**SURVIVAL AND BURROWING ECOLOGY OF PYGMY RABBITS:**

**IMPLICATIONS FOR SAGEBRUSH HABITAT AND ESTIMATION OF**

**ABUNDANCE**

A Thesis

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# AUTHORIZATION TO SUBMIT THESIS

This thesis of Amanda J. Price, submitted for the degree of Master of Science with a major in Wildlife Resources and titled "Survival and Burrowing Ecology of Pygmy Rabbits: Implications for Sagebrush Habitat and Estimation of Abundance," has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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# ABSTRACT

The pygmy rabbit (*Brachylagus idahoensis*) is a cryptic, non-gregarious, burrowing lagomorph of conservation concern. Interest in the pygmy rabbit has increased recently, and United States Fish and Wildlife Service is currently considering a petition to list the entire species under the Endangered Species Act in response to a perceived decline across its range (Federal Register 2008). As part of ongoing research aimed at understanding this species, we evaluated several attributes of the ecology of pygmy rabbits and developed an index that can be used to estimate rabbit abundance.

First, we examined factors potentially influencing survival of juvenile pygmy rabbits (Chapter 1). We modeled survival of radio-tagged juveniles captured shortly after emergence from their natal burrows, and we evaluated the effect of variables (sex, year, study area, and relative date of birth) on survival through 18 weeks of age. Survival varied substantially across multiple factors, and although model selection results did not indicate strong support for any single combination of variables, juveniles born later in the summer experienced lower survival.

Second, we evaluated the effects of foraging and burrowing by pygmy rabbits on the structure and composition of a sagebrush community (Chapter 2). Because of their foraging and burrowing behaviors, pygmy rabbits have the potential to markedly influence the sagebrush-steppe environment in which they live, and such effects might become more pronounced around burrows over time. We evaluated whether duration of occupancy affects vegetation characteristics around burrow systems and if effects of occupancy were more pronounced close to the center of burrowing activity. We detected no influence of distance from center of burrowing activity on the structure and

composition of sagebrush habitat across two study sites in eastcentral Idaho.  However, vegetation differed with the duration of occupancy of burrow systems.  Vegetation around burrows occupied longer had higher browsing intensity, increased seedling density, more open understory, and less visual obstruction.  The changes we observed in vegetation as duration of burrow occupancy by pygmy rabbits increased establishes their role as ecosystem engineers in sagebrush-steppe communities, and suggests that pygmy rabbits have the potential to influence habitat quality for themselves and sympatric species.

Finally, although understanding various aspects of the ecology and habitat relations of pygmy rabbits is important for understanding the basic biology of this species, in order to truly evaluate the status and population dynamics of pygmy rabbits, we need a method for estimating their abundance and monitoring populations.  We developed an index of abundance based on density of active burrow systems at 7 study sites in eastcentral Idaho (Chapter 3) by conducting censuses of burrow systems and using mark-resight surveys and snow-track surveys to estimate abundance of rabbits on each site.  We evaluated patterns of burrow use by individuals, and we used the estimated abundance data to examine the relationship between vegetation structure and density of rabbits.  Density of active burrow systems and density of rabbits varied across sites and the number of burrow systems used by individuals increased with density of available burrows.  Population density increased curvilinearly with density of active burrows accounting for over three-quarters of the variation ($r^2$=0.79) in population estimates across sites.

Overall, this work supports the idea that pygmy rabbit populations might shift across the landscape due to changes in vegetation structure and composition and that high variability in survival over relatively small spatial and temporal scales might contribute to marked fluctuations in their populations. As a result, in order to understand and conserve populations of pygmy rabbits, researchers and managers might consider monitoring multiple populations across broader geographic areas to assess regional trends in abundance and habitat use. Additionally, the density of burrows can serve as an index for monitoring changes in abundance of pygmy rabbits in eastcentral Idaho and also might be useful for monitoring changes in relative abundance over time at other locations. To assess abundance at larger spatial scales or across different regions, however, the index should be calibrated under regional conditions and site-level covariates should be evaluated.

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**THESIS INTRODUCTION**

Interest in the pygmy rabbit (*Brachylagus idahoensis*) has grown since the Columbia Basin population in Washington was listed under the Endangered Species Act (ESA) as an endangered distinct population segment (Federal Register 2003). Additionally, in part because of a perceived decline in the species across its range, a petition to list the species as threatened or endangered throughout its range was submitted, but subsequently denied in May 2005, citing insufficient information to warrant listing. Following litigation, the petition is currently being reconsidered (Federal Register 2008), and the rabbit is again a candidate for listing under the ESA.

The petition for ESA listing of pygmy rabbits has prompted managers to place a high priority on developing a consistent method to survey the species across its range and on developing a better understanding of their ecology. Several questions remain unanswered about how pygmy rabbits select and influence their habitats. In addition, anecdotal evidence has suggested that populations of pygmy rabbits might shift across a landscape over time (Janson 1946, Wilde 1978, Weiss and Verts 1984). A clearer understanding of the potential effects of burrowing and foraging behavior on vegetation and a standardized monitoring method to evaluate abundance would allow researchers to identify such population trends and begin to evaluate factors that shape the dynamics of this species in time and space.

To date, two ecological characteristics about which information is limited for pygmy rabbits are: 1) survival of juveniles and 2) potential influence of pygmy rabbits on vegetation around their burrow systems. Several studies have reported survival rates for

adult pygmy rabbits in the wild (Wilde 1978, Sanchez 2007, Crawford 2008), however, juvenile survival in particular has been identified as a critical parameter influencing population growth rates and trends for some species, and has not been studied in free-ranging pygmy rabbits. Additionally, few studies have examined fine-scale habitat relationships of pygmy rabbits, and none have addressed how rabbits might alter their habitat as a function of burrowing and foraging behaviors. Yet, because of these behaviors, rabbits have the potential to markedly influence the vegetation around their burrow systems.

Because pygmy rabbits are considered a burrowing obligate, use of an index based on burrow systems has been proposed as a monitoring tool for the species across its range. If applicable, the index could be used to estimate abundance of pygmy rabbits, as well as to monitor populations over time, to address questions about distribution, ecology, abundance, and population trends.

The goal of this thesis was to better understand the burrowing and foraging ecology of pygmy rabbits and to develop and apply a monitoring tool for the species based on their burrow systems. The results of this study will enhance our understanding of a species of conservation need and provide a tool for management. Specific objectives for this research were:

1) Estimate survival of juvenile pygmy rabbits;

2) Evaluate the effect of pygmy rabbits on vegetation around burrow systems; and

3) Calibrate an index of abundance based on burrow systems by correlating the index with estimates of population density.

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**CHAPTER 1:**

**Survival of Juvenile Pygmy Rabbits**

ABSTRACT

Until recently, natal behavior of pygmy rabbits (*Brachylagus idahoensis*) was largely unknown, and no information on survival of free-ranging juveniles was available. We evaluated survival of radio-tagged juvenile pygmy rabbits at 2 sites in east-central Idaho during 2004 and 2005. We captured juveniles (n = 58) shortly after they emerged from natal burrows. Mortality rates were high and variable, ranging from 27% for females during 2004 to 63% for males during 2005. Approximately 69% of mortalities were attributed to predation. We evaluated variables influencing juvenile survival through 18 weeks old using known-fate models in Program MARK. We expected survival to decline around the age of natal dispersal and to be lower for young born later in the season. We evaluated 14 candidate models that included sex, year, study area, and relative date of birth within each year. Model selection results did not indicate strong support for any single combination of variables, and 9 competing models all included effects of relative date of birth, year, and study area. These results revealed substantial variability in survival of juveniles across multiple factors, and we documented similar patterns for adult pygmy rabbits. Such high variability in survival over relatively small spatial and temporal scales might contribute to marked fluctuations in populations of pygmy rabbits, and hence, managers interested in monitoring this species might consider

monitoring multiple populations across broader geographic areas to assess regional trends in numbers.

INTRODUCTION

Survival is a fundamental demographic parameter influencing population dynamics; therefore, an understanding of factors influencing survival is necessary for population management and conservation planning (Lebreton et al. 1992).  Juvenile survival in particular has been identified as a critical parameter influencing population growth rates and trends for some species, at least under certain environmental and ecological conditions (Gaillard et al. 1998, Dobson and Oli 2001, Oli and Dobson 2003, Ozgul et al. 2006).  This is especially relevant for short-lived species that typically have high reproductive rates resulting in a high proportion of their populations in the juvenile age class.

One such species is the pygmy rabbit (*Brachylagus idahoensis*) of the western United States.  Recent population viability analyses (PVA) for a captive breeding program that was established for the Columbia Basin pygmy rabbit, a federally endangered distinct population segment (Federal Register 2003), documented that juvenile survival was the demographic parameter with the greatest influence on population persistence, risk of extinction of the captive population, and availability of surplus rabbits for reintroduction (Zeoli et al. 2008). Survival of juvenile pygmy rabbits in captivity was low and highly variable (Elias 2004, Zeoli et al. 2008).  Adult pygmy rabbits in free-ranging populations have relatively high mortality rates (Wilde 1978, Sanchez 2007, Crawford 2008).  Sanchez (2007) estimated the average lifespan of free-

ranging adults to be 1.7 years with individuals usually surviving to participate only in a single breeding season. However, those estimates were for individuals categorized as adults when initially captured and do not include mortality of juveniles. These characteristics suggest a dependency on recruitment of juveniles for population persistence in free-ranging populations of this species, a conclusion that is consistent with PVA analysis for the captive population of Columbia Basin pygmy rabbits (Zeoli et al. 2008).

The pygmy rabbit is a sagebrush specialist that digs and uses residential burrow systems and separate shallow natal burrows (Wilde 1978, Green and Flinders 1980, Rachlow et al. 2005). Parturient females excavate natal burrows and backfill entrances with loose soil effectively concealing the burrows' locations. Young emerge from natal burrows at about 2 weeks old, and pygmy rabbits in captivity can rear up to 3 litters of 4-6 young in a season (Elias et al. 2006). Until recently, the secretive natal behavior of this species was largely unknown, and as a result, no information exists on fecundity of free-ranging females, or behavior and survival of juvenile pygmy rabbits in the wild.

Our objectives were to estimate survival rates and evaluate factors affecting survival of free-ranging juvenile pygmy rabbits. Specifically, we tested for the effects of gender, year, study site, and relative date of birth within a season on survival to 18 weeks old, the age at which juveniles become difficult to distinguish from adults and the age by which most juveniles have dispersed from natal areas (Estes-Zumpf and Rachlow 2009). We expected survival to decline between 6 and 12 weeks old due to the onset of dispersal (Estes-Zumpf and Rachlow 2009), and we also expected that timing of birth within a season would affect survival. Kits born later in the year might have lower survival due to

decreased maternal body condition, resource depletion, or competition with other juveniles.

STUDY AREA

We conducted the study in the Lemhi Valley, located in east-central Idaho near the Montana border. The Lemhi Mountain Range runs along the western edge of the Valley and the Beaverhead Mountains form the eastern boundary, and the land was managed by the Bureau of Land Management (BLM). The Lemhi Valley was characterized by sage-steppe vegetation with the dominant shrubs including Wyoming big sagebrush (*Artemisia tridentate* spp. *wyomingensis*), mountain big sagebrush (*A. t.* spp. *vaseyana*), and green rabbitbrush (*Chrysothamus viscidiflorus*). The understory was composed of a variety of forbs and grasses. Mima-mounds, areas of mounded micro-topography with relatively large, dense sagebrush and deeper soils (Tullis 1995), were common on much of the study area and were used extensively by pygmy rabbits for burrow excavation and foraging.

We delineated two study sites within the Lemhi Valley, Cedar Gulch and Rocky Canyon, which were separated by approximately 6 km of continuous sage-steppe habitat. Cedar Gulch was characterized by patchily distributed vegetation that occurred on mima-mounds with little shrub cover between mounds. Rocky Canyon was characterized by less patchily distributed vegetation, mima-mounds with taller sagebrush, and more continuous shrub cover between mounds (Sanchez 2007). Some common predators of pygmy rabbits documented at both study sites included long-tailed weasels (*Mustela*

*frenata*), coyotes (*Canis latrans*), great horned owls (*Bubo virginianus*), northern harriers (*Circus cyaneus*), badgers (*Taxidea taxus*), and red-tailed hawks (*Buteo jamaicensis*).

METHODS

During May – July of 2004 and 2005, we captured juvenile rabbits shortly after they emerged from natal burrows. We trapped rabbits with Tomahawk live traps, which we set at burrow entrances where we observed juveniles (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA). We checked traps approximately every 15 minutes. We restrained captured juveniles with a cloth handling cone and collected standard measurements of hind foot length (mm), ear length (mm), and weight (g). We implanted all rabbits with Passive Integrative Transponder (PIT) tags. We estimated age for all juveniles based on initial capture weights (Estes-Zumpf and Rachlow 2009). We considered juveniles that weighed <130 g recently emerged young (≤4 weeks old), and we fitted them with 1-g radio transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) using a modified glue-on attachment method (Estes-Zumpf and Rachlow 2007). These transmitters had an average range of 200-300 m and a battery life of 42 days. Once juveniles reached approximately 300 g (about 6 weeks old), we recaptured them using the same techniques and replaced glue-on transmitters with 5-g radio collars (Holohil Systems Ltd.), which had a battery life of 6 months and a range of several kilometers. We located rabbits via homing every 3 to 4 days from date of capture through August and biweekly during September to April. We monitored survival of juveniles, and when possible, we also recorded the age and cause of death. Evidence for determining cause of death included presence of scat, feathers, rabbit remains, and location of carcasses. All

methods were approved by the University of Idaho Animal Care and Use Committee

(Protocol 2003-50).

We evaluated survival of juvenile rabbits post-emergence from natal burrows,

which excluded neonatal mortality that might have occurred in natal burrows during the

first 2 weeks of life.  We first estimated overall patterns of survival with the Kaplan-

Meier (KM) method (Kaplan and Meier 1958).  We estimated weekly survival to 18

weeks old and modeled the effects of predictor variables on survival with the known fate

extension of Program MARK (White and Burnham, 1999).  We constructed a set of 14 *a*

*priori* models for survival analyses based on biologically justifiable combinations of the

following variables: SEX (male or female), AREA (Cedar Gulch or Rocky Canyon),

YEAR (2005 or 2004), and BORN (number of days after earliest birth of a juvenile

caught in that year).  The latter parameter represented the relative date of birth within a

breeding season.  We right censored juveniles with confirmed tag loss or malfunction and

individuals that were initially alive but then not detected through the end of the study.

We used Akaike's Information Criteria corrected for small sample sizes ($AIC_c$) for model

selection (Burnham and Anderson 2002).  We considered models with delta $AIC_c$ values

≤2 as competing models.  We calculated Akaike's weights to evaluate the relative

importance values of predictor variables across all models containing variables YEAR,

SEX, AREA, and BORN (Burnham and Anderson 2002).  We calculated model-averaged

estimates of the probability of juveniles surviving for the duration of the study across all

models in the candidate set.


RESULTS

During the 2004 and 2005 breeding seasons, we captured and tagged 28 juvenile female pygmy rabbits (mean mass = 111 g, mean age = 3.4 wks) and 30 juvenile males (mean mass = 106 g, mean age = 3.2 wks).  We did not tag rabbits directly from their natal burrows, and we captured animals throughout each study site over approximately 2 months each year.  Therefore, we assumed that tagged juveniles had a low probability of being littermates.  Of the 58 tagged juveniles, the glue-on transmitters failed or came off of 4 animals, and we were not able to relocate 4 other animals after several occasions.  Of the remaining 50 individuals, 18 were killed by predators, 8 died from unknown causes, and 24 individuals survived to 18 weeks old.  Only 11 individuals survived to the start of the next breeding season in April of the subsequent year (3 females and 4 males in 2004, and 4 males in 2005).

Contrary to our expectations, survival of juvenile rabbits was fairly consistent throughout the first 18 weeks of life, and survival did not decline around the age of dispersal (6-12 wks).  The KM survivorship curve showed no marked declines in survival, but rather a steady downward trend (Fig. 1).  Similarly, instantaneous weekly survival probabilities from Program MARK also revealed relatively constant survival across the 18 weeks (Fig. 2).

