 11	2	Slope + Moisture
Model 12	3	Height + Shrub + Grass
Model 13	3	Slope + Moisture + Intensity
Model 14	3	Overstory + Understory + Intensity
Model 15	4	Intensity + Height + Shrub + Grass
Model 16	5	Slope + Moisture + Height + Shrub + Grass
Model 17	5	Slope + Moisture + Overstory + Understory + Intensity
Model 18	6	Overstory + Understory + Intensity + Height + Shrub + Grass
Model 19	6	Slope + Moisture + Intensity + Height + Shrub + Grass
Model 20	8	Slope + Moisture + Intensity + Height + Shrub + grass + Overstory, Understory

The number in parentheses lists the number of variables in each model.

Table 4.2. AIC model selection statistics of logistic regression models for pygmy rabbits in the Duck Creek allotment in Rich County, Utah, USA.

Model	k_i	AIC	Δ_i	$L(g_i x)$	w_i
F535					
Model 5	1	68.205	0.000	1.000	0.411
Model 15	4	70.645	2.440	0.295	0.121
Model 14	3	70.469	2.264	0.322	0.133
Model 13	3	72.014	3.809	0.149	0.061
Model 8	1	72.595	4.390	0.111	0.046
Model 7	1	72.687	4.482	0.106	0.044
Model 3	1	73.729	5.524	0.063	0.026
Model 6	1	74.178	5.973	0.050	0.021
Model 10	2	74.364	6.159	0.046	0.019
Model 17	5	74.408	6.203	0.045	0.019
Model 4	1	74.532	6.327	0.042	0.017
Model 2	1	74.680	6.475	0.039	0.016
Model 9	2	74.687	6.482	0.039	0.016
Model 1	1	75.121	6.916	0.031	0.013
Model 18	6	75.528	7.323	0.026	0.011
Model 11	2	75.674	7.469	0.024	0.010
Model 12	3	76.399	8.194	0.017	0.007
Model 19	6	77.314	9.109	0.011	0.004
Model 20	8	77.585	9.380	0.009	0.004
Model 16	5	79.648	11.443	0.003	0.001
F588¹					
Model 8	1	59.854	0.000	1.000	0.130
Model 6	1	60.138	0.284	0.868	0.113
Model 2	1	60.166	0.312	0.856	0.111
Model 7	1	60.214	0.360	0.835	0.109
Model 4	1	60.693	0.839	0.657	0.086
Model 3	1	60.726	0.872	0.647	0.084
Model 1	1	60.745	0.891	0.641	0.083
Model 5	1	60.756	0.902	0.637	0.083
Model 10	2	61.721	1.867	0.393	0.051
Model 9	2	61.888	2.034	0.362	0.047
Model 11	2	62.623	2.769	0.250	0.033
Model 12	3	63.397	3.543	0.170	0.022
Model 14	3	63.715	3.861	0.145	0.019
Model 13	3	64.603	4.749	0.093	0.012
Model 15	4	65.390	5.536	0.063	0.008
Model 16	5	67.370	7.516	0.023	0.003
Model 17	5	67.670	7.816	0.020	0.003
Model 18	6	68.714	8.860	0.012	0.002
Model 19	6	69.457	9.603	0.008	0.001
Model 20	8	72.715	12.861	0.002	0.000

