

AN ABSTRACT OF THE THESIS OF

Troy G. Smith for the degree of Master of Science in Forest Science  
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Wood and Antelope Bitterbrush in Ponderosa Pine Forests of Central Oregon

Abstract approved:

Signature redacted for privacy.

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Chris C. Maguire

Downed wood and antelope bitterbrush (*Purshia tridentata*) are often managed on federal ponderosa pine (*Pinus ponderosa*) forests in central Oregon to prevent catastrophic wildfires and provide wildlife habitat. However, although much is known regarding the roles of downed wood and bitterbrush in wildfire behavior, little is known regarding the relationships of small mammal populations with downed wood and bitterbrush in these pine forests east of the Cascade crest. This study had four primary objectives: 1) to test for differences in population parameters (i.e., density, reproductive condition, and survival) of common small mammals between forested areas with high and low downed wood volumes; 2) to test for differences in these small mammal population parameters between forested areas with high and low shrub cover; 3) to quantify relationships of small mammal population parameters with different habitat features, emphasizing downed wood

volume, bitterbrush cover, and total shrub cover; and 4) to quantify relationships between small mammal population parameters and habitat features across seasons and years to assess temporal variability.

Study units representing five replicates of three combinations of shrub cover and downed wood volume (high shrub cover/high downed wood volume, high shrub cover/low downed wood volume, low shrub cover/low downed wood volume) were selected in the Deschutes National Forest east of the crest of the Cascades Mountains in central Oregon. A total of 2,654 small mammals representing nine species were captured in live traps on the 15 study units during four sampling periods: early summer 2000 (June 25 to July 27), late summer 2000 (August 29 to September 30), fall 2000 (October 2 to October 28), and early summer 2001 (July 3 to August 4). Yellow-pine chipmunks (*Tamias amoenus*), golden-mantled ground squirrels (*Spermophilus lateralis*), and deer mice (*Peromyscus maniculatus*) comprised 98% of the captures.

Golden-mantled ground squirrel survival and density were significantly higher on study units with high versus low downed wood volume. Yellow-pine chipmunk populations did not exhibit significant relationships with downed wood volume, but chipmunk density was higher on study units with high versus low shrub cover. Deer mouse populations failed to exhibit significant relationships with downed wood volume or shrub cover. For the three small mammal species, there was considerable variation among seasons, years, and locations for many of the population parameters examined. Results from this study suggest that

managing downed wood and antelope bitterbrush in ponderosa pine forests of central Oregon may affect the small mammal community through changes in density and survival of golden-mantled ground squirrels and yellow-pine chipmunks. Such impacts on the small mammal community will, consequently, influence other aspects of forest ecology, including fire behavior and shrub regeneration due to the consumption and dispersal of bitterbrush seeds by these chipmunks and ground squirrels.

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SMALL MAMMAL RELATIONSHIPS WITH DOWNED WOOD AND  
ANTELOPE BITTERBRUSH IN PONDEROSA PINE FORESTS OF CENTRAL  
OREGON

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Troy G. Smith

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# SMALL MAMMAL RELATIONSHIPS WITH DOWNED WOOD AND ANTELOPE BITTERBRUSH IN PONDEROSA PINE FORESTS OF CENTRAL OREGON

## CHAPTER 1

### INTRODUCTION

State, federal, and private forests in Oregon are subject to a variety of management practices stemming from multiple objectives. These management goals include, but are not limited to timber, recreation, fire, and wildlife. Often, however, the ecological impacts of management decisions on wildlife are largely unknown.

In forested systems, downed wood is frequently managed for wildlife habitat, and it is well known that many terrestrial vertebrates utilize downed wood for feeding, travel, cover, and reproduction (Maser et al. 1979, Harmon et al. 1986, Freedman et al. 1996, Bull et al. 1997). Consequently, state and federal agencies mandate downed wood targets in managed forests of Oregon to provide wildlife habitat (USDA 1995, ODF 1996). However, the correlative relationships between small mammal populations and downed wood remain poorly defined despite the importance of quantifying these relationships for devising credible downed wood management policies (Harmon 2001).

Shrubs, in addition to downed wood, are important elements of wildlife habitat. Antelope bitterbrush (*Purshia tridentata*) is often a dominant shrub of



ponderosa pine (*Pinus ponderosa*) forests east of the Cascade Mountain crest in central Oregon, and it is an important seed source for small mammals (Vander Wall 1994) and important browse for mule deer (*Odocoileus hemionus*; Guenther et al. 1993). Further, small mammals, such as the yellow-pine chipmunk (*Tamias amoenus*), cache bitterbrush seeds in favorable soil microsites as part of their foraging activities. Because chipmunks and other rodents do not subsequently recover many of these caches, unrecovered seeds often experience greater odds for survival and germination than seeds that are not cached (West 1968, Sherman and Chilcote 1972, Vander Wall 1994, 1995). However, although ecologists recognize the importance of small mammal scatter-hoarding activities for bitterbrush dispersal and regeneration, the relationships between small mammal populations and antelope bitterbrush remain poorly understood.