Timing of birth as well as year and study area may have influenced survival of juveniles.  A set of 9 models was included in the top model set ($\Delta$AICc $\leq$ 2), indicating relatively high model uncertainty (Table 1).  The null model with constant survival ranked ninth in the model set.  As expected, juveniles born later in the season experienced poorer survival.  The most parsimonious model described survival as a single factor adjusted for relative date of birth (BORN, S = 0.41, 95% CI = 0.27-0.55),

and modeled by $S = 3.75-0.17(BORN)$. The top 3 models all included the effect of date of birth (Table 1), however, when model averaged parameter estimates were calculated, this relationship was not significant (Table 2). Model averaging across all *a priori* models resulted in an overall estimate of probability of survival to 18 weeks old as 0.43. The top model set was comprised of most a priori models that included primary and additive effects of date of birth, year, and study area. Relative importance values ranked relative influence of study area, date of birth, and year as roughly equal (Table 2). In contrast, gender (SEX) had a low importance value and was ranked low in the model set, as were any time or trend effects throughout the first 18 weeks old (Table 1.2). Although there was no significant effect of gender, the mean estimate of survival for females was >20% higher (0.44, 95% CI = 0.26-0.64) than for males (0.35, 95% CI = 0.20-0.55). Only in the top model was timing of birth a significant effect based on the 95% confidence intervals (95% CI = -0.33 to -0.0001). However, the importance values and model ranking revealed that variation among years and study areas also might have influenced survival of juveniles. Survival rates were highest on Rocky Canyon in 2005 and lowest on Cedar Gulch in 2004 (Fig. 3).

DISCUSSION

Survival rates of juvenile pygmy rabbits were generally low and highly variable among sites and years, but within each year, survival was fairly consistent across the first 4 months. Onset of dispersal did not markedly influence survival of juveniles as we predicted. At least 2 factors associated with dispersal might have contributed to this result. First, the relatively short duration of natal dispersal movements (3-10 days; Estes-

Zumpf and Rachlow 2009) might reduce the probability of mortality during such events (Gaines and McClenagham 1980). Rapid dispersal by juvenile pygmy rabbits might minimize time moving through unfamiliar territory or less suitable habitat and also might reduce vulnerability to predators or other mortality factors associated with natal dispersal (Weisser 2001). Second, variation among individuals in age at onset of dispersal from 2.5 to 12 weeks old (median = 6.5 wks) and differences in body mass at time of dispersal (73-369 g; Estes-Zumpf and Rachlow 2009), might contribute to individual variability in survival of juveniles during dispersal events. Nevertheless, survival of juvenile rabbits did not exhibit a marked decline associated with dispersal.

Support for an effect of timing of birth on juvenile survival was equivocal. Although our top model included only timing of birth as a significant factor, this effect was not significant when we averaged it across models. Wilde (1978) noted that the first litters of pygmy rabbits seemed to have the greatest survival based on numbers of juveniles recaptured across the summer during sequential trapping. He attributed this apparent trend to the quantity and quality of forage provided by the spring green-up followed by a decline in nutrition as plants senesced throughout the dry summer months. Maternal body condition plays an important role in neonatal survival in some species, and spring green-up also might contribute to better maternal condition during gestation and lactation for earlier litters (King and Allaine 2002, Rödel et al. 2005, Lomas and Bender 2007, Rödel et al. 2009). In addition, abundant forbs and grasses might provide enhanced hiding cover for neonates born earlier in the season. Our results suggest that larger sample sizes are needed to evaluate how timing of birth might influence survival of juvenile pygmy rabbits.

Sample sizes also limited our ability to detect significant differences among years and study sites; however, our data suggested that survival varied both temporally and spatially. Similar results were documented for survival of adult pygmy rabbits in the Lemhi Valley, Idaho, (Sanchez 2007), and in southeastern Oregon and northwestern Nevada (Crawford 2008). Both of those studies reported no significant influence of sex, but they noted high variability in survival of adults between years and study sites. Multiple factors might influence variation in survival of leporids spatially and temporally, including variability in predator populations, climatic conditions, forage quality or quantity, soil characteristics, parasites, and disease (O'Donoghue 1994, Gillis 1998, Bond et al. 2001*a*, Rödel et al. 2004).

Although we do not know the specific causes for the differing rates of survival of juveniles, we noted substantial variability across a relatively small spatial extent (~ 6 km). The apparent variation in survival between study sites might be explained by differences in shrub cover between the 2 study areas. Cedar Gulch vegetation was more patchily distributed on mima-mounds with little shrub cover between mounds, unlike the more even dispersion of shrubs on Rocky Canyon. Bond et al. (2001*b*) observed that cottontail rabbits (*Sylvilagus floridanus*) moved quickly in more open, patchy habitats and experienced greater predation risk as movements increased (Bond et al. 2001*a*). Even though the SE bars overlap for site level survival probabilities, it is apparent that for both years juvenile pygmy rabbits experienced greater survival at Rocky Canyon, which had greater dispersion of vegetative cover (Fig.3).

Variability in survival of juvenile and adult pygmy rabbits might contribute to population fluctuations. If recruitment of juveniles markedly affects population

persistence, then local extirpations should be expected for isolated populations. Indeed, numerous researchers have noted that pygmy rabbit populations are subject to rapid local declines (Janson 1946, Wilde 1978, Weiss and Verts 1984). Such dynamics suggest that pygmy rabbits might persist as metapopulations (Hanski 1999), and that an understanding of connectivity among populations is important for their conservation.

MANAGEMENT IMPLICATIONS

Our findings document that survival of juvenile pygmy rabbits is a highly variable demographic parameter. Consequently, managers interested in monitoring regional trends in populations should be aware that high variability of survival rates over relatively small spatial and temporal scales could result in marked population fluctuations. Therefore, longer-term data across broader spatial scales might be needed to understand and quantify population trajectories.

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Table 1. Candidate model set used to evaluate survival of juvenile pygmy rabbits in the

Lemhi Valley, Idaho, during 2004-2005.  Predictor variables included study area

(AREA), YEAR, and relative date of birth (BORN).

| Model | $AIC_c$ | $\Delta AIC_c$[a] | $w_i$[b] | $k$[c] | Model likelihood |
|---|---|---|---|---|---|
| BORN | 211.18 | 0 | 0.16 | 2 | 1 |
| AREA+BORN | 211.57 | 0.39 | 0.13 | 3 | 0.82 |
| YEAR+BORN | 211.81 | 0.63 | 0.12 | 3 | 0.73 |
| YEAR | 211.97 | 0.79 | 0.11 | 2 | 0.67 |
| YEAR+AREA | 212.19 | 1.00 | 0.10 | 3 | 0.61 |
| AREA | 212.32 | 1.14 | 0.10 | 2 | 0.57 |
| YEAR+AREA+BORN | 212.46 | 1.28 | 0.09 | 4 | 0.53 |
| YEAR*AREA | 212.74 | 1.56 | 0.07 | 4 | 0.45 |
| Constant survival | 213.02 | 1.83 | 0.06 | 1 | 0.40 |
| Linear time trend | 213.78 | 2.60 | 0.04 | 2 | 0.27 |
| AREA+SEX | 213.90 | 2.72 | 0.04 | 3 | 0.26 |
| SEX | 214.66 | 3.47 | 0.03 | 2 | 0.18 |
| Quadratic time trend | 215.73 | 4.55 | 0.02 | 3 | 0.10 |
| Variable time | 225.72 | 14.53 | 0.00 | 14 | 0.00 |

[a] Difference between model's Akaike's Information Criterion (AIC) corrected for small sample size
[b] Akaike wt provides evidence of model likelihood
[c] No. of parameters estimated

Table 2. Model-averaged parameter estimates, standard errors, 95% confidence intervals, and relative importance values of each parameter from analysis of factors influencing survival of juvenile pygmy rabbits in the Lemhi Valley, Idaho, during 2004-2005. Importance values were calculated by summing the Akaike weights across all models in which the variable appeared.

| Parameter | Estimate | SE | 95% confidence interval | | Importance value |
| | | | Upper | Lower | |
| --- | --- | --- | --- | --- | --- |
| Intercept | 3.3308 | 0.5737 | 4.4495 | 2.2121 | |
| BORN | -0.1410 | 0.0877 | 0.0300 | -0.3120 | 0.5000 |
| YEAR | -0.5413 | 0.5408 | 0.5133 | -1.5959 | 0.4800 |
| AREA | 0.6964 | 0.4765 | 1.6303 | -0.2375 | 0.5200 |
| SEX | -0.2567 | 0.3987 | 0.5248 | -1.0382 | 0.0700 |

Figure 1. Kaplan-Meier survival curve for juvenile pygmy rabbits post-emergence from natal burrows in the Lemhi Valley, Idaho, 2004-2005
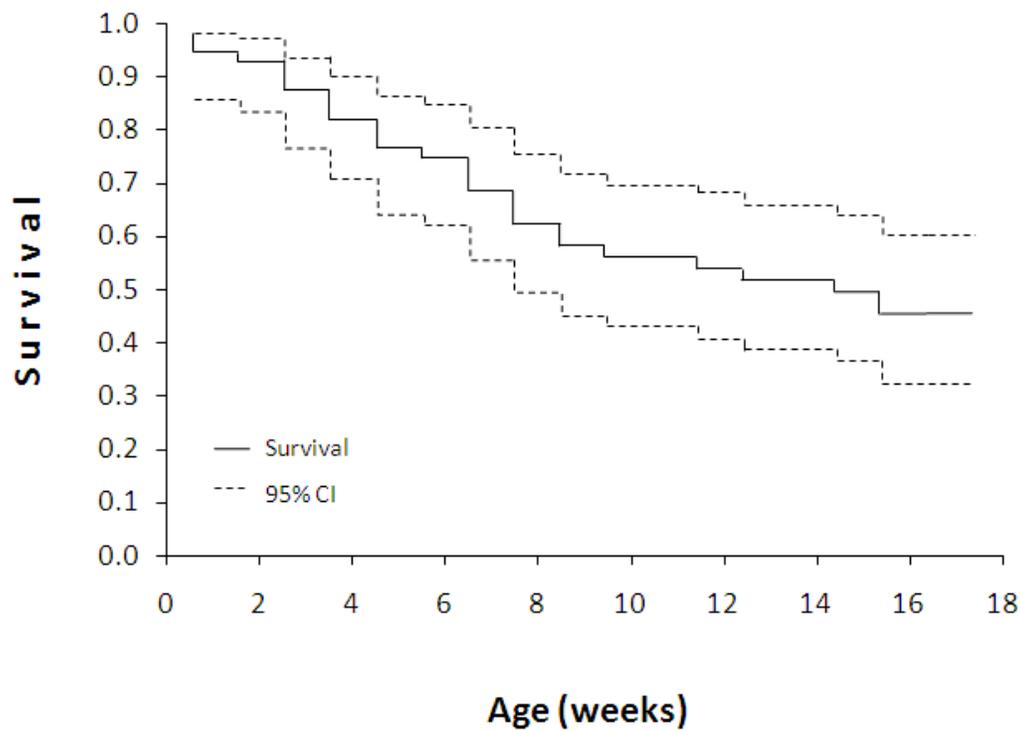
Figure 2. Estimates of weekly survival for juvenile pygmy rabbits in the Lemhi Valley, Idaho, 2004-2005.
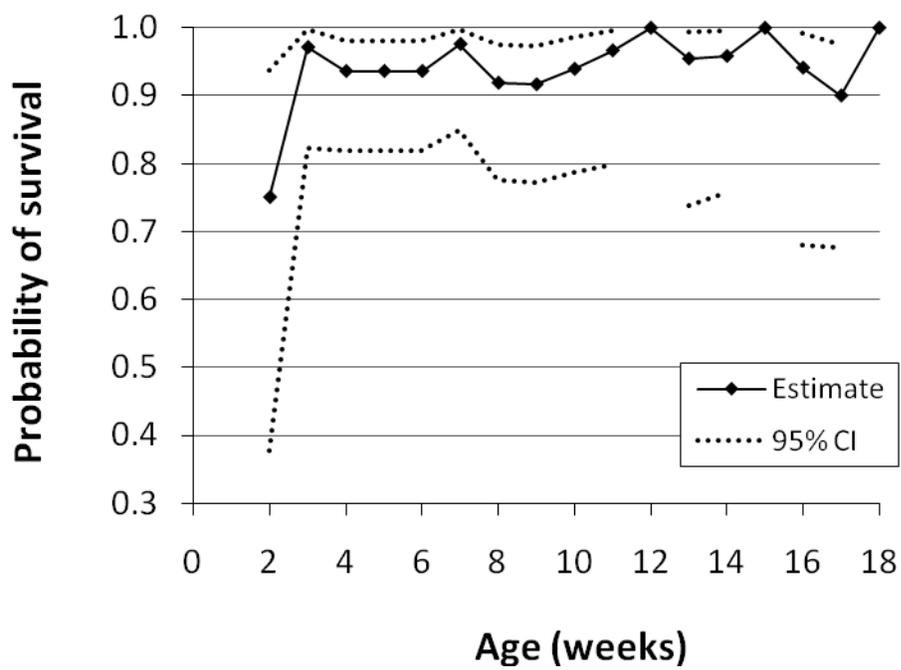
Figure 3. Model-averaged parameter estimates (±SE) for survival of juvenile pygmy rabbits on 2 study sites, Cedar Gulch and Rocky Canyon, in Idaho, 2004 and 2005.
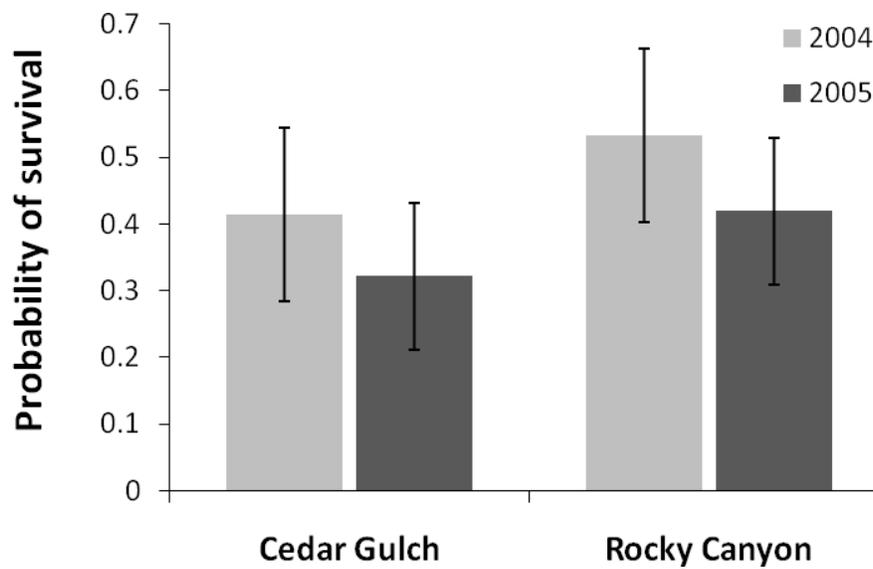
**CHAPTER 2:**

**Effects of foraging and burrowing by pygmy rabbits on the structure and composition of a sagebrush community**

ABSTRACT

Animals can alter their environments directly and indirectly in many ways. Animals can influence vegetation characteristics through foraging and also physically change their habitats through burrowing. Pygmy rabbits are non-gregarious, semi-fossorial herbivores that use sagebrush for both food and cover. Because of their foraging and burrowing behaviors, pygmy rabbits have the potential to markedly influence the sage-steppe environment in which they live, and such effects might become more pronounced around burrows over time. We evaluated whether duration of occupancy affects vegetation characteristics around burrow systems and if effects of occupancy were more pronounced closer to the center of burrowing activity. We detected no significant influence of distance from center of burrowing activity on the structure and composition of sagebrush habitat across two study sites in eastcentral Idaho. However, vegetation differed with the duration of occupancy of burrow systems. Vegetation around burrows occupied for longer periods had higher browsing intensity, increased seedling density, more open understory, and less visual obstruction. We also noted an inverse relationship between cover of sagebrush and cover of rabbitbrush, which is a disturbance-adapted shrub. The changes we observed in vegetation as duration of burrow occupancy increased establishes the role of pygmy rabbits as ecosystem engineers

in sagebrush-steppe communities, and suggests that pygmy rabbits have the potential to influence habitat quality for themselves and other, sympatric species.