Model	k_i	AIC	Δ_i	$L(g_i x)$	w_i
F577					
Model 13	3	175.016	0.000	1.000	0.585
Model 11	2	177.457	2.441	0.295	0.173
Model 17	5	178.903	3.887	0.143	0.084
Model 4	1	179.200	4.184	0.123	0.072
Model 19	6	180.113	5.097	0.078	0.046
Model 16	5	181.143	6.127	0.047	0.027
Model 20	8	182.677	7.661	0.022	0.013
Model 5	1	190.499	15.483	0.000	0.000
Model 3	1	192.034	17.018	0.000	0.000
Model 8	1	192.299	17.283	0.000	0.000
Model 6	1	192.440	17.424	0.000	0.000
Model 1	1	193.051	18.035	0.000	0.000
Model 7	1	193.191	18.175	0.000	0.000
Model 2	1	193.214	18.198	0.000	0.000
Model 14	3	193.426	18.410	0.000	0.000
Model 9	2	194.206	19.190	0.000	0.000
Model 10	2	194.222	19.206	0.000	0.000
Model 15	4	195.555	20.539	0.000	0.000
Model 12	3	196.176	21.160	0.000	0.000
Model 18	6	197.668	22.652	0.000	0.000
F561					
Model 14	3	141.655	0.000	1.000	0.684
Model 17	5	144.333	2.678	0.262	0.179
Model 18	6	146.409	4.754	0.093	0.064
Model 15	4	147.715	6.060	0.048	0.033
Model 20	8	148.570	6.915	0.032	0.022
Model 19	6	150.981	9.326	0.009	0.006
Model 13	3	151.759	10.104	0.006	0.004
Model 8	1	152.715	11.060	0.004	0.003
Model 5	1	153.885	12.230	0.002	0.002
Model 10	2	154.220	12.565	0.002	0.001
Model 6	1	155.883	14.228	0.001	0.001
Model 9	2	156.256	14.601	0.001	0.000
Model 12	3	156.625	14.970	0.001	0.000
Model 7	1	158.116	16.461	0.000	0.000
Model 16	5	158.123	16.468	0.000	0.000
Model 1	1	163.028	21.373	0.000	0.000
Model 4	1	164.519	22.864	0.000	0.000
Model 3	1	164.894	23.239	0.000	0.000
Model 11	2	165.137	23.482	0.000	0.000
Model 2	1	165.212	23.557	0.000	0.000

k_i , the number of variables for model i ; AIC, the Akaike information criterion; Δ_i , the difference of the AIC for model i from that of the best model; $L(g_i|x)$, the likelihood of model i given the data; and w_i , the Akaike weights for model i

¹Model fit for F588 was poor. The parameter estimates were not different from zero.

Table 4.3. Variable importance of logistic regression habitat models for pygmy rabbits in the Duck Creek allotment in Rich County, Utah, USA.

	Under story cover	Grass cover	Soil moisture	slope	Burrow intensity	Shrub height	Shrub cover	Over story cover
F535								
Importance ¹	19.74	16.32	12.51	11.65	76.41	18.52	26.95	23.03
Rank	4	6	7	8	1	5	2	3
Weighted importance ²	3.29	2.72	1.79	1.66	9.55	2.32	2.99	3.84
Rank	3	5	7	8	1	6	4	2
F588³								
Importance ¹	15.78	14.45	13.58	13.72	12.75	19.62	20.41	20.46
Rank	4	5	7	6	8	3	2	1
Weighted importance ²	2.63	2.41	1.94	1.96	1.59	2.45	2.27	3.41
Rank	2	4	7	6	8	3	5	1
F577								
Importance ¹	9.66	5.85	92.70	99.90	72.73	8.59	67.07	9.66
Rank	6	8	2	1	3	7	4	5
Weighted importance ²	1.61	0.98	13.24	14.27	9.09	1.07	7.45	1.61
Rank	6	8	2	1	3	7	4	5
F561								
Importance ¹	95.01	12.50	21.20	21.20	99.42	12.62	13.02	95.28
Rank	3	8	5	4	1	7	6	2
Weighted importance ²	15.83	2.08	3.03	3.03	12.43	1.58	1.45	15.88
Rank	2	6	5	4	3	7	8	1

¹Importance is the sum of the Akaike weights for all models containing the variable multiplied by 100 for easy visual interpretation.

²Weighted importance is the Importance value divided by the number of models containing the variable.

³Model fit for burrows within the homerange for this rabbit was very poor. Importance assignments and rankings have very little information in this case.

Table 4.4 Spearman's correlation between log transformations of Rabbit utilization and burrow intensity for pygmy rabbits in the Duck Creek allotment in Rich County, Utah, USA. Sample = 100 random points

rabbit	<u>Whole UD</u>		<u>Exterior</u>		<u>Interior</u>	
	all burrows	burrows with sign	all burrows	burrows with sign	all burrows	% burrows with sign
F535	0.2903	0.4672	0.2142	0.3060	0.0066	0.1048
F561	0.3872	0.6061	0.2257	0.3988	0.6131	0.7190
F588	0.3605	0.3598	0.3111	0.2531	0.3812	0.4145
F577	0.2409	0.3293	0.1307	0.2502	0.5074	0.5290