To implement forest practices that truly achieve management goals, including small mammal habitat considerations, it is important to first understand the ecological implications of management actions. Thus, the objective of this study was to quantify relationships between small mammal populations, downed wood, antelope bitterbrush, and other associated habitat variables to provide natural resource managers with empirical data on the impacts of downed wood and bitterbrush levels on small mammal communities. Yellow-pine chipmunk, golden-mantled ground squirrel (*Spermophilus lateralis*), and deer mouse (*Peromyscus maniculatus*) population parameters (i.e., density, reproductive condition, and survival) were examined and compared under three environmental conditions: high

shrub cover/high downed wood volume, high shrub cover/low downed wood volume, and low shrub cover/low downed wood volume. Small mammals were live trapped during four sample periods over 14 months in 2000 and 2001. All field research was conducted in the ponderosa pine/antelope bitterbrush vegetation type on the Deschutes National Forest in central Oregon.

Analysis of Variance tests were used to evaluate small mammal population responses across study conditions, while multiple linear and logistic regression, and Akaike's Information Criterion were used to assess the importance of, and to quantify, the relationships of each small mammal population parameter with time and habitat features (Ramsey and Schafer 1997, Burnham and Anderson 1998). Chapter 2 examines small mammal population relationships with varying volumes of downed wood and Chapter 3 examines small mammal population relationships with varying quantities of shrub cover. Chapter 4 summarizes the results from Chapters 2 and 3 and addresses implications of the research.

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## CHAPTER 2

## SMALL MAMMAL RELATIONSHIPS WITH DOWNED WOOD IN CENTRAL OREGON

## ABSTRACT

Downed wood is an important component of ponderosa pine (*Pinus ponderosa*) forests in central Oregon because of its roles in wildfires and wildlife habitat. Although much is understood about how downed wood influences fire behavior in these forests, little is known about affiliations between downed wood and wildlife. This study examined relationships between small mammal populations and downed wood volume, and other habitat features. Small mammals were live trapped during four sample periods from June through October 2000, and July and August 2001 in ponderosa pine/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest in central Oregon. Density, reproductive condition, and survival of the three most abundant small mammal species [yellow-pine chipmunk (*Tamias amoenus*), golden-mantled ground squirrel (*Spermophilus lateralis*), and deer mouse (*Peromyscus maniculatus*)] were estimated on five study units with high ( $\bar{x} = 117.8 \text{ m}^3/\text{ha}$ ) and five units with low ( $\bar{x} = 15.8 \text{ m}^3/\text{ha}$ ) volumes of downed wood. Analysis of Variance tests indicated that only golden-mantled ground squirrel survival was positively correlated with downed wood volume (adjusted  $p = 0.09$ ). Odds for golden-mantled ground squirrel survival were 4.2 times greater on study units with high versus low downed wood volume. Similarly,

regression modeling indicated that, relative to other habitat variables examined, downed wood volume was important only for golden-mantled ground squirrel density. Each 35.1 m<sup>3</sup>/ha increase in downed wood volume coincided with a 10% increase in ground squirrel density. Finally, temporal and spatial variability were important for many population parameters examined, indicating considerable population variation among seasons, years, and location.

## INTRODUCTION

Downed wood is one of the most manageable properties of forest environments and it greatly influences forest biodiversity (Freedman et al. 1996, Huston 1996). Downed wood often significantly impacts processes such as nutrient cycling, carbon storage, and sediment transport, and it contributes to fish and wildlife habitat (Harmon et al. 1986). Further, downed wood can play an important role in determining wildfire potential depending on the size, decay state, and abundance in an area (Maser et al. 1979).

In many Pacific Northwest forests, downed wood has been, and continues to be, heavily affected by timber harvesting and other anthropogenic manipulations (Harmon 2001). Forests in the western United States, dominated by ponderosa pine (*Pinus ponderosa*), have undergone major alterations since European settlers arrived in the mid- to late-1800's (Cooper 1960, Harrod et al. 1999, Moore et al. 1999). These forests have experienced increasing downed wood volume, shrub cover, and average tree density, while densities of large snags and average tree

diameter have decreased. Additionally, current forests often possess a uniform matrix of smaller diameter second-growth trees that are higher in density than pre-settlement forests, which were typically maintained by frequently occurring low intensity fires that left large trees scattered in widely spaced clumps (Cooper 1960, Bork 1985, Morrow 1985, Harrod et al. 1999). Further, old and mature ponderosa pine forests in central Oregon experience annual mortality rates of  $< 1\%$  (Franklin et al. 1987), while second-growth forests, in contrast, exhibit variable mortality as competition and stress in dense stands leave trees more susceptible to insect, disease, and drought-induced mortality (Hessburg et al. 1994, Cochran and Barrett 1995, 1999). As a result, many ponderosa pine forests today have smaller diameter, more abundant, and higher volumes of downed wood with increased residence time when contrasted with pre-settlement periods, largely due to the absence frequently occurring fires on the forest floor (Bork 1985, Agee 1994, Korol et al. in press).

Many of these structural changes in ponderosa pine forests east of the Cascade crest in central Oregon result from land management activities such as grazing, logging, and fire suppression (Agee 1994, Hessburg et al. 1994, Korol et al. in press). These widespread changes have the potential to broadly affect biotic productivity, diversity, and species composition, and to dramatically increase the potential for catastrophic wildfires. However, forest and wildlife managers have recently begun managing forests to emulate pre-settlement structures and patterns (Moore et al. 1999). Although we largely understand how downed wood

influences fire behavior in pine forests, we have limited understanding of the intricate associations of wildlife species and communities with downed wood (Agee 1994, Freedman et al. 1996, Harmon 2001). Even so, in recognition that downed wood improves wildlife habitat in many vegetation types, federal regulations require the retention of specified amounts of downed wood in federally managed forests on the east side of the Cascade crest (USDA 1995).