INTRODUCTION

Organisms not only respond to the environment in which they live, but many also have the ability to alter their environments. Indeed, individuals across many taxa physically modify their environments in diverse ways (e.g., Reichman and Smith 1985, Naiman et al. 1988, Aho et al. 1998, Andersen and Kay 1999, Gutierrez and Meserve 2000, Zhang et al. 2003, Galvez et al. 2008). Jones et al. (1994) introduced the term "ecosystem engineers" to describe organisms that directly or indirectly modify, maintain, or create habitats, thereby changing availability and quality of resources. Allogenic engineers modify their environments by transforming material from one state to another through actions such as biodepositon (deposition of organic matter and nutrients through feces and urine), bioturbation (mixing of sediment or soils), and foraging. These processes can alter nutrient cycles, modify soil physical and chemical properties, change microsite characteristics, and result in a shift in plant species composition (Jones et al. 1997). The combined effects of various forms of habitat alteration and disturbance can have important implications for suitability of the habitat not only for the engineering species, but also for other, sympatric species.

Burrowing animals are classic examples of ecological engineers because their actions directly alter the environment by concentrating or redistributing resources and creating new patches of habitat. Tunneling activities can alter soil properties and composition by loosening soils as a result of tunnel digging, backfilling of burrows, and

production of tailings on the surface (Whitford and Kay 1999). This shifting and mixing of soils can influence nutrient exchanges, water movement, erosion, and mineralization of soils (Jones et al. 1997, Reichman and Seabloom 2002, Davidson and Lightfoot 2008). Also, vegetation can be influenced directly by burrowing behavior that can cause loss of roots, reduction of biomass, changes in recruitment, and alteration of plant competition, all of which can influence species composition (Huntly and Reichman 1994, Bruun et al. 2005). Creation of burrows also can have implications for other animal species by providing refuges and structures for breeding, and by opening new niches (Lomolino and Smith 2003, Machicote et al. 2004, Bangert and Slobodchikoff 2006). Because the prevalence and intensity of burrowing activity differs across species, the impacts of burrowers on their environments can vary markedly from severe but geographically restricted consequences, such as those created by badgers (*Taxidea taxus*) to relatively minor effects that influence entire landscapes such as those resulting from the activity of earthworms (*Lumbricus spp.*; Meadows 1991, Eldridge 2004)

Foraging by herbivores also can alter habitats, influencing characteristics of forage plants and modifying cover and food resources for animals. Herbivores have both direct and indirect effects on the habitats in which they live and the plants on which they feed (Crawly 1983, Huntly and Reichman 1994). The most obvious effect is direct loss of foliage or root stock, which can have fitness consequences for forage plants. Some species exhibit responses to herbivory that include altered growth patterns. For example, compensatory growth and increased vigor were documented in bitterbrush (*Purshia tridentate*) under simulated winter browsing (Bilbrough and Richards 1993), and increased canopy volume of creosote bush (*Larrea tridentata*) was documented following

intense browsing by black-tailed jackrabbits (*Lepus californicus*; Roth et al. 2007). Other responses to herbivory include changes in plant morphology, altered nutritional content, and increased chemical and physical defense mechanisms following browsing events (Shiojiri and Karban 2006, Gowda 1997, Karban and Myers 1989, Agrawal 2000, McNaughton 1983). For example, in response to the selective foraging and removal of branches by beavers (*Castor Canadensis*), cottonwoods (*Populus fremonti*) developed a shrubby growth pattern and delayed sexual maturity (McGinley and Whitham 1985). This shrubby appearance often is a result of the production of suckers that exhibit juvenile characteristics, including increased levels of toxins (e.g., terpenes and phenolic resins), effectively deterring future browsing by herbivores (Reichardt et al. 1984, Bryant et al. 1985, Tahvanainen et al. 1985). Similar responses to herbivory have been documented for quaking aspen (*Populus tremoloides*), balsam poplar (*Populus balsamifera*), Alaska paper birch (*Betula resinifera*), green alder (*Alnus crispa*), and several willow species (*Salix* spp.; Basey et al. 1988, Bryant 1981, Tahvanainen et al. 1985, Reichardt et al. 1984).

One foraging strategy that is common among burrowing animals is central-place foraging, in which animals maximize energy consumption or delivery to a central place; this strategy is expected to influence vegetation to a greater extent around the central location (Andersson 1978, Schoener 1979, Orians and Pearson 1979, Killeen et al. 1981, McGinley and Whitham 1985, Elliot 1988). Many species have been identified as central-place foragers such as beavers (McGinley and Whitham 1985), white-fronted bee-eaters (Hegner 1982; *Merops bullockoides*), eastern chipmunks (Kramer and Nowell 1980; *Tamias striatus*), spider monkeys (Chapman et al. 1989; *Ateles geoffroyi*) and pikas

(McIntire and Hik 2005; *Ochotona* spp.), and all need to balance basic metabolic and nutritional requirements with the cost of traveling between habitat patches, relative quality of forage in patches, and predation risks associated with movement. Because animals are expected to use resources close to the central place more intensely, how long they occupy a central place might influence the suitability of cover and food resources available to the central-place forager and other, sympatric species. Additionally, many species that are considered central-place foragers also partake in burrowing activities, and therefore, the combination of these two habitat-altering behaviors has the potential to act in complementary or synergistic ways.

The pygmy rabbit (*Brachylagus idahoensis*) is a non-gregarious, semi-fossorial herbivore. As a dietary specialist, the pygmy rabbit lives in close association with relatively tall, dense stands of big sagebrush (*Artemisia tridentata*), and is often associated with mounded microtopography called 'mima-mounds'. Sagebrush provides essential nutrition comprising approximately 30 - 50% of the diet of pygmy rabbits during summer and > 90% during winter (Wilde 1978, Green and Flinders 1980, Thines et al. 2004). Sagebrush also is important for providing cover from predators and thermal extremes in the sage-steppe environment, and for providing locations for burrow excavation. Burrow systems of pygmy rabbits have a relatively simple structure (typically 2 - 4 entrances; Wilde 1978, Elias 2004). Rabbits usually occupy and maintain more than one system at a time, and use of burrows differs by season and sex (Green and Flinders 1980, Sanchez and Rachlow 2008). Because of these traits, pygmy rabbits have the potential to markedly influence the sage-steppe habitat through physical manipulation of the soil, mechanical alteration of the shrub community, and alteration of nutrient

availability through pellet deposition. Additionally, their burrow systems provide refuge for a variety of other sage-steppe species such as least chipmunks (*Tamias mimimus*), mountain cottontails (*Sylvilagus nuttallii*), ground squirrels (*Spermophilus* spp.), long-tailed weasels (*Mustela frenata*), and mice (*Peromyscus spp.*; Larrucea and Brussard 2009), as well as larger species that modify their burrow systems including badgers and black-tailed jackrabbits. Therefore, habitat alterations by pygmy rabbits could have implications for the species and the sage-steppe community in which they live.

Because sagebrush, which is relatively slow growing, is a primary component of the diet of pygmy rabbits, we expected that burrowing and foraging by rabbits might influence characteristics of the sagebrush vegetation, especially close to occupied burrow systems. Indeed, field observations suggest that rabbit occupancy often is associated with sagebrush on mima-mounds that show evidence of browsing, such as a decrease in sagebrush cover near ground level and a higher proportion of dead sagebrush around burrow systems. We hypothesized that foraging by rabbits results in altered vegetation cover and potentially, composition, and that the effects would be most pronounced near the center of the burrow system. We expected that burrow systems that have been occupied longer would exhibit greater evidence of browsing by rabbits, have less mature sagebrush, greater cover of disturbance-associated vegetation such as rabbitbrush, (*Chrysothamnus* spp.) and decreased recruitment of seedlings; consequently, we expected that those burrow systems would be more exposed. Additionally, if occupancy by rabbits does decrease sagebrush cover around burrow systems, then we predicted that long term occupancy might reduce suitability of burrow systems over time. This work provides the

first assessment of potential effects of burrowing and foraging by pygmy rabbits on the sagebrush communities in which they live.

METHODS

We conducted our research on two study sites, Cedar Gulch and Rocky Canyon, located in the Lemhi Valley of southeastern Idaho. The Lemhi Valley was characterized by sage-steppe vegetation with the dominant shrubs including Wyoming big sagebrush (*Artemisia tridentate* spp. *wyomingensis*), mountain big sagebrush (*A. t.* spp. *vaseyana*), and green rabbitbrush (*Chrysothamus viscidiflorus*). The understory was composed of a variety of forbs and grasses. Sites were separated by approximately 6 km of continuous sage-steppe habitat. Cedar Gulch was approximately 130 ha and characterized by patchily distributed vegetation that occurred on mima-mounds with little shrub or herbaceous cover between mounds. Rocky Canyon was approximately 80 ha and characterized by less patchily distributed vegetation, mima-mounds with taller sagebrush, and more continuous shrub and herbaceous cover among mounds. Rabbitbrush, a disturbance-associated species, was more prevalent on Rocky Canyon and relatively uncommon on Cedar Gulch (Sanchez 2007). Elevation for sites ranged from 1500 to 2400 m, and all sites were considered high desert sage-steppe ecosystems with < 30 cm of precipitation per year and average minimum and maximum temperatures ranging from -14.6°C to 27.9°C (Western Regional Data Center 2009).

We assessed how long burrow systems were occupied by pygmy rabbits based on data from censuses of burrow systems that were conducted on both study sites each autumn since 2002. We placed burrow systems into 3 categories: occupied for ≥ 6 years,

3-5 years, and 1-2 years. We also identified areas not occupied by rabbits or without presence of burrowing activity. Using images from the National Agricultural Imagery Program (NAIP) collected in 2006 and a GIS (ArcGIS 9.2, ESRI, Redlands, Colorado), we digitized all areas of dense sagebrush vegetation, most of which were associated with mima-mounds on our study sites. These were identified as potential sites for rabbit burrows. We overlaid the locations of burrow systems with the digitized potential sites to identify those areas of potential habitat without records of burrow systems over the last 7 years. We then selected a random sample of these unoccupied mounds at which to conduct vegetation measurements. Once in the field, we confirmed absence of burrowing activity on each mima-mound for all unoccupied sites and verified that classified burrow systems were still active (i.e., associated with fresh rabbit pellets indicating current or recent use).

Vegetation at occupied burrow systems and at potential, unoccupied sites was sampled during May-June of 2009. Because pygmy rabbit burrow systems often have more than one entrance, the center of burrow systems was defined as the center of the mima-mound, or in the absence of mima-mounds, by estimation of the geographic center of burrowing activity. We used the center of the mound or sagebrush clump for unoccupied sites. We selected a random direction and established two 4-m transects radiating in opposite directions out from the center of each mima-mound or burrow system. Along each transect, 4 1-m$^2$ quadrats were established (Figure 1), within which we measured 9 vegetation variables. These included live shrub cover (recorded using the line-intercept method; Canfield 1941), height of the tallest rooted shrub (not counting seed pods or inflorescence), height from the ground to the lowest live branch of a rooted

established shrub, and we enumerated all seedlings within the quadrant within 3

categories: < 5 cm, 5-10 cm, and 10-15 cm.  For seedlings, we also recorded evidence of

browsing.  We estimated the percentage of dead sagebrush and the percentage of browsed

sagebrush stems by visual assessment and consensus between two trained observers;

percentages were placed into categories of 0-5, 6-25, 26-50, 51-75, 76-95, and 96-100 %.

Browsing was estimated only within the bottom 50-cm of sagebrush because this is the

area within reach of an adult pygmy rabbit standing upright on its hind legs.  Clean,

angled cuts on current annual growth were used to identify lagomorph browsing on

sagebrush.

We measured visual obstruction (vertical cover) using a Robel pole in two

different ways (Robel et al. 1970).  First, we took a measurement across each quadrat

plot, reading the pole at a distance of 1 m and eye-height of 1 m (Quadrat-level visual

obstruction).  This measurement examined the pole at approximately a 45º angle,

simulating a view that might be characteristic of avian predators.  Next, we placed the

Robel pole in the center of the mound and took a reading at a standard distance of 4 m

along the transect line in each direction (Mound-level visual obstruction).  This

measurement simulated the view of potential terrestrial predators.  Finally, if the burrow

system or random site was located on a mima-mound, we recorded the distance from the

center to the edge of the mound along the transects in each direction (Figure 1).  These

boundaries were defined as the point along the transect where a distinct change in shrub

height was apparent and a gap of > 1 m between shrubs present.

We used multivariate analysis of variance (MANOVA) to test for differences in

vegetation characteristics among occupancy status categories ( $\geq$ 6yr, 3-5yr, 1-2yr, and

unoccupied) and distances from the center in 1-m increments (1 m, 2 m, 3 m, and 4 m).

We conducted a separate analysis for each study site because of observed differences

between sites in species composition of co-dominant shrubs.  Dependant variables for

both sites included visual obstruction, height to first live sagebrush, horizontal cover of

sagebrush, percent decadent sagebrush, and percent of sagebrush stems that were

browsed.  Additionally, we included cover of rabbitbrush as a dependent variable for the

Rocky Canyon site because it was a common disturbance-adapted species on that site and

we predicted that prevalence of rabbitbrush would increase with duration of occupancy.

We followed significant MANOVAs with univariate analysis of variance (ANOVA) to

evaluate the influence of occupancy and distance from the mound center on each

dependent variable.  We used Tukey's Honestly Significant Difference test (HSD) to

evaluate pairwise comparisons of least-square means.  We conducted a second

MANOVA on mound-level measures of visual obstruction and seedling counts to test for

differences across occupancy status for those variables. We pooled seedling data across

distance categories and seedling class for each site for this analysis.  We transformed data

before analysis when needed to ensure homoscedasticity and normal distributions (Zar

1999).  All analyses were conducted using SYSTAT 11 (Cranes Software International,

Chicago, IL) and $\alpha = 0.05$ was used to determine statistical significance.


RESULTS

We sampled vegetation at 103 burrow systems that differed in duration of

occupancy by pygmy rabbits.  On Cedar Gulch, we sampled 15 burrow systems from

each of the $\geq$ 6 yr, 1-2 yr, and unoccupied categories, and 14 burrows that had been

occupied for 3-5 years. On Rocky Canyon, we sampled 12 burrow systems from $\geq 6$ yr

and unoccupied categories, and 10 each from the 1-2 yr and 3-5 yr categories. Sample

sizes differed between the study sites because fewer known-status burrows were available

at the Rocky Canyon site. At that site, we sampled all burrows with known status that

fell within each category, and at Cedar Gulch, we randomly selected 15 burrows to

sample in each category except the 3-5 yr one for which we sampled all burrows.

Duration of occupancy by pygmy rabbits, but not distance from the center of a

burrow system significantly influenced the vegetation characteristics we measured. We

did not detect a significant interaction between occupancy status and distance for either

Cedar Gulch (Wilks' Lambda = 0.82, $F_{45,897}$ = 0.90, p = 0.666) or Rocky Canyon (Wilks'

Lambda = 0.75, $F_{54,779}$ = 0.82, p = 0.813), and therefore, we evaluated the main effects of

each. Although there was variation in mean values for some vegetation variables, we did

not detect a significant main effect of distance from the center of a burrow system on

either site (Cedar Gulch: Wilks' Lambda = 0.94, $F_{15,552}$ = 0.90, p = 0.569; Rocky Canyon:

Wilks' Lambda = 0.89, $F_{18,430}$ = 1.04, p = 0.417). Duration of occupancy by pygmy

rabbits, however, significantly influenced the vegetation at both sites (Cedar Gulch:

Wilks' Lambda = 0.81, $F_{15,552}$ = 3.01, p < 0.001; Rocky Canyon: Wilks' Lambda = 0.80,

$F_{18,430}$ = 2.02, p = 0.008).

Evidence of browsing on shrubs increased with duration of occupancy of burrow

systems by pygmy rabbits (Table 1). Across sites, browsing at all occupied burrow

systems ($\geq 6$ yr $\mu$ = 31.5%, 3-5 yr $\mu$ = 21.1%, and 1-2 yr $\mu$ = 15.7%) was 6.3 to 12.6

times more intense than levels documented on unoccupied sites ($\mu$ = 2.5%). Pair-wise

comparisons at both study sites revealed that percent browsing around burrows occupied

for ≥ 3 years was significantly greater than intensity of browsing on unoccupied sites and around burrow systems occupied for ≤ 2 years (Figure 2).