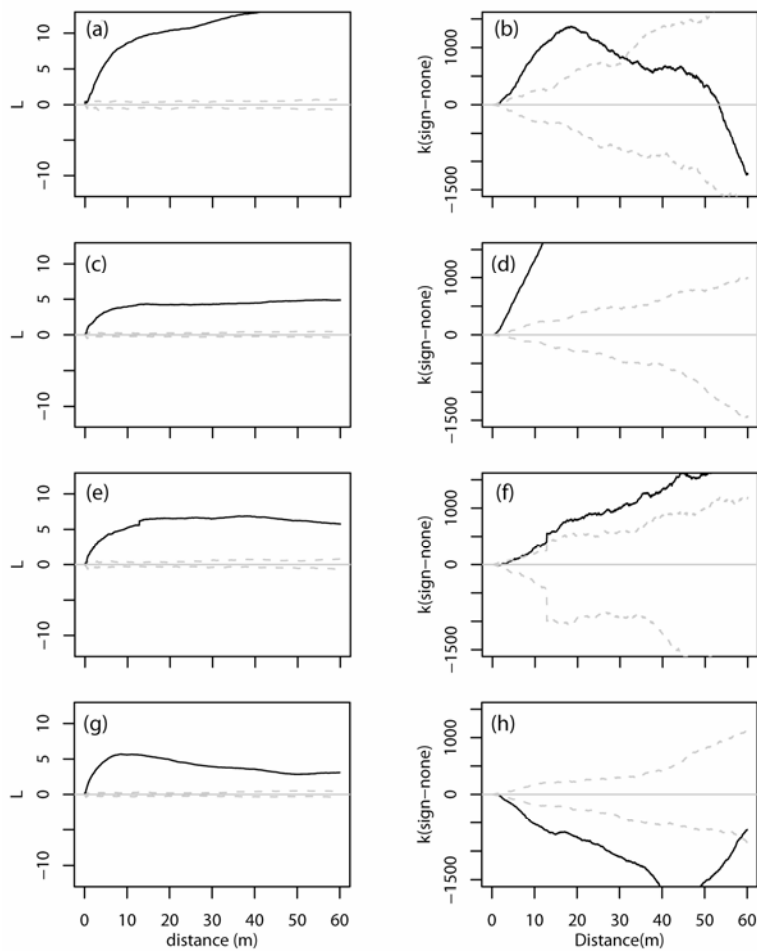


Fig. 4.1. K statistics for pygmy rabbits in the Duck Creek allotment in Rich County, Utah, USA. The rows represent the four rabbits: F535 = (a,b), F561 = (c,d), F588 = (e,f) F577 = (g,h). The columns represent the K-function tested. Column 1, (a),(c),(e), and (g), is the L-function for all burrows. Significant clustering is noted if the black line extends above the gray dashed lines. Column 2, (b),(d),(f), and (h), represents the random labeling K-function. Significant clustering of burrows with sign within all burrows is observed if the black line extends above the gray dashed lines, random if it is within the dashed lines, and regularly spaced if the black line extends below the dashed lines.

CHAPTER 5
CONCLUSION
SYNTHESIS

Processes affecting animal distribution, abundance, and movement operate across multiple scale domains (Johnson 1980). These processes, and the patterns they create, must be understood if ecologists are to make predictions about species distribution now and in the future, whether in response to changes in landuse, landcover, or climate. A hierarchical approach also facilitates the ability of managers and conservationists to evaluate resources necessary to maintain or increase populations. Therefore successful animal species conservation requires understanding of spatial processes at multiple scales of observation. The task of the ecologist is to link process to pattern as best as possible given the constraints and challenges imposed within this hierarchical framework.

The collection of papers presented here examines pygmy rabbit distribution, habitat selection, and resource use at landscape, home range, and within home range levels of organization. Chapter 2 combines the ideas of species distribution models (Guisan and Zimmermann 2000) and patch occupancy (MacKenzie et al. 2002) to present spatially explicit models of pygmy rabbit distribution and relative abundance on a landscape that was known to be occupied. Chapter 3 evaluates the effects of sagebrush restoration treatments on pygmy rabbit habitat selection at two hierarchical levels of observation. Finally, Chapter 4 evaluates within-home-range resource selection. These

papers advance our knowledge of pygmy rabbit space use at multiple scales of resolution, thereby aiding in their conservation. More generally, the papers represent a nested hierarchy of research that presents a complete picture of how an organism operates at multiple scales.