Much of the available information on wildlife relationships with downed wood comes from mesic forests of the Pacific Northwest (Loeb 1996), and it often focuses on small mammals. Researchers have examined small mammal use of downed wood by individual animals and populations, and across scales from individual logs through landscapes (McMillan and Kaufman 1995, Bowman et al. 2000). Small mammals may utilize logs for travel routes, visual cues and navigational landmarks, nesting, and predator avoidance (Olszewski 1968, Hayes and Cross 1987, Barnum et al. 1992, Planz and Kirkland 1992, Carter 1993, Tallmon and Mills 1994, McMillan and Kaufman 1995, McCay 2000). Further, some small mammals utilize downed wood for lookout sites, feeding perches, and foraging sources for invertebrates and fungi (States 1976, Maser et al. 1979). Evidence links small mammals with highly decayed wood and increasing downed wood volume, but these trends are not universal within or among species or regions (Hayes and Cross 1987, Barnum et al. 1992, Tallmon and Mills 1994, Craig 1995, Lee 1995, Loeb 1999, Bowman et al. 2000, Butts and McComb 2000, McCay 2000, Maguire in press).

In many ponderosa pine forests of central Oregon, yellow-pine chipmunks (*Tamias amoenus*), golden-mantled ground squirrels (*Spermophilus lateralis*), and deer mice (*Peromyscus maniculatus*) dominate the small mammal community. These animals have significant ecological roles as consumers and dispersers of seed (Tevis 1952, Sullivan 1979, Vander Wall 1992, 1994) and hypogeous fungi (Tevis 1952, 1953, Maser et al. 1978), and as prey for avian and mammalian predators (Sutton 1992, Bartels and Thompson 1993, Verts and Carraway 1998). Currently we have sparse data on the relationships between these small mammals and downed wood in semi-arid ponderosa pine forests, but available data from other forest types and related species suggests that these mammals will have significant positive correlations with downed wood, particularly downed wood volume.

The objectives of this study, therefore, were: 1) to test for differences in yellow-pine chipmunk, golden-mantled ground squirrel, and deer mouse density, reproductive condition, and survival between forested study units with high and low downed wood volumes; 2) to identify associations of small mammal population parameters with different habitat features, with an emphasis on downed wood volume; and 3) to quantify small mammal habitat relationships across different seasons and years to assess temporal variability in trends. Results from this study will contribute to our knowledge of eastside forest ecology and can be applied to the development of forest management plans that account for habitat needs of forest small mammals.



## METHODS

### Study Area

This study took place on the Bend/Fort Rock Ranger District of the Deschutes National Forest in central Oregon in areas supporting the ponderosa pine/antelope bitterbrush (*Purshia tridentata*)/Idaho fescue (*Festuca idahoensis*) plant association which typically occurs on pumice soils (Franklin and Dyrness 1988, Volland 1988). Across the study area, annual precipitation ranges from approximately 300 to 540 mm, mostly in the form of snow (National Weather Service recording stations near Bend and Wickiup Dam, Oregon; USDC 2002).

Initially, I located forested areas on the Deschutes National Forest based on the plant association and stand age from GIS maps, and then visually assessed the areas according to homogeneity of the plant community, the estimated number of trees per hectare, mean tree diameter, and amount of shrub cover. I then evaluated the most current vegetation survey data from the Deschutes National Forest which provided a reference of the range of downed wood volumes across the forest. In conjunction with these data, I selected paired study units (blocks) based on a visual assessment of downed wood volume; one study unit possessed relatively low (range: 6.3 to 37.2 m<sup>3</sup>/ha) and the other high (range: 72.8 to 234.2 m<sup>3</sup>/ha) downed wood volume (Figure 2.1). Subsequently, I will refer to these study unit conditions as “low” and “high” downed wood, respectively. Due to logistical limitations in small mammal sampling and to ensure that animals could not move among blocks,