Structure of sagebrush and other vegetation around burrow systems also differed with duration of occupancy by rabbits. Height to first live shrub vegetation differed significantly across occupancy categories on the Cedar Gulch site (Table 1). Burrow systems occupied for ≥6yr (μ = 11.94 cm) had significantly less live vegetation near the ground than sites occupied for 1-2 yrs (μ = 4.8 cm) or unoccupied sites (μ = 3.4 cm; Figure 3). Additionally, both horizontal cover of sagebrush (Figure 4) and visual obstruction differed significantly across occupancy categories at the Rocky Canyon site (Table 1). Corrected pair-wise comparisons did not reveal statistically significant differences, however, sites occupied for a longer period (≥ 6 years) exhibited reduced sagebrush cover. Although not statistically significant, we noted the same pattern as on Cedar Gulch. Contrary to our expectations, burrow systems on Rocky Canyon occupied for ≥6 yr also had significantly greater visual obstruction (≥6yr μ = 28.5 cm vs. 3-5yr sites μ = 16.3 cm). This contradiction is potentially related to increased growth of rabbitbrush on long-occupied sites at Rocky Canyon. Although cover of rabbitbrush did not differ significantly in the ANOVA (Table 1), the mean values suggested increased growth of rabbitbrush around long-occupied burrow systems. Post hoc analysis revealed a significant negative correlation ($r$ = -0.351 p < 0.001) between cover of sagebrush and cover of rabbitbrush across all 44 occupied burrow systems measured at the Rocky Canyon study site.

Finally, variables examined only at the level of the burrow system, which included our second visual obstruction measurement (collected at the mound-level from a

4-m distance) and counts of seedlings, revealed marked variation with duration of

occupancy by rabbits.  The main effect of occupancy was significant for both Cedar

Gulch (Wilks' Lambda = 0.39, $F_{6,108} = 0.67.11$, p < 0.001) and Rocky Canyon (Wilks'

Lambda = 0.70, $F_{6,78} = 0.24.8$, p = 0.027).  This effect was attributed to differences in

seedling density, but not visual obstruction (Table 1).  Pair-wise comparisons revealed

that for Cedar Gulch, number of seedlings was significantly higher at burrow systems in

the $\geq$ 6yr category ($\mu$ = 146.2) than any other category, and that even occupancy for 3-5

years resulted in significantly more abundant seedlings ($\mu$ = 45.4)  than we documented

at recently occupied (1-2yr $\mu$ = 15.3) or unoccupied sites ($\mu$ = 18.4; Figure 5a).  Occupied

burrows at the Rocky Canyon study site also exhibited a trend of increased establishment

of seedlings around burrow systems occupied for longer durations, however, the pattern

differed somewhat (Figure 5).  Overall, however, the mean number of seedlings on

occupied mounds at Rocky Canyon was 4.8, which is <7% of the mean number on

occupied burrows (69.5) on the Cedar Gulch site, indicating that sagebrush recruitment in

general was markedly lower on Rocky Canyon.  Although we noted some browsing on

seedlings, the percentage of browsed seedlings pooled across sites was only 6.2%,

indicating that > 93% of seedlings exhibited no evidence of browsing.


DISCUSSION

        As hypothesized, foraging and burrowing behaviors of pygmy rabbits influenced

characteristics of the shrub community around occupied burrow systems at both of our

study sites.  These behaviors might alter succession of shrub species by opening canopy

cover and providing loose soil for seedling establishment. On Cedar Gulch, we observed

a higher number of sagebrush seedlings in association with burrow systems occupied for longer durations. Burrowing behavior of rabbits often creates mounds of loose soil or tailings outside the burrow entrance, an effect that was more pronounced around burrow systems with numerous and larger burrow entrances. These characteristics were associated with longer durations of occupancy of burrow systems; indeed, burrow systems that were occupied for many years often had a larger number of collapsed as well as open burrow entrances. The low incidence of browsing on sagebrush seedlings suggested that rabbits and other browsers avoided foraging on the seedlings (Bryant and Fox 1984). Thus, burrowing activity by pygmy rabbits might enhance establishment leading to successful recruitment of sagebrush seedlings around their burrow systems. Additionally, accumulation of feces around burrow openings and around heavily browsed sagebrush plants could enhance nutrient composition of soils in those areas, also contributing to favorable conditions for seedling establishment (Hobbie 1992, Bruun et al. 2005, Galvez et al. 2008). We had expected browsing, disturbance, and potentially trampling to decrease recruitment of sagebrush, however, our results supported the opposite trend.

Disturbance of the soil by burrowing pygmy rabbits likely removes existing herbaceous vegetation providing opportunities for seedling establishment, however, which species benefit from this disturbance might depend, in part, on the existing plant community. We documented a pattern on the Rocky Canyon site that was similar to the Cedar Gulch site with respect to seedling establishment around occupied rabbit burrows (Figure 5), but the number of sagebrush seedlings was dramatically lower on Rocky Canyon. One explanation for the marked difference in recruitment of sagebrush might be

the prevalence of rabbitbrush on that site.  Rabbitbrush is a seral species, which

establishes readily on repeatedly disturbed soils; in contrast, although most sagebrush

species also readily establish from seed, they are slow-growing shrubs that can take up to

10 years to reestablish after disturbances such as fire (Young and Evans 1974, Bunting et

al. 1987, Young et al. 1990, Colket 2003, Van Dyke and Darragh 2006).  The disturbance

of soil by burrowing activities coupled with browsing on mature sagebrush likely creates

microhabitat characteristics that increase opportunities for colonization by disturbance-

adapted species.  This pattern of growth was not consistent across sites because

rabbitbrush is uncommon on the Cedar Gulch site.  However, we did notice a trend of

increasing percent of dead sagebrush across mounds with increasing duration of

occupancy.  On Cedar Gulch, these open areas tended to be colonized by sagebrush

seedlings and often also prickly pear cactus (*Opuntia spp*.), another disturbance-adapted

species.  These observations suggest that disturbance by pygmy rabbits might interact

with the existing plant community to influence vegetation changes.  On sites where

disturbance-adapted species like rabbitbrush are common, this interaction might cause a

shift in species composition favoring disturbance-related species (Gibson 1989, Guo

1996, Kotliar et al. 1999, Eldridge 2004, Roth et al. 2007).

Contrary to our expectations, we did not observe significant changes in vegetation

structure and composition with distance from the center of the mound or burrow system.

Central-place foraging theory proposes that animals should maximize energy intake on

forage closest to their central location (Schoener 1979, Orians and Pearson 1979).

Additionally, as a prey species, pygmy rabbits must balance foraging and vigilance

behaviors.  Two factors likely influenced our ability to detect an effect of distance from

the center of the burrow system.  First, pygmy rabbits use more than one burrow system seasonally and even daily, and they often partake in burrow switching behaviors (Wilde 1978, Sanchez and Rachlow 2008).  Therefore, they likely follow more of a multiple central place foraging strategy (MCPF; Chapman et al. 1989) because they choose between limited numbers of central places.  This behavior could diminish effects at the center of any particular burrow system.  Also, because burrow systems often are associated with mima-mounds, and burrow systems usually have more than one entrance, the center of the mima-mound from which we measured might not represent the center of the burrow entrances.  On several mima-mounds, burrow entrances were located close to the edges or spread out across the mound.  These characteristics suggest that the influence of rabbits on vegetation is distributed more diffusely around occupied burrow systems rather than localized right outside of individual burrow entrances.

Because browsing consistently and significantly increased with duration of burrow occupancy by pygmy rabbits, their cumulative foraging activities might have implications for plant chemical and nutritional composition.  We observed browsed sagebrush that exhibited a stunted or shrubby appearance known as "hedging."   These hedged branches had high percentages browsed stems, as well as increased abundance of fresh, green ephemeral leaves.  Hedged branches likely provide decreased cover and may have higher concentrations of volatile chemicals produced by the plants to deter future foraging.  In addition, browsed sagebrush has the ability to stimulate herbivory resistance in neighboring shrubs via airborne cues. (Cook and Stoddard 1960, Karban et al. 2006, Shiojiri and Karban 2006).  Chemical defense mechanisms likely inhibit some herbivores, but their effect on browsing by pygmy rabbits is unknown.  Sagebrush is

naturally high in terpenes and is consumed in higher quantities by relatively few herbivores (e.g., sage grouse; *Centrocercus* spp., mule deer; *Odocoileus hemionus,* Pronghorn antelope, *Antilocarpa americana*), however, pygmy rabbits likely have developed adaptations that allow them minimize toxic effects while maximizing energy intake from sagebrush. Such relationships have been established for other herbivores that specialize on chemically defended plants including koalas (*Phascolarctos cinereus*) foraging on Eucalyptus (*Eucalyptus* spp.; Boyle et al. 2000) and the Stephen's woodrat (*Neotoma stephensi*) feeding on one-seed juniper (*Juniperus monosperma*; Sorenson et al 2004). Snowshoe hares (*Lepus americanus*) also show a tolerance for chemical compounds in their diet, and they choose forage based on nutritional value rather than levels of toxins (Wirsing and Murray 2002, Bryant 2003). Regardless, intensive herbivory on sites occupied by rabbits for longer periods of time might reduce nutritional quality of browse to the point that the effort required to consume and digest the forage of heavily browsed plants is not worth the reward and rabbits move to new patches of sagebrush.

Pygmy rabbits alter sagebrush habitat in ways that could affect themselves and other animal species. The decrease in ground-level sagebrush likely increases the visibility of rabbits to predators, especially on sites where there is little herbaceous vegetation, or during late in summer after grasses have senesced or been grazed. Increased visibility might require rabbits to spend more time vigilant and less time foraging. Vigilance behavior by chipmunks (*Tamias striatus*), which involved repetitive head-raising and pausing, was found to increase at the expense of time spent foraging when exposed to new patches (Trouilloud et al. 2004), however, adult degus (*Octodon*

*degus*) adjusted quality not quantity of vigilance behaviors, spending more time in bipedal stances when grass cover was high (Ebensperger and Hurtado 2005). These conflicting examples illustrate that although species responses to changes in cover can differ in regard to foraging and vigilance, there may be a cost associated with the loss of ground-level vegetative cover. Whether the observed decrease influences vigilance behavior, movements, or foraging behavior of pygmy rabbits was not tested directly in our study, but changes in vegetation structure resulting from rabbit activities could affect survival through increased exposure to predators, decreased time spent foraging, and possibly increased movement among burrow systems or foraging areas. In addition, decreases in ground-level vegetation could alter microhabitat characteristics, which might be more or less favorable for moderation of thermal extremes (Katzner and Parker 1997, Zollner et al. 2000, Bacigalupe et al. 2003).

As with many prey species, the pygmy rabbit must balance its needs for cover and food resources with its nutritional requirements (Sih 1980, Schmitz et al. 1992). A shift in shrub composition around occupied burrow systems towards rabbitbrush potentially alters the quality or quantity of cover resources around burrows. Loss of sagebrush also might reduce essential winter forage and require individuals to either move to other burrow systems or to spend more time traveling away from the burrows to meet their nutritional needs. Additional movement has implications for survival of rabbits because of increased metabolic costs and potential risk of mortality from increased exposure to predators (van Gils and Tijsen 2007, Litvaitis et al. 2008).

Long term occupancy might reduce the suitability of the burrow systems for rabbits and have fitness consequences for individuals by decreasing cover from predators

and thermal extremes, initiating increased toxin production in sagebrush, decreasing nutritional quality, and requiring more investment in vigilance behaviors and movement activities. Anecdotal evidence suggests that pygmy rabbits shift across the landscape, both regionally and locally. While analysis of these patterns is beyond the scope of this paper, we have demonstrated that pygmy rabbits have the potential to turn suitable burrow system locations into less suitable ones. Assuming that shrub cover, composition, and forage quality determine suitability of burrow systems, then rabbits occupying systems with decreased sagebrush resources might experience lower survival and/or reproduction, and they might need to forage farther from the burrow systems in order to meet energy needs. These factors combined might cause rabbits to abandon burrow systems and shift to new burrowing areas or for populations to shift to more suitable habitats over time.

We propose that the pygmy rabbit can be considered an ecosystem engineer for several reasons. First, they have the ability to markedly affect the physical architecture of the sagebrush shrub community through concentrated foraging activities around their burrow systems. Second, their burrowing activities appear to alter seedling recruitment and potentially, plant succession. Third, although not tested directly in our study, their burrowing activities likely alter soil properties such as water holding capacity and nutrient composition. Consequently, their behaviors likely affect the shrub and herbaceous plant community composition. In addition, burrows of pygmy rabbits provide refuge for several other animal species that do not dig their own burrow systems directly, and therefore, possibly play an important role in fitness of these species. Pygmy rabbits appear to fall into the category of ecosystem engineers that have large impacts

over geographically restricted areas (Jones et al. 1997). Their behaviors and presence likely play a key role in dynamics of the sage-steppe ecosystem as documented for other lagomorphs in other ecosystems (Krebs et al. 1995, Smith and Foggin 1999, Havstad et al. 1999, Delibes-Mateaus et al. 2007). Our study represents a first step in examining the fine-scale impacts of pygmy rabbits on the sage-steppe community, however, additional work is needed to more fully explore the impacts of their browsing on sagebrush nutrition and chemical composition, diet choices of pygmy rabbits in the wild, influences of soil properties on burrowing behavior of rabbits and growth of sagebrush, and additional fine-scale variables that might influence the shifting of burrow system use by pygmy rabbits.

## ACKNOWLEDGEMENTS

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Table 1. Results of univariate ANOVA tests for differences in vegetation characteristics around burrow systems of pygmy rabbits occupied for different durations (occupancy categories: 1-2 yr, 3-5 yr, $\geq$ 6 yr, and unoccupied). Measurements were collected at two sites (Cedar Gulch and Rocky Canyon) in eastcentral Idaho during May-June 2009.

| Variable | Cedar Gulch | | Rocky Canyon | |
|---|---|---|---|---|
| Quadrant-level: | $F_{3, 204}$ | p | $F_{3, 157}$ | p |
| Visual Obstruction* | 0.30 | 0.829 | 3.01 | 0.032 |
| Cover Sagebrush* | 1.50 | 0.217 | 3.00 | 0.032 |
| Cover Rabbitbrush | - | - | 0.82 | 0.487 |
| Height to Live* | 3.58 | 0.015 | 1.49 | 0.221 |
| Percent Decadent | 0.33 | 0.805 | 0.24 | 0.866 |
| Percent Browsed* | 8.02 | <0.001 | 4.43 | 0.005 |
| | | | | |
| Mound-level: | $F_{3, 55}$ | p | $F_{3, 40}$ | p |
| Visual Obstruction | 1.10 | 0.358 | 1.56 | 0.216 |
| Seedlings* | 25.06 | <0.001 | 4.10 | 0.013 |

* Indicates significance at $p < 0.05$ at one or both study sites.