In Chapter 2, I present a spatially explicit model of pygmy rabbit distribution and relative abundance using indirect indicators of presence (i.e. burrows and fecal pellets) that had natural hierarchical structure. Through this modeling exercise, heterogeneity in the expected pygmy rabbit distributions is shown within an area that was known to be occupied. Rigorous spatial predictions are made about the relative abundance of pygmy rabbit burrows as well as the probability of occupancy. This modeling framework can be extended to encompass both larger extents and other species for which direct estimation of abundance is difficult.

In Chapter 3, I evaluated the effects of mechanical, sagebrush-reduction treatments on habitat selection at two levels of resolution. I found no evidence of treatment effects at the level of home range placement. However, I observed within-home range selection for rabbits living very close to treated patches. These results are useful for managers planning sagebrush manipulations.

In Chapter 4, I evaluate within home range resource selection as it pertains to burrows and burrow arrangement. I found that burrows are spatially clustered and that pygmy rabbit use as evidenced by fecal pellets is clustered within burrows. Pygmy rabbit utilization distributions contained many burrow entrances and clusters. I also found a weak positive relationship between burrow intensity and utilization. These

observations are consistent with behavior of a central-place forager that is partially dependent on burrow systems or complexes. Both cover and neighborhood characteristics were important for predicting pygmy rabbit burrow use. Explicit attention to burrow arrangement should improve both population trend monitoring based on burrows and pygmy rabbit reintroduction efforts.

MANAGEMENT RECOMMENDATIONS

Monitoring pygmy rabbits presents a significant challenge for resource managers. Their lack of unique markings and cryptic behavior make population enumeration in the field costly and difficult. The method I presented in Chapter 2 should be extended to incorporate multi-year data as inputs, allowing relative abundance trends to be monitored over time with inexpensive burrow surveys. Use of pellets as indicators of pygmy rabbit occupancy is subject to both false absence (missed observation of pygmy rabbit pellets) and false presence (misclassification of cottontail pellets). Further effort should be expended to quantify these measurement uncertainties and incorporate them into the modeling framework I developed. Remote cameras (Larrucea and Brussard 2008) or genetic testing of pellets could also be used to evaluate the frequency of false presence and absence of rabbits given pellet observations, so that these errors can be modeled with informed priors.

I would caution against using numbers from our census of burrows in pygmy rabbit home ranges and output from our burrow abundance model to estimate of the number of pygmy rabbits in Duck Creek. This is because the relationship between the number of burrows and the number of rabbits is unknown for our study area. Price

(2009) found a non-linear relationship between rabbit populations and burrow counts. This was largely because rabbits with access to more burrows used more burrows (Price 2009). Robust estimation of pygmy rabbit population size is necessary to calibrate burrow counts to estimate true population size. Population estimation remains invasive, costly and difficult for pygmy rabbits, but recent advances in the development of genetic markers hold promise for improvement.

Some managers may wish to use counts of burrow clusters instead of burrow entrances for pygmy rabbit monitoring. Defining clusters in the field is subjective and would be difficult to standardize amongst observers. Use of an objective method for defining clusters would likely require a complete understanding of burrow distribution (census). Burrow censuses are time consuming and costly because of the effort required to find and record the locations of all burrows. Use of burrow systems or clusters for census techniques should be avoided until these challenges have been adequately addressed.

On-going sagebrush manipulations are planned for sagebrush-dominated rangelands throughout the western United States. Widespread application of these sagebrush manipulation projects has the potential to affect large areas of pygmy rabbit habitat. I found that pygmy rabbits are not extirpated from areas where treatments have been implemented, but that they use the treated patches less than expected. This suggests that treatment patches may limit pygmy rabbit movement at the treatment edge. Furthermore, Zeoli et al. (2008) suggest that pygmy rabbit populations may exist in a metapopulation where patches blink in and out of occupancy from year to year.

This underscores the potential importance of both recently occupied burrow systems, and unoccupied sagebrush steppe for recolonization and dispersal corridors, respectively. Therefore, a landscape approach would assist managers wishing to conduct sagebrush manipulation in the vicinity of occupied and recently occupied pygmy rabbit burrow systems (e.g. WDFW 1995).