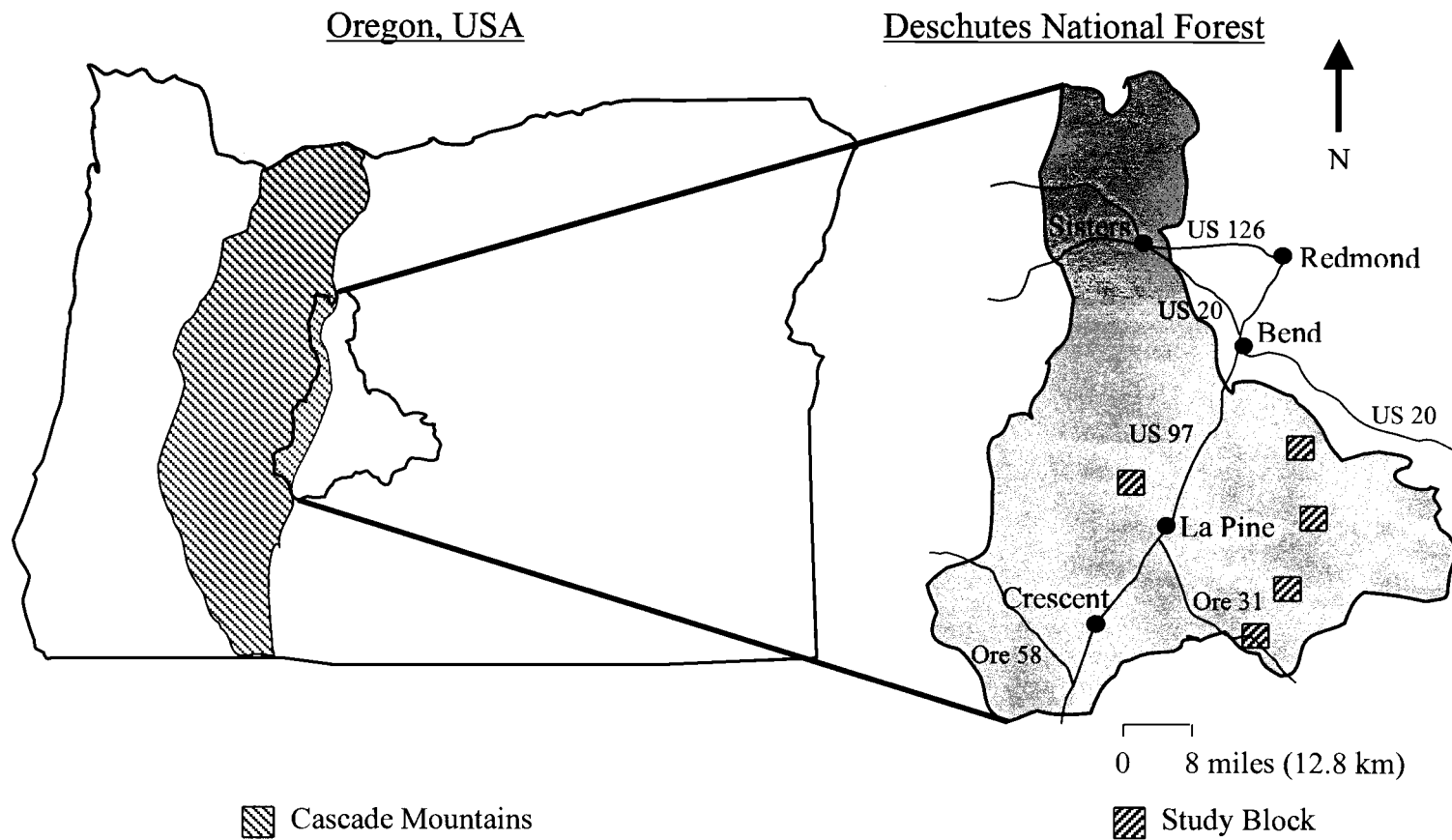


Figure 2.1. The locations of five study blocks in ponderosa pine (*Pinus ponderosa*) forests on the Deschutes National Forest, east of the Cascade crest, Oregon. Each block is comprised of one study unit with high downed wood volume ( $\bar{x} = 117.8 \text{ m}^3/\text{ha}$ ) and one unit with low downed wood volume ( $\bar{x} = 15.8 \text{ m}^3/\text{ha}$ ).

only five geographically scattered blocks (separation of each block > 16 km) were included in the research.

The 10 study units selected range in elevation from 1285 to 1505 m and were characterized by discontinuous overstory canopies with medium to large ponderosa pines dominating the overstory (USDA 1995); a small number of lodgepole pines (*Pinus contorta*) were found on four of the study units. The mean diameter of ponderosa pines on the 10 units ranged from 21 to 46 cm, mean density ranged from 33 to 137 trees/ha, and canopy cover was 14 to 42%. Antelope bitterbrush comprised 82 to 99% of the shrub cover on the 10 units, while rabbitbrush (*Ericameria bloomeri*), rubber rabbitbrush (*E. nauseosus*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*) were less common. Idaho fescue, western needle grass (*Achnatherum occidentale*), and squirreltail (*Elymus elymoides*) were common grasses. All 10 units were probably railroad logged between 1920 and 1950, and three of the five low downed wood units received shelterwood cuts in the early 1980's (M. Deppmeier, Deschutes National Forest, pers. com.). Additionally, the five low downed wood units were used in a concurrent study examining small mammal relationships with varying quantities of antelope bitterbrush cover (identified as high shrub cover study units in Chapter 3).

### Habitat Sampling

On each 0.64-ha study unit I established one 8- x 8-sampling grid with 10-m spacing between grid points (Figure 2.2). On each unit, I measured eight habitat