Figure 1. Diagram of the sampling design for vegetation measurements collected on mima-mounds around pygmy rabbit burrow systems. The shaded area represents the mound or area of relatively dense sagebrush shrubs. Measurements were collected at 2 study sites in the Lemhi Valley, Idaho, during May-June 2009.
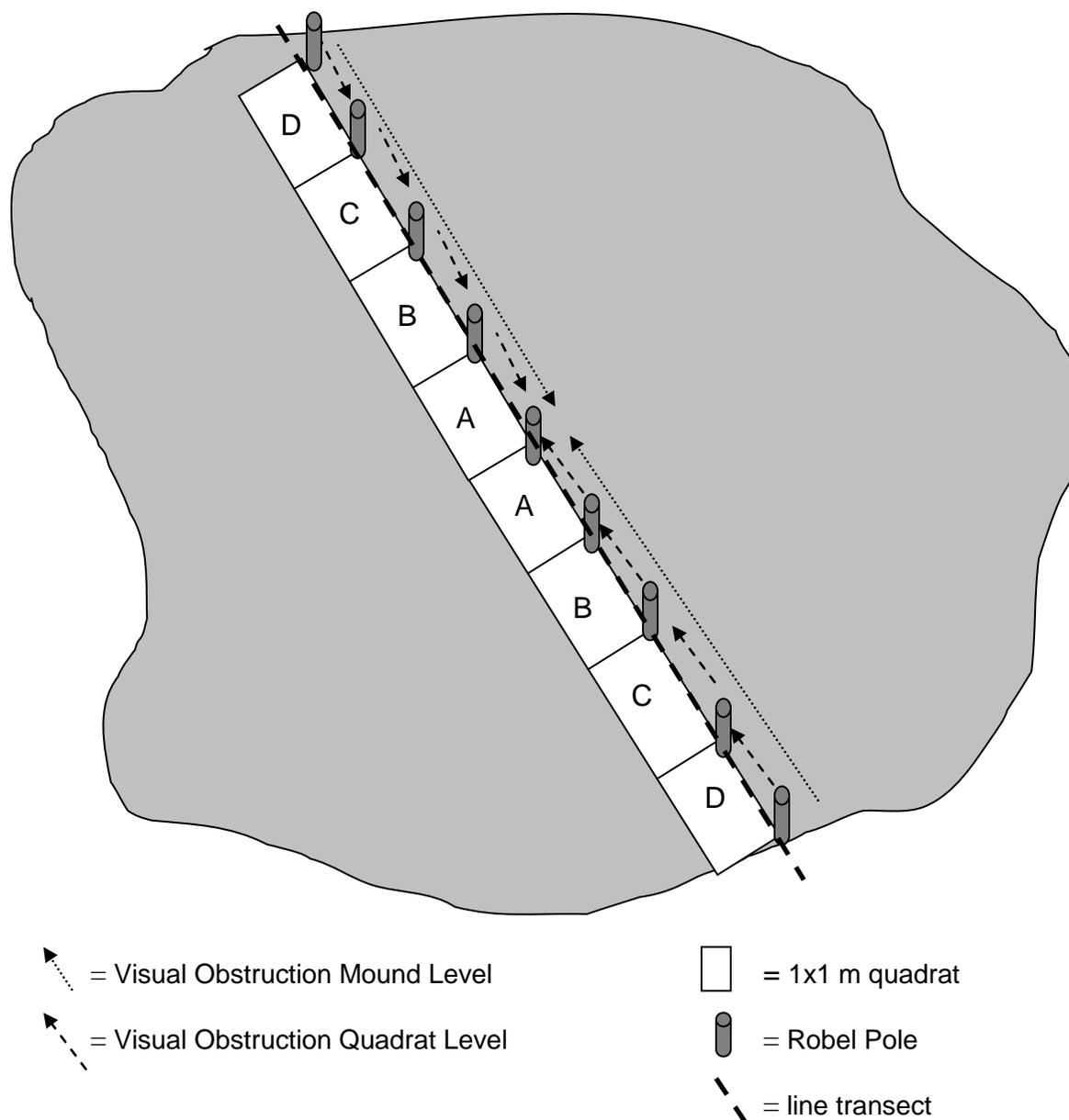
Figure 2. Percent (mean ±SE) of sagebrush stems within 50 cm of the ground that were browsed around burrow systems occupied for different durations by pygmy rabbits and on randomly selected unoccupied sites at the Cedar Gulch (a) and Rocky Canyon (b) study sites, Idaho.  Letters within graphs represent occupancy categories that were significantly different at the α = 0.05 level.
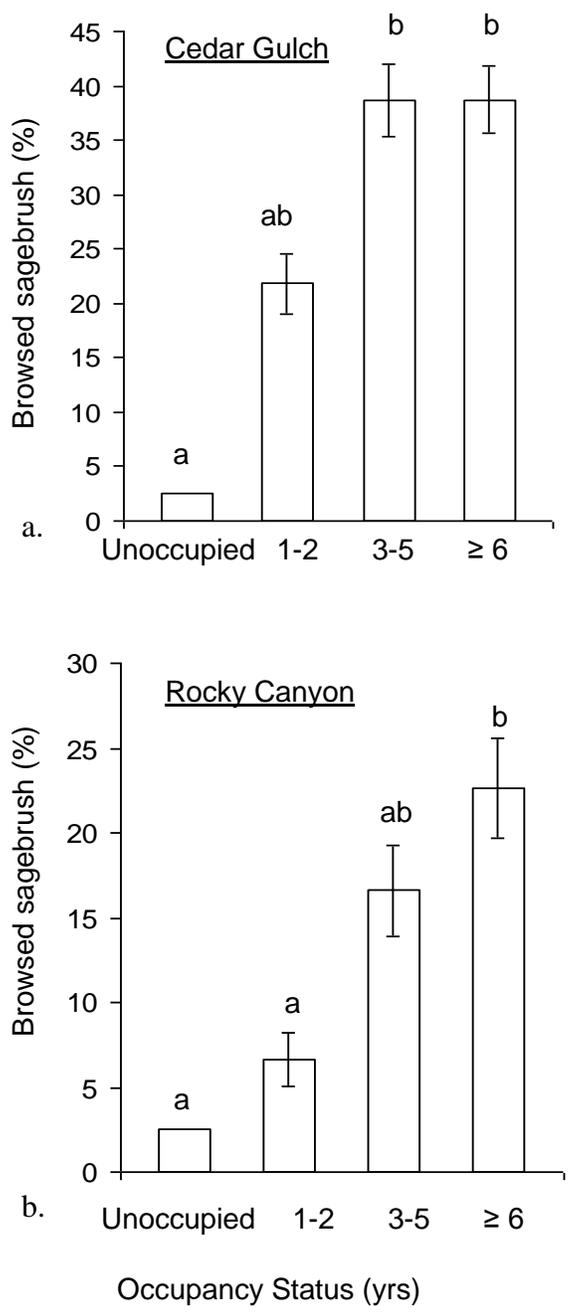
Figure 3. Height to first live sagebrush branch (mean ±SE) around burrow systems occupied for different durations by pygmy rabbits and on randomly selected unoccupied sites at the Cedar Gulch study site, Idaho. Letters represent occupancy categories that differ significantly at the $\alpha = 0.05$ level.
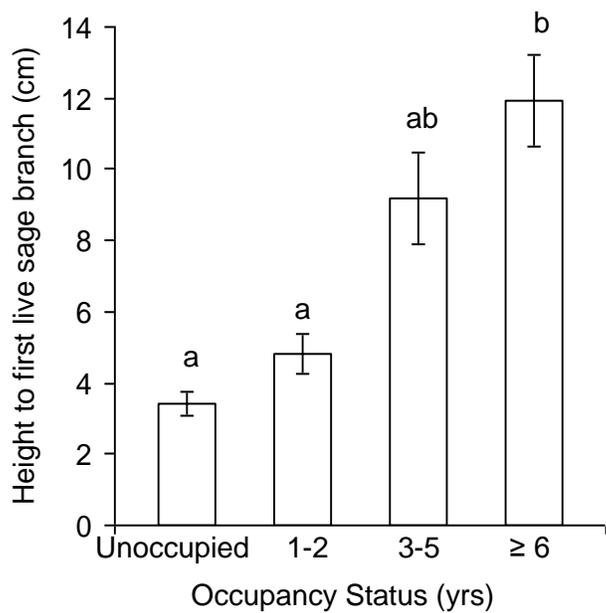
Figure 4. Percent cover of sagebrush (mean ±SE) across occupancy categories of pygmy

rabbit burrow systems for Rocky Canyon (a) and Cedar Gulch (b).  ANOVA results

indicated a significant differences among categories of occupancy status for Rocky

Canyon, but not for the Cedar Gulch site.  Letters within graphs represent occupancy

categories that were significantly different at the α  = 0.05 level.
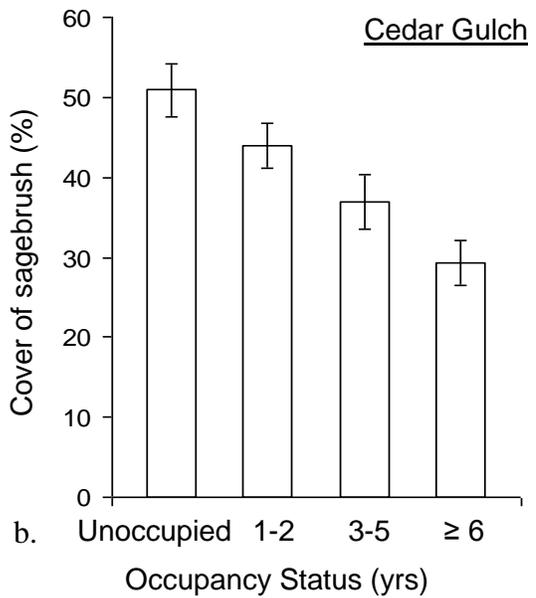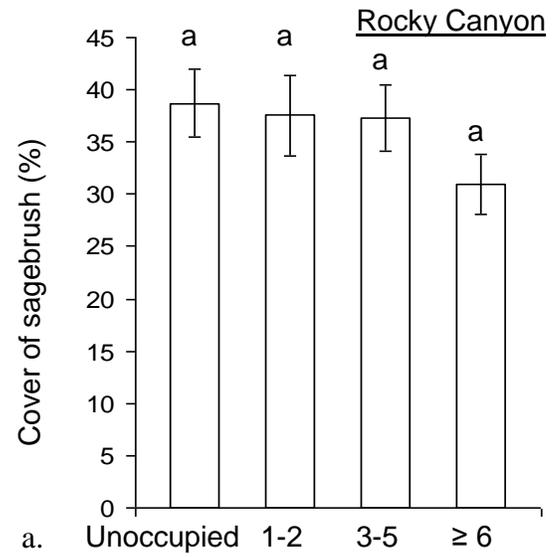
Figure 5. Number of seedlings (means ±SE) counted around burrow systems that differ in duration of occupancy at Rocky Canyon (a) and Cedar Gulch (b). Letters within graphs represent occupancy categories that were significantly different at the α = 0.05.
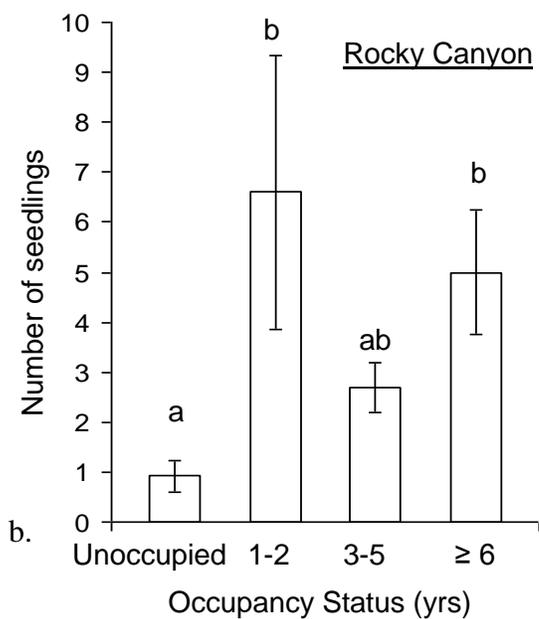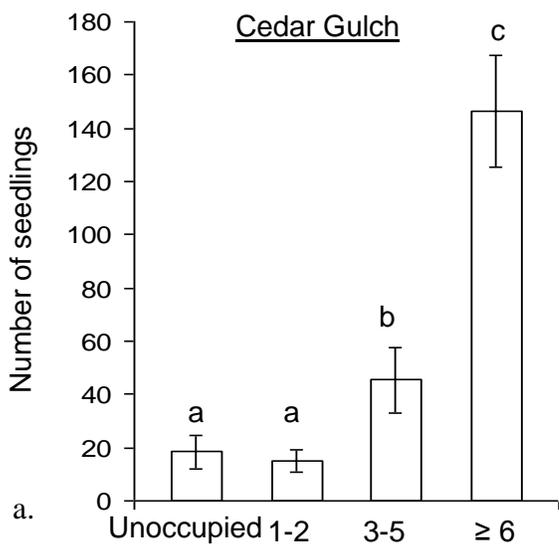
**CHAPTER 3:**


**Development of an Index of Abundance for Pygmy Rabbit Populations**

ABSTRACT

The pygmy rabbit (*Brachylagus idahoensis*) is a cryptic, burrowing lagomorph of

conservation concern for which an efficient method to monitor populations is needed for

conservation planning.  We developed an index of abundance based on density of active

burrow systems at 7 sites (57.2-118.5 ha) in eastcentral Idaho.  We conducted censuses of

burrow systems and used mark-resight surveys of 80 radio-collared individuals to

estimate density of rabbits.  At 5 sites, we also used a second method to estimate rabbit

numbers based on presence of tracks in snow around burrow systems.  We evaluated

patterns of burrow use by individuals and examined the relationship between vegetation

structure and density of rabbits.  Density of active burrow systems varied from 0.19 to

3.46/ha and density of rabbits ranged from 0.02 to 0.46/ha.  Number of burrow systems

used by individuals increased with density of available burrows, which supported a non-

linear relationship between abundance of burrows and rabbits.  Population density

increased curvilinearly with density of active burrows accounting for over three-quarters

of the variation ($r^2$=0.79) in population estimates across sites.  We documented a positive

relationship between visual obstruction of vegetation and density of rabbits across 6 of

the study sites.  These results suggested that density of burrows can serve as an index for

monitoring changes in abundance of pygmy rabbits in eastcentral Idaho and that this

index also might be useful for monitoring changes in relative abundance over time at

other locations. To assess abundance at larger spatial scales or across different regions, the index should be calibrated under regional conditions and site-level covariates should be evaluated.

INTRODUCTION

Estimating abundance and distribution of animal populations is a critical yet challenging component of wildlife science. Accurate estimates are essential to an understanding of the current status of species and population trends over time (Rosenberg et al. 1995). Many species, however, are either patchily distributed, uncommon, or elusive, or they occur at low densities that make traditional techniques for estimation of abundance infeasible (Bodkin and Udevitz 1999, McDonald et al. 1999, Williams et al. 2002). Additionally, although estimates of absolute abundance often are preferred, techniques required to obtain such estimates, for example mark-recapture surveys, can be time and resource-intensive and invasive; many also have underlying assumptions that are not practical for use across large areas or for estimating abundance of species that are cryptic or difficult to mark (Rosenberg et al. 1995, Sargeant et al. 2002, Ganey et al. 2004, Stanley and Royle 2005). Consequently, use of indices of abundance based on animal sign (scat, tracks, and burrows) have been developed and used extensively by wildlife professionals as tools for monitoring and estimating population densities for a wide variety of taxa (e.g. Mallick et al. 1997, Hubbs et al. 2000, Karels et al. 2004). Such indices can be important for gathering baseline demographic data needed to understand population trends, both temporally and spatially (Engeman 2005).

Burrow entrances can provide evidence of occupancy by fossorial and semi-fossorial species. Counts of burrow entrances also have been used to estimate abundance for several obligate burrowing species, including ground squirrels (*Spermophilus townsendii*; Van Horne et al. 1997, *Spermophilus columbianus*; Weddel 1989, prairie dogs *(Cynomys ludovicianus;* Biggins et al. 1993, Powell et al. 1994, Severson and Plumb 1998, Johnson and Collinge 2004)*, kangaroo rats *(Dipodomys stephensi;* O'Farrel 1992, Brock and Kelt 2004)*, pocket gophers *(Thomomys talpoides;* Reid et al. 1966)*, European rabbits *(Oryctolagus cuniculus;* Parer and Wood 1986, Palomares 2001, Ballinger and Morgan 2002)*, badgers *(Meles meles;* Wilson et al. 2003)*, and gopher tortoises (*Gopherus polyphemus;* Breininger et al. 1991). Several studies have documented positive and significant relationships between burrow counts and species abundance (Parer 1982, O'Farrel 1992, Biggins et al. 1993, Vreeling and Tietje 1999, Ballinger and Morgan 2002, Johnson and Collinge 2004), while others identified no significant relationship between the two parameters (Powell et al. 1994, Van Horne et al. 1997, Severson and Plumb 1998, Palomares 2002). While controversy exists over the applicability of burrow counts as indicators of abundance for burrowing species, most researchers agree that the relationships are variable.

Usefulness of burrow counts for indexing abundance relies on multiple factors. The spatial scale of the study can be important. For example, Johnson and Collinge (2004) and Biggins et al. (1993) reported a positive relationship between burrow entrances and number of prairie dogs at relatively large spatial scales (22-39 colonies), while Severson and Plumb (1998) and Powell et al. (1994) did not find a significant relationship between the two when examined at smaller spatial scales (5-12 colonies).

The objectives of the study (e.g. long or short term monitoring, population trend analysis, habitat suitability), level of precision needed, scope of inference, and resources available to conduct surveys all can influence the efficacy of burrow counts as indices of abundance. In addition, the burrowing and social behavior of the species in question (gregarious, solitary, use of one or many burrows, seasonal changes in burrow use or movement patterns) can add variability to relationships between burrows and populations (Palomares 2001, Biggins et al. 2006). In studies of European rabbits, Parer and Wood (1986) documented a significant relationship between warren counts and rabbit numbers in Wales, but only during the non-breeding season. In contrast, Ballinger and Morgan (2002) identified a significant relationship between burrow counts and rabbit numbers in Australia, but they did not report an influence of the breeding season, perhaps because climatic conditions of that region allow for a longer and more variable breeding season. Biologists must carefully consider the best way to index abundance based on the natural history of a species, research needs, and available resources.