Until the population and genetic structure of wild pygmy rabbits is known, I conservatively recommend that currently and recently occupied sagebrush steppe not be targeted for sagebrush treatment. I show no evidence, however, that treatments in the Duck Creek allotment affected the general placement of pygmy rabbit home ranges within treated plot. This suggests that wide no-treatment buffers around occupied habitats may not be warranted. I therefore recommend that, in all sagebrush rangelands within the vicinity of pygmy rabbits, treated patches remain small relative to the grain of habitat selection by pygmy rabbits, especially in occupied and recently occupied habitat where treatments cannot be avoided. It would help managers to think of the resulting landscape looking like several small treated patches in a matrix of sagebrush, rather than the more common practice of leaving sagebrush remnants in a treated matrix.

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APPENDICES

APPENDIX A

COAUTHOR AND REPRINT PERMISSION LETTERS

10 May 2010

Tammy L. Wilson
5230 Old Main Hill
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James B. Odei
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APPENDIX B

PRELIMINARY DATA ANALYSIS
FOR EMPIRICAL BAYESIAN HIERARCHICAL MODEL

GEOSTATISTICS

We assumed that the linear models for burrow intensity and utilization,

$$\log(\lambda) = \mathbf{X}_\lambda \boldsymbol{\beta} + \boldsymbol{\varepsilon} \quad \text{eqn S1}$$

$$\Phi^{-1}(\boldsymbol{\theta}) = \mathbf{X}_\theta \boldsymbol{\alpha} + \boldsymbol{\eta} \quad \text{eqn S2}$$

were affected by spatial structure. Due to a lack of a-priori information about the nature of this spatial structure, we fit $\boldsymbol{\varepsilon}$ and $\boldsymbol{\eta}$ using traditional geostatistical methods (Cressie 1993). The large-scale trend was first evaluated using non-spatial linear models with transformed response variables and the spatial covariates. We used backward selection to select a trend model that maximized prediction and parsimony as measured by adjusted R^2 (Table S1). Recall that burrow intensity and utilization were unobserved processes in our model. We therefore performed model fitting on counts as surrogates for the latent processes (number of burrows and number of burrows with sign/number of burrows, respectively).

Table S1 Backward selection of linear models. Selected models are indicated with bold text.

Candidate models for $\log(\lambda)$	R^2_{adj}
$\sim X + Y + \text{SLOPE} + \text{ASPVAL} + \text{ASPWEST} + \text{NIR_M} + \text{RED_M} + \text{WATER}$	0.510
$\sim X + Y + \text{SLOPE} + \text{ASPVAL} + \text{NIR_M} + \text{RED_M} + \text{WATER}$	0.523
$\sim X + Y + \text{SLOPE} + \text{ASPVAL} + \text{NIR_M} + \text{WATER}$	0.535
$\sim X + \text{SLOPE} + \text{NIR_M} + \text{WATER}$	0.533
Candidate models for $\Phi^{-1}(\boldsymbol{\theta})$	R^2_{adj}
$\sim X + Y + \text{SLOPE} + \text{ASPVAL} + \text{ASPWEST} + \text{NIR_M} + \text{RED_M} + \text{WATER}$	0.2527
$\sim X + \text{SLOPE} + \text{ASPVAL} + \text{ASPWEST} + \text{NIR_M} + \text{RED_M} + \text{WATER}$	0.2754
$\sim X + \text{SLOPE} + \text{ASPVAL} + \text{NIR_M} + \text{RED_M} + \text{WATER}$	0.2313

We used the geoR package (Ribeiro Jr. & Diggle 2001) to fit geostatistical models to the residuals resulting from the selected trend model; the best spatial models were selected using AICc. The spatial dependence for $\boldsymbol{\varepsilon}$ and $\boldsymbol{\eta}$ can respectively be described by the isotropic exponential correlation function $r_\varepsilon(d) = \exp(-d/v_\varepsilon)$ and isotropic spherical correlation function $r_\eta(d) = [1 - 1.5d/v_\eta + 0.5(d/v_\eta)^3]$, where d is the distance between two locations and v_ε and v_η are spatial dependence parameters, $v_\varepsilon, v_\eta > 0$ (Fig. A.1). These covariance parameters were used in the hierarchical model. In the case of $\boldsymbol{\varepsilon}$, we modified the burrow counts by the probability of burrow detection (φ ; described below), such that $\log(Y/\varphi)$ was used as a surrogate for λ to get an empirical estimate for v_ε . We then modeled σ_ε^2 as a random parameter in the hierarchical model.