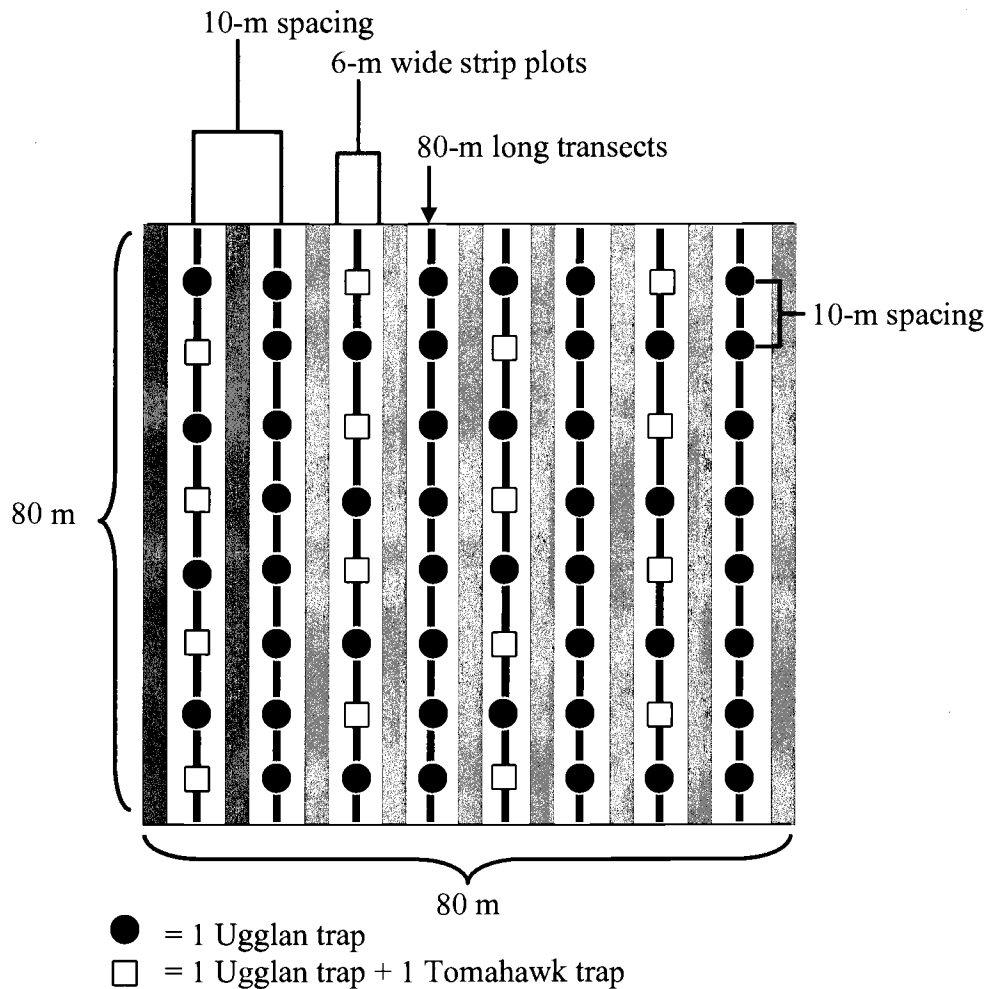


Figure 2.2. Study unit sampling design. Downed wood volume and decay class were sampled by complete census within each 80- x 80-m study unit. Additional habitat features were measured on the eight 80-m transects and within the 6-m wide strip plots. Small mammal traps were placed every 10 m in an 8-x 8-grid.

features with potential for influencing small mammal abundance, reproduction, and survival based on previous life history and habitat relationship studies. I quantified downed wood volume ( $\text{m}^3/\text{ha}$ ) by complete census on each study unit and measured the large-end (LED) and small-end diameters (SED) and total length for each wood piece  $> 0.5\text{-m}$  long with  $\text{LED} > 10\text{ cm}$  and  $\text{SED} > 1\text{ cm}$ . I calculated the volume for each wood piece using the formula for a frustum of a cone (Harmon and Sexton 1996),

$$V = L(\text{LED} + (\text{LED} \times \text{SED})^{0.5} + \text{SED})/3 \quad (1)$$

where,  $V = \text{volume } (\text{m}^3)$

$L = \text{piece length (m)}$

$\text{LED} = \text{large-end diameter (m)}$

$\text{SED} = \text{small-end diameter (m)}$ .

I estimated downed wood decay class using three structural classes (Parks et al. 1997) based on the amount of bark and branches, ground contact, wood decay, and log intactness. Class-1 logs were hard and still possessed much bark and foliage, while class-3 logs were soft and exhibited substantial decay.

I calculated tree basal area ( $\text{m}^2/\text{ha}$ ) from the diameter at breast height (dbh) of all ponderosa pine trees  $> 4\text{-cm}$  dbh within 3 m either side of each transect (i.e., 80- x 6-m strip plots). Mean tree dbh for each unit was calculated as the sum of all ponderosa pine dbh values divided by the total number of ponderosa pine trees on that unit. Because the major perceived benefit of trees for small mammals is the combination of seeds for forage and shade from large canopies, lodgepole pines

were excluded from the analyses due to their low frequency among and within study units, and their small size relative to ponderosa pines on the study units (mean dbh: lodgepole = 16.4 cm, ponderosa = 32.6 cm).

Percent total shrub cover was quantified using the line-intercept method (Bonham 1989) along eight 80-m parallel transects passing over each grid point. Shrub cover was measured in centimeters as the continual distance of all shrub components separated by < 5.0 cm that crossed the vertical plane of the horizontal transect. Additionally, I visually estimated the percent of live antelope bitterbrush cover crossing each transect as an index of plant vigor and potential seed production. Hereafter, the term “bitterbrush cover” will be used when discussing live bitterbrush cover.