The pygmy rabbit (*Brachylagus idahoensis)* is an uncommon and cryptic species for which neither distribution nor abundance are comprehensively documented across much of their range. As a dietary specialist, the pygmy rabbit lives in close association with tall dense stands of big sagebrush (*Artemisia tridentata*), which provides essential forage and cover. The pygmy rabbit is one of only 2 North American rabbits known to dig and use residential burrows, and it is considered a solitary, semifossorial species (Green and Flinders 1980). Although multiple pygmy rabbits are rarely observed together at burrow systems, individuals use more than one system and often participate in burrow switching throughout the year (Wilde 1978, Sanchez and Rachlow 2008). The

geographic range of the species spans most of the Great Basin and surrounding intermountain areas (Green and Flinders 1980, Wiess and Verts 1984, Rachlow and Svancara 2006). However, there is concern about the status of the species throughout this range because of their patchy distribution and dependence on declining sagebrush-steppe habitats (Weiss and Verts 1984, Rauscher 1997, Rachlow and Svancara 2006).

Interest in the pygmy rabbit has increased since the Columbia Basin population in Washington was listed in 2003 as a distinct population segment under the Endangered Species Act (ESA; Federal Register 2003). In 2005, the United States Fish and Wildlife Service (USFWS) rejected a petition for ESA listing for the entire species, in part because insufficient information on abundance and population trends was available (Federal Register 2005). Presently, the USFWS is reconsidering the petition in response to a perceived decline across the species range (Federal Register 2008). These petitions have spurred researchers and managers to place a high priority on developing a consistent method to survey the species across its range. Because pygmy rabbits are obligate burrowers, a calibrated index of burrow density and activity might provide an efficient method to acquire baseline estimates of pygmy rabbit distribution and abundance (Oliver 2004, Sanchez et al. *in press*)

The goal of our research was to evaluate use of burrow systems as an index of abundance of pygmy rabbits. We estimated population densities using mark-resight techniques and evaluated the relationship between population densities and burrow densities. We hypothesized that density of rabbits would be positively related to density of active burrow systems because this species uses residential burrows throughout the year. We also examined use of burrow systems by individuals. We expected that

individual rabbits would use a consistent number of burrow systems within a season, and we tested whether number of burrow systems used varied with density of available burrow systems. Finally, we asked whether density of rabbits was correlated with vegetation characteristics across study sites. Because sagebrush is a primary source of both food and cover for this species (Wilde 1978, Green and Flinders 1980, Wiess and Verts 1984), we expected that study areas with greater shrub cover might support greater densities of pygmy rabbits, and we used our estimates of abundance to evaluate the relationship between vegetation cover and abundance. This work provides the first examination of the relationship between density of pygmy rabbits and their burrow systems, and evaluates a potential management tool for monitoring this species of conservation concern.

METHODS

We delineated 7 sites for this study in southeastern Idaho. Sites were selected to cover a range of rabbit and burrow densities. Six sites were located in the Lemhi Valley along the Montana border and one site was located on the southern end of the Idaho National Laboratory (INL). Most sites were approximately 100 ha (range 57.2-105.7 ha). Five of the sites in the Lemhi Valley were located along the base of the Beaverhead mountain range on the northeast side of the valley and spanned a total distance of 16 km, and one site was located at the base of the Lemhi Range on the southwest side of the valley (Figure 1). All sites were characterized by the presence of mounded micro-topography called mima-mounds that support relatively tall, dense clumps of sagebrush, and most sites also included patches of more continuous sagebrush cover. The primary

vegetation component for all sites was Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), with varying degrees of other sagebrush species such as low sagebrush (*A. arbuscula*), black sagebrush (*A. nova*), and three-tip sagebrush (*A. tripartita*). Sites also varied in apparent amount of herbaceous cover, bare ground, and distance between mima-mounds. Elevation for sites ranged from 1500 to 2400 m, and all sites were considered high desert sage-steppe ecosystems with < 30 cm of precipitation per year with average annual temperatures ranging from -4.8°C to 12.8°C (Western Regional Data Center 2009). Three additional lagomorph species, black-tailed jackrabbits (*Lepus californicus*), white-tailed jackrabbits (*Lepus townsendii*), and mountain cottontails (*Sylvilagus nuttalli*), also occurred infrequently on the study sites.

We censused burrow systems during September of 2007 and 2008. For each burrow system we recorded the location using handheld global positioning system (GPS) units, counted number of entrances to the burrow system, and evaluated the activity status. Activity was categorized based on criteria modified from Roberts (2001), which places systems into 4 categories: active, recently active, old, and very old (Sanchez et al. *in press*). Active burrow systems were associated with fresh pellets and open burrow entrances and represented burrows that had been used during the previous year. Recently active burrows had weathered pellets that were distinguishable by their faded color. Old burrows had open entrances but no pellets present, and very old burrow systems also had no pellets but the burrow entrances were partially collapsed (Sanchez et al. *in press*). We chose to conduct burrow censuses in September because movements of pygmy rabbits are more restricted and there is less overlap in pellet sizes between juvenile cottontails and adult pygmy rabbits than during the breeding season (Sanchez et al. *in press*). At burrow

systems associated with pellets of an intermediate size for which species identification was unclear, we collected pellets for DNA testing to verify species. We also collected a sample of pellets from active pygmy rabbit burrows for species validation purposes. Censuses were completed by 4-8 observers using GPS units as guides to walk in parallel on transect belts that were 25-50 m wide. To ensure a complete census and consistency of burrow system classification, observers were trained offsite before conducting the censuses. Additionally, in areas with denser sagebrush, more time was spent searching for burrows and in areas of continuous sage, width of transects was decreased to aid in thorough coverage of the area. Burrow census counts were compiled and transformed into estimates of burrow density within each activity status category on each site.

We trapped rabbits from September to November of 2007 and 2008. Trapping lasted from 4 to14 days per site and rabbits were trapped using Tomahawk live traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin) placed in burrow entrances where rabbits were observed. We collected standard mammalian measurements (body mass, hind foot length, ear length), recorded sex, fitted each adult with a 5-g radio collar with an external antennae (Holohill Inc., Toronto), and implanted each with a uniquely numbered Passive Integrated Transmitter (PIT). Rabbits were tracked 1-2 days post collaring to ensure proper collar fit and condition of the rabbit. Radio-collars had a maximum battery life of 6 months, and collars were removed prior to battery failure. Radio-collars served as marks for the mark-resight surveys and also facilitated locating individuals after resighting surveys were completed. All procedures were approved by the University of Idaho Animal Care and Use Committee (Protocol # 2007-23) and were

in compliance with recommendations of the American Society of Mammalogists for use of wild mammals in research (Gannon et al. 2007).

We used mark-resight techniques to estimate population sizes on 4 of our higher density sites. Because pygmy rabbits often remain close to burrow systems, we used maps of burrow systems created during the burrow censuses and GPS units to navigate to all burrow systems categorized as active or recently active to maximize resight probabilities. We avoided conducting surveys on days with extreme weather conditions such as high wind, heavy snow or rain, because these conditions likely influence behavior of rabbits and consequently, probabilities of resighting individuals. To eliminate a potential bias associated with time of day, starting locations for each resight survey were randomly chosen at each study site. Observers then began walking to all active and recently active burrow systems navigating to the closest systems first and extending out from the starting location to search all burrow systems in those categories. We did not follow systematic search paths, but rather, covered the area in a different order with each resight survey. When an animal was sighted, we recorded: 1) the presence of a mark (collar) using a scanning telemetry receiver; 2) GPS location of the sighted rabbit; and 3) confirmed survival. Occasion-specific conditions were assessed at the start of each resighting survey from the center of the study site; these included weather (categories: rain, snow, sunny, overcast), temperature, snow cover (4 cover classes: 0, <2.45 cm, 2.54-12.7 cm, > 12.7 cm), and wind (categorized into 5 classes: 0 = calm, 1 = gentle breeze, 2 = moderate breeze, 3 = strong breeze, 4 = gale; modified Beauford scale; Huler 2004). After completing resight surveys, we located all collared animals that were not

detected during the resight event to determine whether they were within the boundaries of the study site during the resighting survey.

Resight histories were analyzed using mixed logit-normal resight models (McClintock 2008) and an AIC model selection approach in Program MARK (White and Burnham 1999). This modeling framework assumes that rabbits are individually marked, sampling is conducted with replacement, and the population in each study site is demographically closed. A set of 6 models were chosen *a priori* for the analysis; variables assessed for their potential influence on resight probabilities included time, individual heterogeneity, and wind strength. Individual heterogeneity was measured mathematically from capture histories of individual collared rabbits. Snow cover and ambient temperatures were measured in the field but not included in *a priori* models because of limited variability. Wind remained in the model set because it has been shown to negatively influence emergence of other lagomorh species, and therefore, potentially influences the sightability of pygmy rabbits (Ballinger and Morgan 2002, W. Estes-Zumpf *per. comm.*). We did not assess influence of site-level characteristics (e.g., vegetation cover) on resight probabilities because the models were constructed independently for each study site. Model averaging across all models with weight of evidence ($w_i>0$) was used to calculate abundance estimates and resight probabilities (Burnham and Anderson 2002). This process incorporates model uncertainty into the final parameter estimates.

A second method was used to estimate abundance based on snow-track surveys on 3 of our low density sites and 2 higher density sites. We surveyed all active and recently active burrow systems < 1 day after snowfall to document signs of rabbit

activity.  Pygmy rabbits are diligent about cleaning debris and snow away from entrances of occupied burrow systems and therefore, current occupancy of a burrow system can be assessed.  Surveys were not completed during snowfall or if more than 1 day had passed since snowfall had ended.  A pilot study in the Lemhi Valley documented that this method was both practical and accurate for evaluating burrow occupancy, however, the track surveys need to be completed shortly after a snowfall and before rabbits begin moving among burrow systems.  Observers used maps and GPS units to navigate to all active and recently active burrow systems and recorded presence of recent digging in snow at burrow entrances.  If sign was present, radio frequencies were scanned to determine whether the burrow system was occupied by a collared or uncollared rabbit. After completing completion of the track survey, we radio-tracked all remaining collared rabbits to identify whether they were within the study site during the survey but had not been detected, or whether they had moved off of the study site.  Data on collared rabbits also were used to evaluate the probability of detection and we used the proportion of collared rabbits to adjust our estimate for uncollared rabbits that might not have been counted during surveys because they had not emerged from burrows or were occupying burrow systems categorized as old or very old, or one that was not identified during the burrow census.  Snow-tracking was completed 2-3 times per site for the 3 low density sites to estimate abundance.  We calculated an abundance estimates for each survey occasion and used the largest to provide an abundance estimate for each site.  In addition, we conducted snow-track surveys 1 time per site for 2 of the high density sites (Cedar Gulch and Rocky Canyon) to provide a qualitative comparison to abundance estimates determined via mark-resight techniques.

We evaluated spatial distribution of burrow systems and patterns of burrow system use by rabbits at each study site to test the assumption that rabbits used the same number of burrow systems across the landscape. A subset of telemetry data were collected from mark-resight surveys and standardized for 6-7 locations per 3-week time period for each rabbit. To assess burrow use, we evaluated the number of burrow systems occupied by an individual during the 3-week period. To estimate the number of burrow systems available to each individual rabbit, we calculated the geometric center of the telemetry locations for each individual,placed a 100-m buffer around that location in a GIS (ArcGIS 9.2, ESRI, Redlands, CA), and counted the number of active burrows within the buffer. We used linear regression to evaluate the relationship between burrow use and density of available active burrow systems. If the number of burrow systems used by individuals varied with density of available burrows, then the relationship between rabbit density and burrow density would be non-linear.

Using information from burrow censuses and abundance estimation, we calibrated the index of abundance. Model averaged abundance estimates for each site were transformed into density estimates for each site. We then used regression analysis to test the relationship between density of rabbits and density of active burrow systems across our 7 sites. We only included density of active burrow systems in the analysis because these systems reflect the most current and reliable information about rabbit activity. To determine whether a linear or curvilinear regression was appropriate, we used the results from our analysis of burrow use across burrow densities. All analyses were conducted using SYSTAT 11 (Cranes Software International, Chicago, IL) and $\alpha = 0.05$ was used to determine statistical significance.

We measured shrub cover and visual obstruction at all sites in the Lemhi Valley to evaluate whether those vegetation characteristics might influence density of rabbits on a site. Ten random locations were selected within each study site, from which we ran 50-m transects in a random directions. Cover was measured using the line-intercept method (Canfield 1941), and visual obstruction was measured using a Robel pole (Robel et al. 1970) at 3 locations (0 m, 25 m, and 50 m), which were then averaged for a total of 10 obstruction measurements per site. We used multivariate analysis of variance (MANOVA) and Tukey's Honestly Significant Difference test (HSD) to test for site differences in estimates of cover (arcsine-square root transformed) and visual obstruction. Finally, we performed linear regression to test for an influence of vegetation on rabbit density.

RESULTS

Systematic burrow censuses yielded density estimates that differed markedly across study sites. Number of active burrows ranged from 23 to 198 burrows, which corresponded to densities of 0.19 to 3.46 burrow systems/ha (Table 1). All samples of pellets that we could identify to species using DNA analysis (n=37) were identified as pygmy rabbit pellets. We were unable to confirm the species for 12 samples because of insufficient quantity or quality of DNA available from the pellet sample (L. Waites, *unpub data*).

We captured 1 to 24 rabbits per site for a total of 80 individuals that were collared over 2 seasons (Table 2). Of those, 43 were females and 37 were males, with fairly even sex ratios on each study site (Table 2). No mortalities occurred from trapping, however,

8 rabbits died before the resighting surveys began, and were not included in the mark-resight analyses.  Three others died between resight occasions therefore were not included in analysis.

Resight occasions were conducted every 1 to 3 days depending on year and site.  During 2007, a total of 5 resight occasions were conducted on 3 sites (Rocky Canyon, Atomic City, and Cedar Gulch).  In 2008, resight effort was increased due to the availability of additional resources.  A total of 18 resight occasions were completed on Middle, 19 on Warm Springs, and 8 each on Ten Mile and Bull Creek.  Numbers of rabbits sighted during surveys varied markedly among study sites.  Percentages of collared animals that were resighted per occasion ranged from 0 to 87%, with total sightings of rabbits (both collared and uncollared) ranging from 1 to 161 across study sites (Table 2).

Models predicting abundance of pygmy rabbits from our 4 higher density sites (Cedar Gulch, Rocky Canyon, Middle, and Warm Springs) revealed that no single model was the top model across all sites.  For each site, only 1 or 2 models had most of the model weight indicating low model uncertainty (Table 3), however, those models were not consistent across the study sites.  The best models ($< 2 \Delta AIC$) for Middle and Warm Springs sites indicated that the probability of resighting individuals varied across resight occasions, however, top models for Cedar Gulch and Rocky Canyon did not support time effects on resight probabilities (Table 3).  Additionally, there was some support for the influence of individual heterogeneity on resight probabilities on the Middle and Cedar Gulch sites (Table 3).  Contrary to our expectations, wind was not an influential factor in resighting pygmy rabbits in the field.  The 95% confidence intervals

of mean resighting probabilities overlapped among all sites (Figure 2), which suggested

that site-level variables did not markedly influence resighting probabilities, or did not do

so in a consistent manner.

Model averaged abundance estimates varied in level of confidence. Estimates

were 24.5 rabbits (SE = 0.97) for the Middle study area, 24.6 (4.12) for Cedar Gulch,

24.9 (4.97) for Rocky Canyon, and 26.2 (2.76) for Warm Springs. The width of 95%

confidence intervals for the estimates varied from 1.9 to 9.7 rabbits. The Middle study

site had the narrowest confidence intervals (22.6-26.4), followed by Warm Springs (20.8

– 31.6), Cedar Gulch (16.6 – 32.7), and Rocky Canyon (15.2 – 34.6).

On the 3 low density sites, we used snow-track surveys to estimate abundances

because densities were so low that the mark-resight methods were not feasible. Three

surveys were completed on both Bull Creek (maximum estimate = 3 rabbits) and Ten

Mile (maximum estimate = 5 rabbits), and 2 surveys were conducted on the Atomic City

site (maximum estimate = 13 rabbits). During the surveys, collared rabbits that were

onsite were always detected via sign at active or recently active burrows; therefore, we

had a 100% detection rate and did not apply correction factors for detectability.