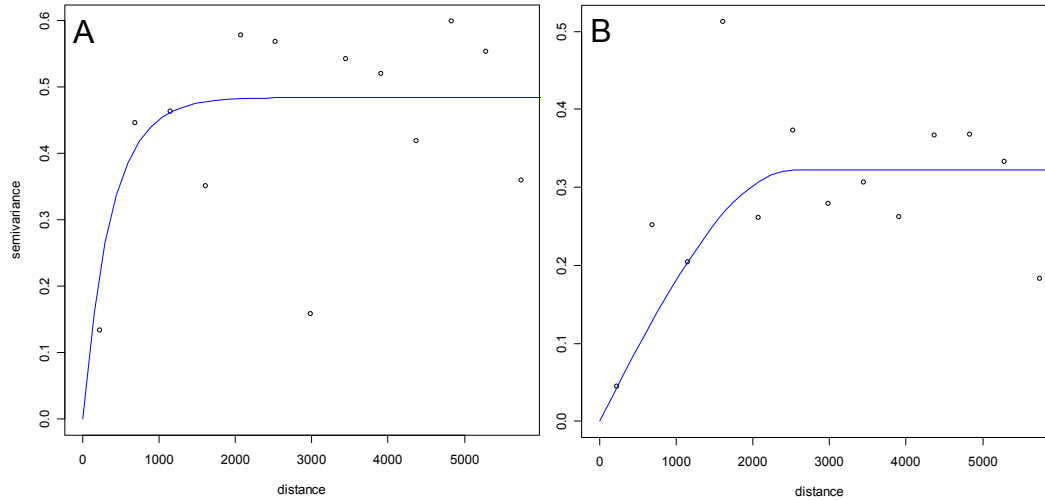


Fig. A.1 Variograms used to model spatial structure of ε (A) and η (B). The estimated parameters describing ε are range = 592m and sill = 0.4, and η are range = 2529m and sill = 0.3.

DETECTION PROBABILITY

We estimated probability of burrow detection using distance sampling methods (Buckland *et al.* 2004). Distance sampling assumes that object detection directly on the transect line is perfect and the probability of detecting additional objects decreases as the distance of that object from the transect line increases. This decrease in detection is modeled by a detection function. We used program DISTANCE (Thomas *et al.* 2006) to fit detection functions and estimate the detection probability of burrows for all sites within the study area separately. The half-normal or half-normal with the cosine key detection functions were used to estimate the probability of detection for the sampled region at each sampled site (Table S2). There were no systematic differences in burrow detection attributable to observers between sites. This is because the same observers conducted sampling at all sites and observer tasks were randomised five times at each site. Additionally, the spatial covariates available for the entire prediction domain (i.e. X, Y, ELEV, SLOPE, NIR) were not appropriate for modeling detection by observers. We therefore assume that probability of detection was homogenous throughout the study area, but was treated as a random variable in the hierarchical model to account for uncertainty in detection (*sensu* Hooten *et al.* 2007). Thus, we modeled detection as a probit transformed random variable coming from a normal distribution: $\Phi^{-1}(\varphi) \sim \text{Norm}(\mu_\varphi, \sigma_\varphi^2)$, where μ_φ is the mean of the detection probabilities estimated for 33 sites and σ_φ^2 is the standard deviation (Table S2).

Table S2. Results of Distance analysis. We excluded sites with insufficient numbers of burrows for the adequate estimation of φ (5 of 38 sites). The results are summarized such that $\mu_\varphi = 0.559$ and $\sigma_\varphi^2 = 0.115$.

site	Burrows detected	φ	Standard Error	Detection function
1	72	0.641	0.068	Half Normal
2	79	0.390	0.033	Half Normal
3	88	0.388	0.028	Half Normal
4	206	0.575	0.033	Half Normal
5	54	0.419	0.044	Half Normal
6	92	0.518	0.046	Half Normal
7	161	0.612	0.041	Half Normal
8	40	0.581	0.080	Half Normal
9	37	0.641	0.087	Half Normal
10	62	0.367	0.046	Half Normal with 2 nd order cos key
11	28	0.493	0.069	Half Normal
12	234	0.476	0.023	Half Normal
13	237	0.607	0.034	Half Normal
14	208	0.639	0.039	Half Normal
15	111	0.395	0.032	Half Normal
17	63	0.470	0.046	Half Normal
18	140	0.476	0.030	Half Normal
19	246	0.589	0.031	Half Normal
20	37	0.529	0.072	Half Normal
21	24	0.321	0.064	Half Normal
23	113	0.544	0.071	Half Normal with 2 nd order cos key
25	84	0.589	0.048	Half Normal
27	44	0.696	0.114	Half Normal
28	42	0.538	0.080	Half Normal
29	170	0.533	0.057	Half Normal with 2 nd order cos key
30	37	0.788	0.133	Half Normal
31	102	0.734	0.070	Half Normal
32	216	0.612	0.067	Half Normal with 2 nd order cos key
33	65	0.597	0.115	Half Normal with 2 nd order cos key
34	51	0.630	0.081	Half Normal
35	106	0.636	0.055	Half Normal
37	163	0.734	0.054	Half Normal
38	52	0.696	0.095	Half Normal