Tree and shrub regeneration were combined into the single category “tree/shrub regeneration” as a measure of live shoots available for consumption by small mammals. I measured regeneration as seedlings per hectare in 0.5- x 0.5-m plots at 2-m intervals along each transect. Tree regeneration included seedlings < 1.4-m tall, and shrub regeneration included seedlings < 2-yr old based on height, typically < 7.5 cm tall, and absence of branching (Hormay 1943). Percent herb cover was estimated using point intercepts along each transect at 0.5- and 1-m intervals and was defined as the percent of ground cover on each unit that consisted of broad-leafed and non-woody plants, grasses, or sedges.

### Small Mammal Sampling

An 8- x 8-trapping grid was overlain on the sampling grid of each study unit (Figure 2.2). At each grid point, I placed one multi-capture Ugglan® model 3 (250 x 78 x 65 mm) wire-mesh live-trap (64 traps/study unit). Additionally, one Tomahawk® model 102 (406 x 127 x 127 mm) wire-mesh live-trap was placed at alternating grid points on alternating rows (16 traps/study unit). All traps were placed in protective cardboard containers and thoroughly covered with available bark pieces, wood, or vegetation to minimize animal exposure to heat and precipitation. Each trap was locked open and pre-baited with sunflower seeds four days prior to trapping. While live trapping, each trap was baited with one grape and several black-oil sunflower seeds, and provided with cotton or wool for thermal insulation.

I simultaneously trapped small mammals on both study units in one block for four consecutive days (24-hour periods). I randomly trapped each of the five blocks consecutively, one per week, for five weeks within a sample period. All blocks were trapped a total of four sample periods in 2000 and 2001, with the exception that block 3 was not trapped in fall 2000 due to unexpected snow in October 2000, precluding access to the block. Small mammal trapping spanned 14 months and included: early summer 2000 (June 25 to July 27), late summer 2000 (August 29 to September 30), fall 2000 (October 2 to October 28), and early summer 2001 (July 3 to August 4). Hereafter, the terms “season” and “year” will

be used when discussing different sample periods within and between years, respectively.

Each captured animal received two uniquely numbered ear tags, one in each ear. I also recorded the capture status (new or recapture), species, weight, sex, and female reproductive condition (reproductive or nonreproductive) of each individual captured. Females with distended abdomens (pregnant), large fleshy mammae, and visible lactation were recorded as reproductively active. Minimum weights from known adult yellow-pine chipmunks ( $> 35$  g) and golden-mantled ground squirrels ( $> 113$  g), based on their capture histories (i.e., captured in both 2000 and 2001;  $n = 88$  and 35, respectively), were used to classify the remaining individuals as adults or juveniles. Because only one deer mouse was captured in both 2000 and 2001, adult mice ( $> 15$  g) were differentiated from juveniles based on the lowest weight of reproductively active individuals.

Because of the difficulty in distinguishing the yellow-pine chipmunk from its congener, the least chipmunk (*Tamias minimus*), in the field (Carraway and Verts 1995) coupled with the previously cited rarity of the least chipmunk within tree lines (States 1976, Chappell 1978), I assumed that all captured chipmunks were yellow-pine chipmunks. If least chipmunks were captured, their infrequent encounters should not have significantly influenced the results.

The Institutional Animal Care and Use Committee at Oregon State University approved all mammal-sampling methods (permit no. 2419). All animals



were captured under Oregon Department of Fish and Wildlife Scientific Taking Permit nos. 097-00 and 113-01.

### Density

Because enumeration methods (e.g., number of individuals captured) may be negatively biased and potentially inappropriate for interspecific or habitat comparisons due to possible violation of the assumption of equal capture probabilities (Nichols and Pollock 1983, Nichols 1986), I used closed population models in the population estimation program, CAPTURE (Otis et al. 1978; Rexstad and Burnham 1991), to estimate population size on each study unit for each sample period. CAPTURE adjusts population estimates according to differing capture probabilities due to influences of time, behavior, and heterogeneity. As a result, population comparison among habitats and species should be more accurate (Nichols and Pollock 1983, Nichols 1986, Slade and Blair 2000). I independently selected a single population size estimator for each small mammal species to minimize estimation differences of population size due to biases among estimators.

For each species I calculated the mean maximum distance moved (MMDM) in CAPTURE to estimate the effective trapping area on each study unit (Wilson and Anderson 1985). This distance was used to calculate the boundary strip width (W) where,

$$W = 0.5 \times \text{MMDM}, \quad (2)$$

and this width was added to all sides of the respective study unit. Population estimates were divided by the effective trapping area for each species on each unit to obtain density estimates (individuals/ha).

### Reproductive Condition

As expected, the majority of females exhibiting signs of reproductive activity were captured during the two early summer sample periods (Jameson 1953, Broadbooks 1958, McKeever 1964). Consequently, only data from these periods in 2000 and 2001 were used to estimate the proportion of reproductively active females in the entire adult population for each species on each study unit. I used these proportions as an index of adult reproductive potential. Due to problematic data (e.g., low observer certainty), golden-mantle ground squirrel reproductive condition was not analyzed.

### Survival

I used program MARK (Version 2.0; White and Burnham 1999) to calculate a single estimate of monthly apparent survival on each study unit over the period of study. MARK provides estimates of apparent survival for marked animals based on re-encounter histories and performs model comparisons using Akaike's Information Criterion (AIC) involving time, group, and habitat effects to evaluate their relative importance (White and Burnham 1999). The term apparent survival is the probability that an animal is alive and available for recapture when

death and emigration cannot be differentiated (White and Burnham 1999).