We also completed snow-track surveys on 2 of the higher density sites, Cedar

Gulch and Rocky Canyon, which provide qualitative comparisons to abundance estimates

based on mark-resight analyses. Rabbits were always detected if they were present at a

surveyed burrow (i.e., all burrows in the active and recently active categories). However,

a few of the collared rabbits (n=2) were tracked to old, very old, or unidentified burrows,

and therefore, were not counted during snow surveys. We used the proportion of collared

rabbits missed during surveys (0.11-0.14) as a correction factor to account for uncollared

rabbits that might not have been counted because they occupied unsurveyed burrows. The count of uncollared rabbits was increased by an equivalent proportion. The corrected population estimate for Cedar Gulch was 21.9 rabbits and for Rocky Canyon, the estimate was 29.2 rabbits. These values were within 12-16% of the mark-resight abundance estimates (within 3-4 individuals), and were contained within the confidence intervals for those estimates, which suggests that the two estimation methods produced comparable results.

Number of burrows used by individual rabbits was variable. Collared rabbits used from 1 to 6 different burrow systems during the 3-week period when resight surveys were conducted. Active burrow systems available within a 100-m radius of the center of each animal's activity varied from 1 to 21 burrow systems. Regression analysis revealed a significant relationship between the number of burrows used by an individual and the density of active burrows available for use ($r^2 = 0.54$, Figure 3). As the density of burrows increased, individuals used more burrow systems.

Estimates of rabbit density differed markedly across our study sites. Estimates ranged from a low of 0.02 rabbits/ha for Bull Creek to a high of 0.46 rabbits/ha for Warm Springs (Table 5). Linear regression analysis documented a significant positive relationship between rabbit density and burrow density ($y = 0.117x + 0.082$, $r^2 = 0.69$, $p = 0.021$). However, because the analysis of burrow use revealed a significant positive relationship between the number of burrow systems used per individual and the density of available burrow systems, we fitted a curvilinear relationship for the density of rabbits against density of burrows. A log regression of these data resulted in substantial

improvement of fit (Figure 4). The regression revealed that rabbit density increased at a slower rate as burrow density increased.

Our measurements of vegetation identified differences across sites in availability of shrub resources for rabbits. Sites differed in both percent cover (F = 4.03, p = 0.004) and visual obstruction (F = 2.99, $p$ = 0.019, Table 4). Percent cover of shrubs was significantly different between Rocky Canyon and Ten Mile ($p$ = 0.002), and between Rocky Canyon and Bull Creek ($p$ = 0.02), but not among any other sites (Figure 5). Although visual obstruction differed overall, pairwise tests did not identify significant differences among sites. Even though our study sites differed only moderately in vegetation characteristics, there was some support that rabbit abundances might be related to differences in vegetation structure across our study sites. Mean rabbit density was positively correlated with visual obstruction, although the relationship was marginally non-significant across the 6 sites for which we had vegetation data ($r$ = 0.80, $p$ = 0.056). In contrast, no such relationship was supported between rabbit density and horizontal shrub cover ($r$ = 0.17, $p$ = 0.756).

DISCUSSION

Our results revealed a significant positive relationship between the density of active burrows and the density of pygmy rabbits. Contrary to our expectations, however, numbers of burrow systems used by individuals varied with the density of available burrow systems. At higher burrow system densities, rabbits occupied more burrow systems. Other studies also documented variability in number of burrow systems used by individual pygmy rabbits, although density of available burrows was not evaluated

(Sanchez and Rachlow 2008, Crawford 2008). Because rabbits used a different number of burrow systems as the density of available burrow systems changed, a non-linear index of abundance best described the rabbit to burrow relationship. Similar non-linear relationships between burrow systems and animal numbers were noted by Reid et al. (1966) for pocket gophers (*Thomomys talpoides*) and by Lisicka et al. (2007) for the common vole (*Microtus arvalis*).

The utility of an index of abundance is influenced by the methods used to develop and calibrate it (Caughley 1966, Williams et al 2002). For our study, we used mark-resight techniques as one method to estimate absolute abundance to calibrate the index. Mark-resight techniques produce robust estimators of abundance when model assumptions are met (White and Burnham 1999). Additionally, because mark-resight methods require that animals only be captured once, they are useful for species that are difficult to trap and they are less invasive than traditional mark-recapture methods (Krebs 1999). Mark-resight estimators have been used for many species ranging from Eurasian badgers (*Meles meles*; Tuyttens et al. 1999) to prairie chickens (*Tymparuchus cupido pinnatus*; Clifton and Krements 2006) to bighorn sheep (*Ovis canadensis canadensis*; McClintock and White 2007). The logit-normal modeling approach that we used enabled us to meet modeling assumptions because the number of animals marked in the population was known, and heterogeneity models allowed demographic closure to be violated via mortality independent of mark status (McClintock 2008). Our modeling approach also allowed incorporation of individual and event-level covariates such as individual heterogeneity and wind strength.

Our analysis revealed similar resight probabilities across the study sites. We had expected that increased wind strength would decrease resight probabilities. Wind has been shown to influence emergence behavior of European rabbits (Ballinger and Morgan 2002), but did not appear to influence this behavior in pygmy rabbits enough to suppress our ability to resight animals during our surveys. However, we did not conduct resights on extremely windy days and consequently, the variation in wind strength experienced during our field surveys might not have been marked enough to detect differences with our models. Additionally, because vegetation was a site-level variable rather than an event-level covariate, it could not be included in the modeling of resight probabilities. We did not test for an influence of vegetation on resight probabilities across sites because these probabilities did not differ among our study sites. Nonetheless, dense shrub cover and strong winds might reduce visibility of rabbits during field surveys.

Snow-track surveys can serve as an alternative method to estimate abundance of pygmy rabbits. Comparison of estimates from mark-resight modeling and snow-track abundance calculations produced similar results for 2 moderate-density sites. Advantages of the snow-track technique are that it provides extremely high detection rates, and it is applicable on sites with low densities of rabbits where encounter rates might be too low for calculation of abundance using mark-resight modeling. This method can be challenging, however, because it is weather-dependant and requires prior censuses of burrows for identification of active and recently active systems.

We offer some caveats associated with the index we developed for estimating pygmy rabbit abundance based on burrow systems. First, although we succeeded in sampling across a spectrum of rabbit densities, we recognize that there is a gap in our

data between the moderate-density sites and our highest density site. Consequently, the Warm Springs site has a large effect on the regression that defines the index. Previous surveys for pygmy rabbits conducted throughout Lemhi and Custer Counties, Idaho, during the late 1990s noted an apparent high density of rabbits in the Warm Springs area, which suggests that this site has supported robust rabbit populations for almost a decade (Roberts 2001). Therefore, our high population estimates for this site are not anomalous or unexpected. Nonetheless, future studies in the region that evaluate abundance on other sites with relatively high densities could be used to fill in the gap in our regression and test the relationship at intermediate population densities.

A second caveat relates to the classification of activity status of burrow systems. Because the index is based on counts of active burrow systems, which are determined by the presence of fresh fecal pellets, density of active burrow systems likely reflects the population that has recently resided on the site, not necessarily the immediate number. Sanchez et al. (*in press*) documented that although pygmy rabbit pellets persisted for 24-36 months, pellets retained their appearance of "fresh" for a much shorter duration of time. Their work suggested that burrows classified as active during the autumn were used by rabbits during the current calendar year. Because that period would include both the breeding season (April – August) and periods of mortality following breeding, the relationship between density of active burrows and population abundance during autumn could vary across sites or years. Also, because pygmy rabbits are a prey species and can experience high rates of mortality (Sanchez 2007, Crawford 2008, Price et al. 2010), density of active burrows will not reflect immediate losses of animals during periods of rapid decline.

We used our population estimates to evaluate the potential influence of vegetation on rabbit density at our study sites. Our results suggested that visual obstruction, which incorporates both herbaceous and shrub components, might be an important measure of cover resources for pygmy rabbits. Although visual obstruction and horizontal cover were positively correlated, only visual obstruction was positively related to density of rabbits on a site. These results suggest that vertical cover might be a useful measure of cover resources for this species. While horizontal cover provides protection from predators (especially avian species), the added protection of vertical cover might provide important concealment from terrestrial predators. Many studies have documented the importance of horizontal cover for small mammals (e.g., Duncan and Jenkins 1998, Jensen et al. 2003), however, others have noted that the 2 types of cover can have different influences on animal behavior and perceptions of risk (Ebensperger and Hurtado 2005). Vertical cover also might provide important concealment for semi-fossorial species that are more conspicuous and possibly less vigilant when excavating burrows.

Before using our index to estimate absolute abundance of pygmy rabbits outside of our study area, additional calibration studies should be conducted for each new region. Our index was calibrated under specific conditions that may not be pertinent in other geographical regions (Eberhardt and Simmons 1987). Site or region-specific factors that might affect the relationship between burrow density and rabbit density, as well as factors that might influence patterns of burrow use by pygmy rabbits should be considered when calibrating the index for a specific geographic area. Variation in predation risk, soil structure, regional climate and precipitation, snow cover, presence of other burrowing animals, land management practices, and vegetation structure all might play important

roles. Examination of these factors could provide greater insight into what drives the dynamics of burrow use and site occupancy by pygmy rabbits and why rabbit densities vary across sage-steppe habitats. Finally, the index based on burrows also can be employed as a tool for tracking relative population trends over time, even if absolute estimates are not necessary. However, it is important to note that there could be a delay in detecting rapid population declines. Also, because the relationship is non-linear, the index will be less informative at high densities sites over which the slope of the relationships between density of rabbits and burrows becomes shallower.

MANAGEMENT IMPLICATIONS

We have demonstrated that counts of active burrow systems can be used to index abundance in populations of pygmy rabbits. Because burrow system counts are noninvasive and require minimal resources to complete, they are more pragmatic for application across multiple populations than other, more intensive methods. We recommend that burrow censuses should be conducted during autumn and that activity status of burrows should be categorized based on the presence of fresh rabbit pellets. In areas where sympatric lagomorph species are present, we recommend testing a sample of pellets to confirm species identity. If the index is to be used to estimate absolute abundances across other regions, then calibration of the relationship between burrows and rabbits should be conducted in each new geographic area. Mark-resight techniques and snow-track surveys could provide the necessary abundance estimates for calibration. If the index is to be used to track relative population trends over time regardless of absolute abundance, then the index could be used as presented here. However, we caution that use

of the index at higher burrow densities might be less informative.. Depending on the management goals, this index provides managers with an efficient tool for monitoring population trends and studying population dynamics in this species of conservation concern.

ACKNOWLEDGEMENTS

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Table 1. Results from censuses of pygmy rabbit burrows conducted in eastcentral Idaho during September 2007 and 2008.  Total burrows reflects the count of all burrow systems in all four activity categories (active, recently active, old, and very old), and densities are expressed as burrow systems per hectare (bs/ha).

| Site | Total Burrows | Burrow Densities  (bs/ha) | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | | Total | Active | Recent | Old | Very Old |
| Cedar Gulch | 106 | 1.23 | 0.62 | 0.34 | 0.08 | 0.23 |
| Middle | 290 | 3.09 | 0.87 | 1.25 | 0.58 | 0.39 |
| Bull Creek | 414 | 3.49 | 0.19 | 0.5 | 2.12 | 0.68 |
| Atomic City | 425 | 4.02 | 0.75 | 1.33 | 0.93 | 1.01 |
| Rocky Canyon | 485 | 4.71 | 1.01 | 1.25 | 1.37 | 1.08 |
| Ten Mile | 566 | 5.5 | 0.57 | 1.21 | 2.89 | 0.83 |
| Warm Springs | 748 | 13.08 | 3.46 | 1.33 | 5.42 | 1.17 |

Table 2. Numbers of pygmy rabbits radio collared and numbers resighted during mark-resight surveys at 7 study sites in eastcentral Idaho during autumn 2007 and 2008. Numbers of males and females represent rabbits that were initially fitted with radio-collars and do not account for mortalities that occurred post-capture.  The marked, unmarked, and total columns represent counts of rabbits resighted after pooling data across all resight occasions.  Individual identification of marked rabbits was recorded during each resight occasion.

| | Radio collared | | | Resighted | | |
|---|---|---|---|---|---|---|
| Site | Male | Female | | Marked | Unmarked | Total |
| Cedar Gulch | 5 | 8 | | 20 | 42 | 62 |
| Rocky Canyon | 7 | 7 | | 25 | 22 | 47 |
| Middle | 10 | 14 | | 112 | 49 | 161 |
| Warm Springs | 10 | 11 | | 88 | 64 | 152 |
| Ten Mile | 3 | 2 | | 0 | 1 | 1 |
| Bull Creek | 0 | 2 | | 4 | 1 | 5 |
| Atomic City | 1 | 0 | | 3 | 7 | 10 |

Table 3. Modeling results from Program MARK for mark-resight surveys on 4 sites in the Lemhi Valley, Idaho, during 2007 and 2008. The logit-normal modeling method was used to test for differences in 6 *a priori* models that included variation in time, wind strength, and individual heterogeneity on resight probabilities. Model parameters are for the resighting probability (p), including no variation p(.), variation among resight events p(t), or variation among 4 categories of wind strength p(wind). Individual heterogeneity in resighting probabilities (s) was modeled as either s(.), which accounts for heterogeneity, or s(.)=0, which does not include heterogeneity.

| Site | Model | AICc [a] | $\Delta$ AICc [b] | $w_i$ [c] | k [d] | Deviance |
|------|-------|----------|-------------------|-----------|-------|----------|
| Middle | {p(t) s(.)=0} | 27.86 | 0.00 | 1.00 | 19 | 369.86 |
| | {p(t) s(.)} | 127.28 | 99.42 | 0.00 | 20 | 367.28 |
| | {p(.) s(.)=0} | 424.46 | 396.60 | 0.00 | 2 | 419.66 |
| | {p(.) s(.)} | 426.21 | 398.35 | 0.00 | 3 | 418.50 |
| | {p(wind) s(.)=0} | 428.64 | 400.78 | 0.00 | 4 | 417.56 |
| | {p(wind) s(.)} | 431.36 | 403.50 | 0.00 | 5 | 416.36 |
| | | | | | | |
| Cedar Gulch | {p(.) s(.)} | 72.25 | 0.00 | 0.51 | 3 | 62.25 |
| | {p(.) s(.)=0} | 72.34 | 0.09 | 0.49 | 2 | 66.62 |
| | {p(wind) s(.)=0} | 81.92 | 9.68 | 0.00 | 4 | 65.92 |
| | {p(wind) s(.)} | 86.27 | 14.03 | 0.00 | 5 | 61.27 |
| | {p(t) s(.)=0} | 105.70 | 33.45 | 0.00 | 6 | 65.70 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | {p(t) s(.)} | 130.94 | 58.69 | 0.00 | 7 | 60.94 |
| Rocky Canyon | {p(.) s(.)} | 84.53 | 0.00 | 0.93 | 3 | 76.13 |
| | {p(wind) s(.)} | 89.87 | 5.34 | 0.06 | 5 | 72.37 |
| | {p(.) s(.)=0} | 95.16 | 10.63 | 0.00 | 2 | 90.07 |
| | {p(wind) s(.)=0} | 100.39 | 15.86 | 0.00 | 4 | 87.94 |
| | {p(t) s(.)} | 103.37 | 18.84 | 0.00 | 7 | 70.71 |
| | {p(t) s(.)=0} | 111.10 | 26.57 | 0.00 | 6 | 87.10 |
| Warm Springs | {p(t) s(.)} | 161.71 | 0.00 | 0.78 | 20 | 289.71 |
| | {p(t) s(.)=0} | 164.25 | 2.54 | 0.22 | 19 | 316.25 |
| | {p(.) s(.)} | 330.29 | 168.59 | 0.00 | 3 | 322.29 |
| | {p(wind) s(.)} | 335.78 | 174.08 | 0.00 | 5 | 319.78 |
| | {p(.) s(.)=0} | 348.44 | 186.73 | 0.00 | 2 | 343.51 |
| | {p(wind) s(.)=0} | 353.04 | 191.33 | 0.00 | 4 | 341.40 |

[a] Akaike's Information Criterion corrected for small sample size (AICc)

[b] Difference between model's AICc values

[c] Akaike weight provides evidence of model likelihood

[d] Estimated number of parameters

Table 4. Vegetation measurements collected from 6 sites in the Lemhi Valley, Idaho, during 2007 and 2008.  Shrub canopy cover represents mean horizontal cover of all shrub species and visual obstruction records vertical cover of both shrub and herbaceous species.  Both measures are reported as mean values ± standard deviation.

| Site | Shrub Canopy Cover (%) | Visual Obstruction (cm) |
|------|------------------------|-------------------------|
| Cedar Gulch | 18.5 (± 7.0) | 16.0 (± 9.8) |
| Rocky Canyon | 29.8 (± 11.3) | 25.3 (± 12.0) |
| Middle | 21.2 (± 4.6) | 22.0 (± 14.5) |
| Warm Springs | 18.3 (± 4.9) | 24.7 (± 13.0) |
| Ten Mile | 15.4 (± 6.5) | 11.7 (± 7.6) |
| Bull Creek | 19.2 (± 9.1) | 12.0 (± 9.7) |

Table 5.  Estimates and 95% confidence intervals for population densities of pygmy

rabbits at 7 sites in eastcentral Idaho.  Estimates were used in development of an index of

abundance based on active burrow systems.

| Site | Density (rabbits/ha) | 95% Confidence Interval | |
| --- | --- | --- | --- |
| | | Lower | Upper |
| Warm Springs | 0.46 | 0.36 | 0.55 |
| Cedar Gulch | 0.29 | 0.19 | 0.38 |
| Middle | 0.26 | 0.24 | 0.28 |
| Rocky Canyon | 0.24 | 0.15 | 0.34 |
| Atomic City | 0.12 [a] | - | - |
| Ten Mile | 0.05 [a] | - | - |
| Bull Creek | 0.02 [a] | - | - |

[a] Estimate calculated using snow-track survey methods for which confidence intervals

were not calculated.