INFORMATION ABOUT PARENT MANUSCRIPT

Material is in supplement to: Hierarchical spatial models for predicting pygmy rabbit distribution and relative abundance

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APPENDIX C

DERIVATION OF RATE PARAMETER

Here we derive the estimation of the rate parameter ($\hat{\lambda}$) used for simulations testing third order habitat selection.

Given the probability density function of the exponential distribution,

$$\begin{aligned} f(x) &= \lambda e^{-\lambda x}, \quad 0 \leq x \leq \infty \\ &= 0 \text{ otherwise.} \end{aligned} \quad (1)$$

For $f(x) > 0$ we obtain,

$$\int_0^{\infty} f(x) dx = \int_0^{\infty} \lambda e^{-\lambda x} dx = \left[-e^{-\lambda x} \right]_0^{\infty} = 1. \quad (2)$$

To find the probability that an arbitrary X less than a known value x_0 we find,

$$P(x_0 \leq X \leq \infty) = P(X \geq x_0) = 1 - P(0 \leq X \leq x_0) \quad (3)$$

and thus,

$$1 - P(0 \leq X \leq x_0) = \int_0^{x_0} \lambda e^{-\lambda x} dx = \left[-e^{-\lambda x} \right]_0^{x_0} = e^{-\lambda x_0}. \quad (4)$$

To estimate the rate parameter ($\hat{\lambda}$), we substitute d^* for x_0 , and rearrange the equation to obtain,

$$e^{-\hat{\lambda}d^*} = 1 - P(0 \leq X \leq d^*). \quad (5)$$

We now solve for λ ,

$$-\hat{\lambda} = \frac{\ln(1 - P(0 \leq X \leq d^*))}{d^*}. \quad (6)$$

If we assume that the radius of the 95% minimum convex polygon home ranges from rabbits in Idaho approximates the 95% quantile of observed locations, we can estimate $\hat{\lambda}$,

$$-\hat{\lambda} = \frac{\ln(0.05)}{d^*}. \quad (7)$$

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PROFESSIONAL EXPERIENCE

- Graduate Research Assistant (Ph.D.)- Utah State University, Logan, UT
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- Wildlife Technician- Colorado Division of Wildlife, Montrose, CO
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- GIS Analyst- Southwest Data Center, Ridgway, CO
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- GIS Analyst- Natural Resources Ecology Laboratory, Fort Collins, CO
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- Biological Science Technician- Bureau of Land Management, Montrose, CO
Summers of 1999, 1998, 1997, 1995, and 1994.
- Natural Resources Park Ranger- South Platte Park, Littleton, CO
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- Biological Technician- Missouri Department of Conservation, Columbia, MO
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June 1993 to December 1993

PUBLICATIONS

Peer reviewed:

Wilson, T.L., F.P. Howe, T.C. Edwards Jr. *Conditionally accepted*. Effects of sagebrush treatments on multi-scale resource selection by pygmy rabbits. *Journal of Wildlife Management*.

Wilson, T.L., J.B. Odei, M.B. Hooten, T.C. Edwards Jr. 2010. Hierarchical spatial models for pygmy rabbit distribution and relative abundance. *Journal of Applied Ecology* 47: 401-409. doi: 10.1111/j.1365-2664.2009.01766.x⁵

⁵ Featured on the BBC news web page in the big picture section 14 January 2010, and on the journal cover.