Hereafter, the term “survival” will be used when discussing apparent survival.

Only adult individuals were used in the survival analyses to reflect longevity in the territorial breeding population rather than mobility of immigrating and emigrating juveniles. Due to insufficient adult recaptures among sample periods that would affect the reliability of survival estimates, not all study units or species were analyzed. Survival was estimated for yellow-pine chipmunks on all 10 study units, golden-mantled ground squirrel survival was estimated on seven units, and deer mouse survival was not estimated.

#### Analysis of Variance

A blocked Analysis of Variance (ANOVA) was performed for each species to test for differences in small mammal density, reproductive condition, and survival between study units with high and low downed wood volumes. Density and reproductive condition analyses included repeated measures to account for the repeated population sampling and interaction terms for season or year and downed wood volume. Because a single mean monthly survival estimate was calculated for each study unit, survival tests did not include repeated measures or interactions.

Due to problematic data, differences in golden-mantled ground squirrel reproductive condition (e.g., low observer certainty) and deer mouse survival (e.g., infrequent adult captures and recaptures) were not tested. Because real differences can be masked by natural variability in observational field studies, ANOVA results

were tested at  $\alpha = 0.1$  to increase the ability to detect small mammal population differences. In addition, Tukey-Kramer adjustments and Dunnett's tests (Ramsey and Schafer 1997) were used to calculate confidence intervals around means reflective of multiple comparisons among sample periods and studies (i.e., low downed wood units were also used in a companion shrub study: see Chapter 3), and the resulting p-values are denoted as "adjusted p." All ANOVA analyses were performed in SAS, Version 8 (SAS Institute, Inc. 1999).

### Model Selection

AIC, and multiple linear and logistic regression were used to examine small mammal density, reproductive condition, and survival relationships with habitat features (Burnham and Anderson 1998). This approach engages the concept of model selection and uncertainty, best inference given the data, and a priori model development (Anderson et al. 2000). In practice, I utilized the second order criterion,  $AIC_c$  (Anderson et al. 2001),

$$AIC_c = -2\log(\mathcal{L}(\hat{\theta}|y)) + 2K + (2K(K+1)/(n-K-1)) \quad (3)$$

where,  $(\mathcal{L}(\hat{\theta}|y))$  = maximized log-likelihood value

$K$  = number of parameters in a model

$n$  = sample size when  $n/K < 40$ .

Additionally, I checked the data for overdispersion (Ramsey and Schafer 1997) and when present, used the quasi-likelihood model selection (Burnham and Anderson 1998),  $QAIC_c$ ,

$$\text{QAIC}_c = [-2\log(\mathbb{E}(\hat{\theta}|y))]/\hat{c} + 2K + (2K(K+1)/(n-K-1)) \quad (4)$$

where,  $\hat{c}$  = variance inflation factor.

Models were ranked according to the difference between the AIC value for a given model and the lowest AIC value in the candidate set,

$$\Delta_i = \text{AIC value} - \text{AIC min} \quad (5)$$

where, AIC min = the smallest value in the candidate set.

The value,  $\Delta_i$ , allows a strength of evidence comparison among models, where increasing  $\Delta_i$  values correspond with decreasing plausibility of the fitted model being a “best” approximating model(s) in the set (Anderson et al. 2000). I interpreted only those models with  $\Delta_i < 2$ , as having substantial support for explaining variation in the data (Burnham and Anderson 1998). Alternatively, models were interpreted as having weak support when their  $\Delta_i \geq 2$  or their AIC values were within 2 units of a null model (e.g., a model that does not include a habitat variable). Finally, I examined Akaike weights ( $w_i$ ), which represent the relative likelihood for a model ( $i$ ) being a best model relative to another ( $j$ ) in the same set as  $w_i/w_j$  (Anderson et al. 2000).

For analyzing density and reproductive condition data, I created nine a priori explanatory models that included time and habitat variables of interest (Table 2.1). Null models only estimated variation among seasons (density analyses) or years (reproductive condition analyses). All density models were examined using multiple linear regression, and I assessed the assumptions of normality and constant variance and performed natural log ( $\log_{(n)}$ ) transformations on all small mammal

Table 2.1. Variable descriptions for models examined as predictors of small mammal density, reproductive condition, and survival. The models were used for small mammals captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon in 2000 and 2001. For measurement descriptions and criteria see the Methods section of this chapter.

Variable	Description
Season <sup>a</sup>	Null model. Time effects associated with repeat sampling across multiple seasons
Year <sup>b</sup>	Null model. Time effects associated with repeat sampling across multiple years
Block <sup>c</sup>	Null model. Spatial and/or temporal effects associated with sampling different blocks
Downed Wood Volume	Downed wood volume (m <sup>3</sup> /ha; large end diameter > 10 cm, small end diameter > 1 cm, and length > 0.5 m)
Downed Wood Decay Class	Downed wood decay class (1 – solid, 2 – moderate decay, 3 – severe decay)
Tree Basal Area	Ponderosa pine basal area (m <sup>2</sup> /ha)
Mean Tree dbh	Mean diameter at breast height for ponderosa pine (cm; dbh > 4 cm)
Total Shrub Cover	Total ground cover of shrubs (%)
Bitterbrush Cover	Ground cover of live bitterbrush (%)
Tree/Shrub Regeneration	Tree and shrub seedlings (#/ha)
Herb Cover	Combined ground cover of grasses, sedges, and broad-leafed forbs (%)

<sup>a</sup> – Early summer 2000, late summer 2000, fall 2000, and early summer 2001; used for density analyses.