Figure 1. Seven study sites delineated for estimation of abundance of pygmy rabbits in eastcentral Idaho during 2007 and 2008.
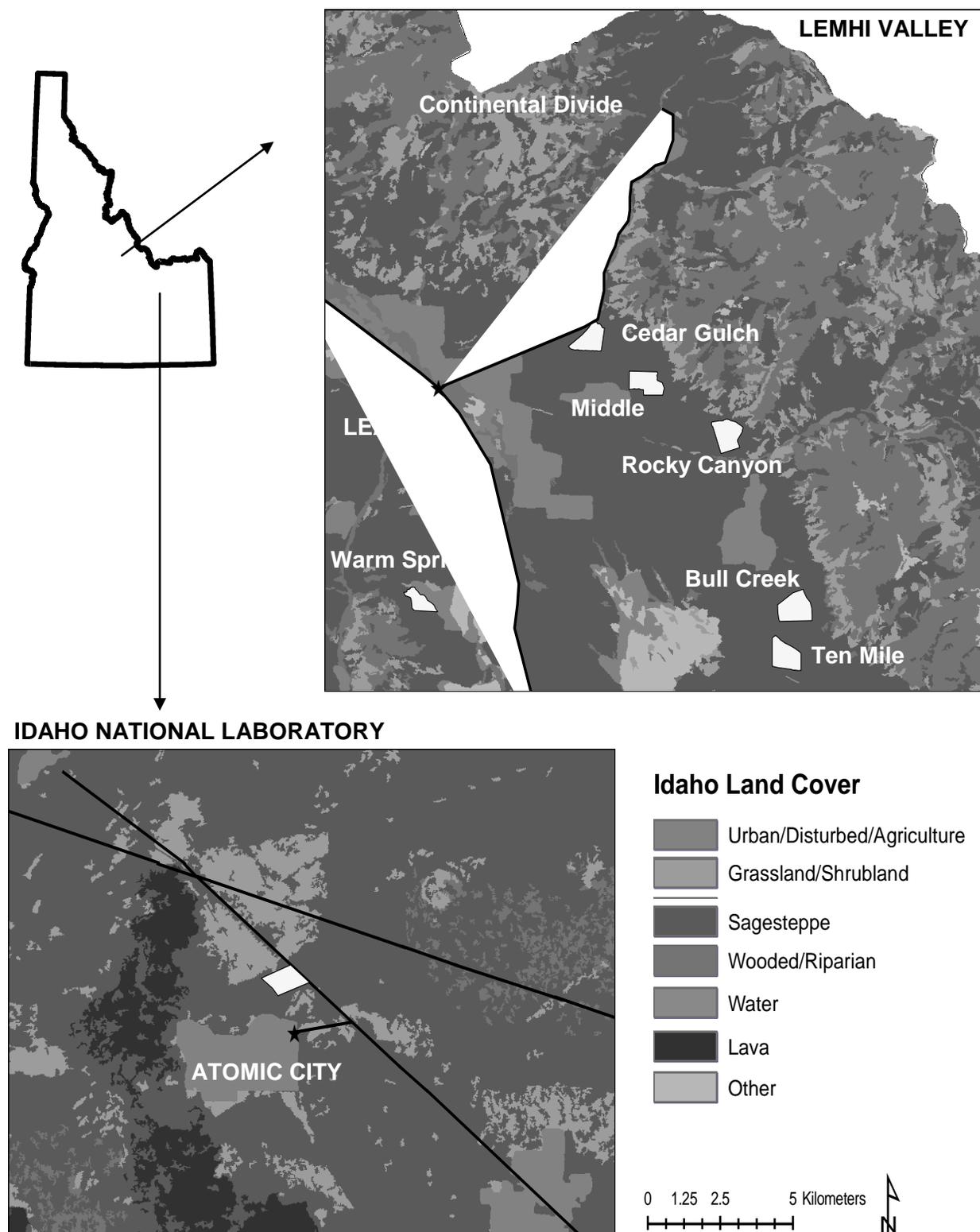
Figure 2. Model-averaged resighting probability for mark-resight surveys of pygmy

rabbits completed at 4 sites in eastcentral Idaho during 2007-2008.  Values are expressed
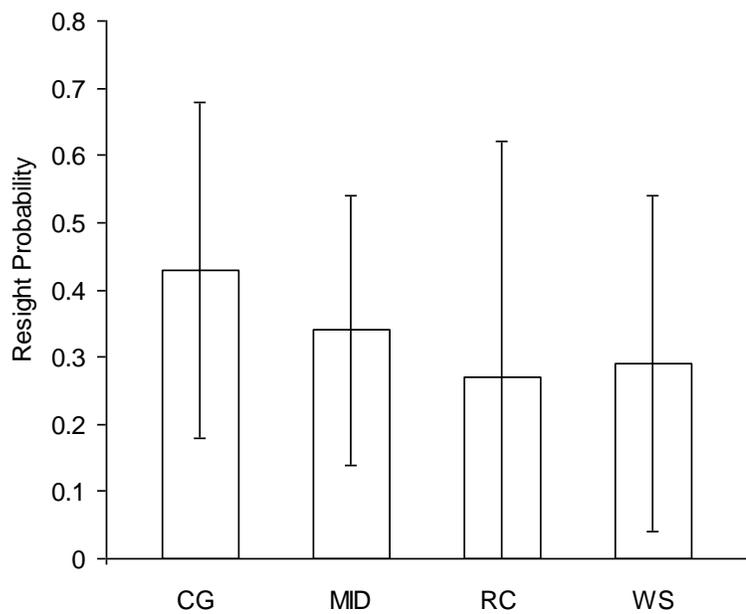
as means and 95% confidence intervals.

Figure 3. Regression results for number of burrows used by individual pygmy rabbits as a function of the density of available burrow systems.  Data were collected on 61 rabbits fitted with radio-collars across 7 sites in eastcentral Idaho during 2007 and 2008.  Burrow use represents a standardized 3-week subset of telemetry locations for collared rabbits and burrow density represents all active burrows present within a 100-m radius of the mean center of the telemetry locations for each individual.
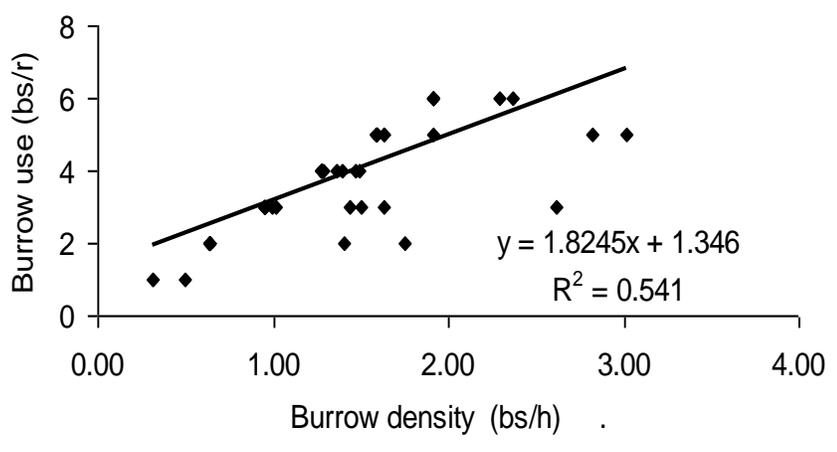
Figure 4.  Relationship between density of pygmy rabbits and density of active burrow systems at 7 sites in eastcentral Idaho, 2007 and 2008.  The curvilinear relationship reflects the use of a greater number of burrows by individuals as density of available burrows increased (see Figure 3).
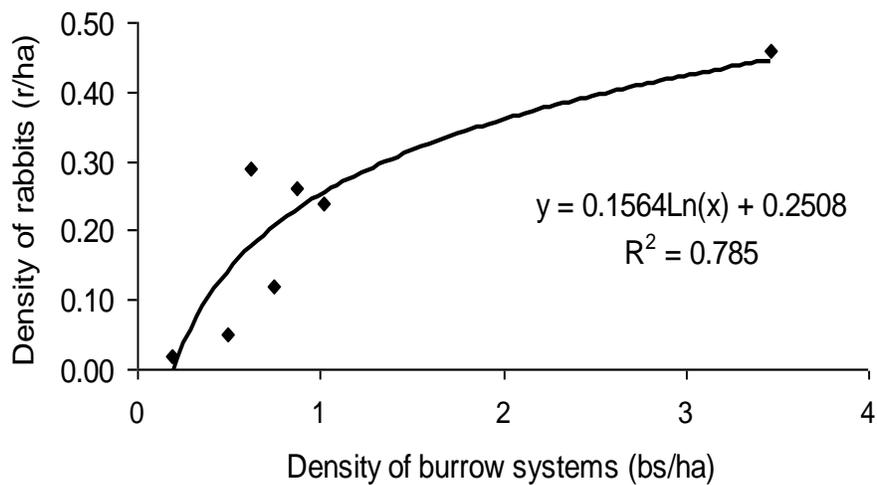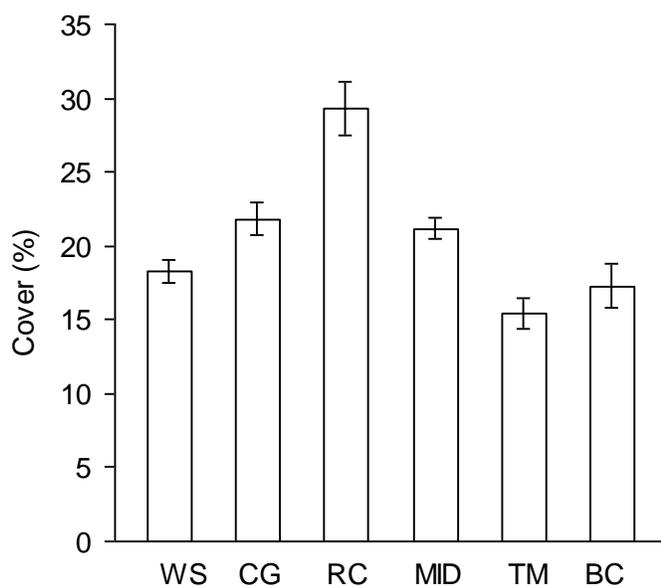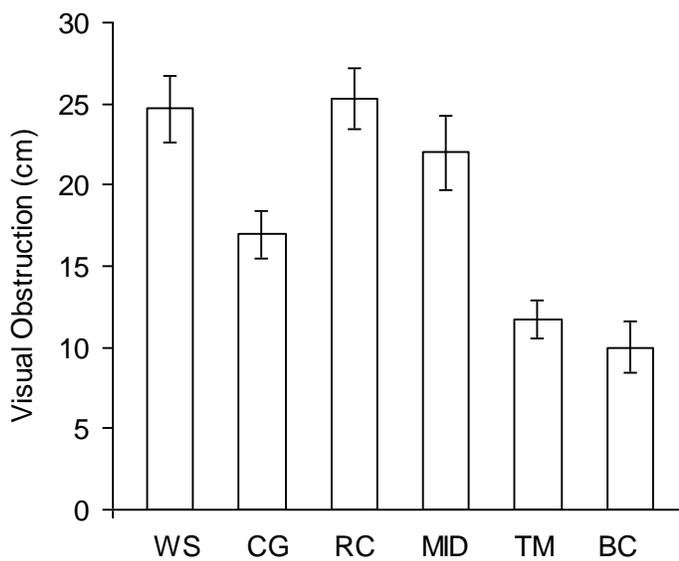


$y = 0.1564Ln(x) + 0.2508$

$R^2 = 0.785$

Figure 5. Mean values (± standard errors) of horizontal cover of shrubs (a) and visual

obstruction (i.e., vertical cover; b) of all vegetation at 6 sites in the Lemhi Valley, Idaho,

measured during 2007-2008.



a.



b.

Fig 5.

**THESIS CONCLUSION**

In addition to a perceived decline of the pygmy rabbit across its range, the sagebrush habitats on which it relies have been reduced and modified by conversion to uses such as dryland agriculture, irrigated agriculture, energy production, and residential development (Knick and Rotenberry 2002). Several researchers have suggested that the species might be subject to local population declines and potentially shift across the landscape though time (Janson 1946, Wilde 1978, Weiss and Verts 1984). Our work, in part, suggests a mechanism for shifts in habitat use over time, even in relatively unmodified habitats. Rabbits might shift due to changes in vegetation created by their own foraging and burrowing behaviors.

Pygmy rabbits markedly influence the vegetation and habitat around their burrow systems by decreasing cover and forage resources. Rabbits act as "ecosystem engineers" by modifying sagebrush-steppe through foraging and burrowing behaviors, potentially turning suitable habitat into unsuitable habitat (Jones et al. 2004). Intense levels of browsing noted at burrow systems that had been occupied for several years indicated that rabbits not only influence cover resources, but also might change the composition and quality of forage. These impacts might be severe enough to cause rabbits to abandon old burrow systems for new, higher quality burrow systems in adjacent areas. Over time, if the rabbit densities are high enough, these impacts could cause entire populations to shift or risk severe local population decline.

Additionally, because the juvenile mortality rate is high and variable, and survival declined for later-born litters, successful recruitment of early-born young might be

essential for population persistence in an area. High variability in survival over relatively small spatial and temporal scales might further contribute to marked population fluctuations of rabbit populations, beyond those impacts imposed by habitat alteration.

As a result of the potential of population fluctuations and local extirpations, researchers might consider monitoring populations across broader geographical areas to assess regional trends in abundance and habitat use. Density of burrow systems can serve as an index for monitoring changes in abundance in eastcentral Idaho and might be a useful monitoring tool for detecting changes in relative abundance over time throughout their range. An improved understanding of the dynamics of this species across space and time is needed to help shape range-wide conservation plans and land management strategies.

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**APPPENDIX**

APPENDIX A:  University of Idaho Animal Care and Use Committee Approval

**University of Idaho**
**Animal Care and Use Committee**

Date:   Wednesday, January 24, 2007
To:     Janet Rachlow
From:   University of Idaho
Re:     Protocol 2007-23
        Abundance Estimation and Development of an Index of Abundance for Pygmy Rabbits (M.S. Project)

Your animal care and use protocol for the project shown above was reviewed by the University of Idaho on Wednesday, January 24, 2007.

This protocol was originally submitted for review on: Friday, November 10, 2006
The original approval date for this protocol is: Wednesday, January 24, 2007
This approval will remain in affect until: Thursday, January 24, 2008
The protocol may be continued by annual updates until: Sunday, January 24, 2010

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.

*Brad Williams DVM*

_____
IACUC Representative

APPENDIX B: Classification protocols used for estimating activity levels of pygmy rabbit burrow systems based on sign and integrity of burrow entrances. Criteria were adapted from protocols developed for use in Roberts (2001) and as presented in Sanchez and Rachlow (*in press*).

| Burrow system activity class | Integrity of entrance(s) | Pellet characteristics | Evidence of recent excavation |
|---|---|---|---|
| Active | entrance open and intact | fresh pellets present | fresh diggings evident/abundant[a] |
| Recent | entrance open and intact | old/weathered pellets present | diggings old, few, or absent |
| Old | entrance open and intact or slightly obstructed | pellets absent | diggings old, few, or absent |
| Very old | entrance collapsed[b] | pellets absent | diggings old, few, or absent |

[a]Detection of fresh pellets resulted in an "active" ranking, regardless of excavation evidence.

[b]Collapsed openings were only considered to be a burrow system entrance if the top half of the arch remained identifiable as an opening likely to have been associated with pygmy rabbit use.