- Larsen, R.T., J.A. Bissonette, J.T. Flinders, M.B. Hooten and **T.L. Wilson**. 2010. Summer spatial patterning of chukars in relation to free water in western Utah. *Landscape Ecology* 25: 135-145. doi:10.1007/s10980-009-9407-z
- Wilson, T.L.**, E. J. Johnson, and J.A. Bissonette. 2009. Relative importance of habitat area and isolation for bird occurrence patterns in a naturally patchy landscape. *Landscape Ecology* 24:351-360. doi: 10.1007/s10980-008-9309-5

Technical reports:

- Edwards, T.C., Jr., F.P. Howe, R.E. Norvell, **T.L. Wilson**, J. Ripplinger, and J. Gibson. 2009. Disturbance as a management tool: effects on selected wildlife species in Rich County, Utah. Final Project Report No. 2009-3, USGS Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan
- Bissonette, J.A., E.J. Johnson, and **T.L. Wilson**. 2006. Sagebrush-Dominated Mountain Meadows Bird and Small Mammal Community Dynamics. Project Report No. 2006-4. USGS Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan Utah.

Theses:

- Wilson, T.L.** 2010. A multi-scale evaluation of pygmy rabbit space use in a managed landscape. Dissertation. Utah State University, Logan.
- Wilson, T.L.** 2005. Landscape Dynamics of bird and small mammal communities in sagebrush-dominated mountain meadows in the Wasatch-Cache National Forest: part of a hierarchical, multi-level study. Thesis. Utah State University, Logan.

PRESENTATIONS

- Contributed Seminar, 16th Wildland Shrub Symposium, Logan, UT. 2010. "Effects of seismic exploration on pygmy rabbits."
- Seminar, USGS National Headquarters, Reston, VA. 2010. "Overcoming the challenges of monitoring rare and cryptic species: the pygmy rabbit as an example."
- Seminar, Patuxent National Wildlife Research Center, Laurel, MD. 2010. "Multiscale investigations of pygmy rabbit spatial ecology."
- Invited Seminar, Utah Cooperative Fish and Wildlife Research Unit Coordinating Committee Meeting, Salt Lake City, UT. 2010. "A multiscale evaluation of pygmy rabbit space use."
- Contributed Seminar, US-International Association for Landscape Ecology, Athens, GA. 2010. "Spatial patterns of burrow use by pygmy rabbits."
- Post-project seminar, Utah State University, Logan UT. 2010. "Pygmy rabbit space use in a managed landscape: a multi-scale evaluation."
- Poster, Restoring the West, Logan, UT. 2009. "Effects of sagebrush restoration treatments on pygmy rabbit space use."
- Contributed seminar, US-International Association for Landscape Ecology, Snowbird, UT. 2009. "Hierarchical spatial models for pygmy rabbit distribution and abundance."
- Poster, Ecological Society of America, Milwaukee, WI. 2008. "Improving habitat models for rare and inconspicuous species."
- Poster, US-International Association for Landscape Ecology, Tucson, AZ. 2007. "Evaluating habitat use and connectivity using occupancy and density indices."

- Pre-project seminar, Utah State University, Logan UT. 2006. "Responses of pygmy rabbits (*Brachylagus idahoensis*) to sagebrush removal treatments in Rich County, Utah."
- Poster, US-International Association for Landscape Ecology, San Diego, CA. 2006. "Moving beyond area-density relationships- a challenge for conservation planning."
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- Poster, The Wildlife Society, Calgary, AB. 2004. "An examination of meadow and landscape characteristics in bird and small mammal species diversity- Technical considerations."

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- Co-mentor 2009-2010: Drew White
Effects of sagebrush restoration on thatch mound ant distribution.
- Co-instructor 2009: USIALE workshop: Bayesian Methods for Landscape Ecologists
Assisted with laboratory exercises, and presented applications.
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- Teaching Assistant 2008: Biometry
Prepared and conducted lectures and labs.
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- Teaching Assistant 2006-2008: Junior block field course
Designed and led research-based exercise for field and lab.
- Field Crew Supervisor 2006-2009: Shrubmap Project
Instructed and mentored undergraduate students conducting field research with the goal of building knowledge, confidence and self-sufficiency while performing resource monitoring and assessment tasks.

GRANTS AND AWARDS

- 2010 Cover article in Volume 47, Issue 2 of Journal of Applied Ecology
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- 2010 Consultant, Wild About Utah radio program on pygmy rabbits.
- 2010 Seminar, Coordinated Resource Management Committee: Sagebrush management recommendations for pygmy rabbits.

- 2008 Seminar, Coordinated Resource Management Committee: Rich county Project progress report.
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