<sup>b</sup> – Early summer 2000 and 2001; used for reproductive condition analyses.

<sup>c</sup> – Five geographically separated blocks; used for survival analyses.

density estimates to meet these assumptions. Female reproductive condition models were examined using multiple linear regression with logit transformations of the proportion of reproductively active females among each adult population. All models for density and reproductive condition using AIC were calculated using maximum likelihood estimators, included blocks, incorporated repeated measures to account for repeated population sampling, and were performed in SAS, Version 8 (SAS Institute, Inc. 1999).

For analyzing survival data, I created nine a priori explanatory models (Table 2.1); null models only estimated variation among blocks. I then utilized logistic regression and the design matrix in MARK (White and Burnham 1999) to compare monthly survival estimates for each species. All models for survival were calculated using maximum likelihood estimators, included blocks, and all re-encounter probabilities were modeled as constant. All survival analyses using AIC were performed in MARK (Version 2.0; White and Burnham 1999).

In all analyses using AIC, I limited the number of models examined to nine to minimize situations where the number of models exceeded the sample size (Anderson et al. 2001). All analyses possessed a larger sample size ( $n = 10$ ) than the number of models ( $n = 9$ ) except for ground squirrel survival, which could only be reliably estimated on seven study units ( $n = 7$ ). Additionally, to reduce the likelihood of over-fitting models, I limited each model to a single time (or block) and/or habitat variable and avoided interaction terms, trading the ability to identify more complex model effects for curtailing the likelihood of obtaining spurious

results (Burnham and Anderson 1998). Finally, some models in the density and female reproductive condition analyses included two variables (i.e., time and one habitat variable) but possessed different numbers of model parameters (K) due to different correlation structures associated with repeated measures analyses and/or lack of variance among blocks.

## RESULTS

Mean downed wood volumes were 15.8 m<sup>3</sup>/ha (SD = 12.7 m<sup>3</sup>/ha) and 117.8 m<sup>3</sup>/ha (SD = 66.4 m<sup>3</sup>/ha) for the five low and high downed wood study units, respectively. Values for additional habitat features measured during the study, and a correlation matrix for habitat variables, are presented in Table 2.2 and Figure 2.3, respectively. For comparison, downed wood volumes and linear dimensions for pieces that qualify as suitable leave logs on each study unit according to the Regional Forester's Decision Notice to Eastside Forest Plan, Amendment No. 2 (USDA 1995) are presented in Appendix A.

During the four small mammal sample periods, 1,911 individuals from nine small mammal species were captured and marked. Yellow-pine chipmunks, golden-mantled ground squirrels, and deer mice made up 97% of the captures (Table 2.3). Capture probabilities across sample periods for chipmunks, ground squirrels, and mice ranged between 0.43 to 0.99, 0.77 to 0.99, and 0.71 to 0.99, respectively. The jackknife population estimator ( $M_h$ ; Burnham and Overton 1978, 1979) was ultimately selected for all three species based on apparent heterogeneity



Table 2.2. Values for the eight habitat features measured on 10 study units on five blocks in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon.

Study Unit	Downed Wood Volume (m <sup>3</sup> /ha)	Downed Wood Decay Class (1–3) <sup>a</sup>	Tree Basal Area (m <sup>2</sup> /ha)	Mean Tree dbh (cm)	Total Shrub Cover (%)	Bitterbrush Cover (%)	Tree/Shrub Regeneration (seedlings/ha)	Herb Cover (%)
<i>High Downed Wood Volume</i>								
Block 1	234.22	2.18	4.62	21.09	42.77	23.19	842.40	9.80
Block 2	102.32	2.86	5.38	27.77	23.01	10.83	936.00	27.34
Block 3	72.84	2.79	8.52	35.66	27.41	11.28	5803.20	28.08
Block 4	101.32	2.79	7.75	46.62	17.18	4.75	530.40	25.83
Block 5	78.40	2.80	7.25	27.51	20.26	9.31	967.20	19.65
Mean	117.82	2.68	6.70	31.73	26.13	11.87	1815.84	22.14
SD	66.40	0.28	1.64	9.80	10.03	6.83	2235.69	7.65
<i>Low Downed Wood Volume</i>								
Block 1	12.54	2.59	16.14	25.42	41.77	21.86	1872.00	3.71
Block 2	6.66	2.61	10.21	36.47	21.00	11.39	998.40	31.49
Block 3	6.32	2.67	5.57	34.38	31.57	10.90	2464.80	35.61
Block 4	16.48	2.82	6.56	44.28	24.68	8.54	1934.40	31.75
Block 5	37.17	2.56	7.46	27.24	37.00	14.94	11169.60	22.92
Mean	15.84	2.65	9.19	33.56	31.20	13.52	3687.84	25.09
SD	12.66	0.10	4.25	7.59	8.54	5.19	4215.37	12.82
Total Mean	66.83	2.67	7.95	32.64	28.66	12.70	2751.84	23.62
Total SD	70.14	0.20	3.31	8.32	9.18	5.79	3330.53	10.08

<sup>a</sup> – 1 = solid, 2 = moderate decay, 3 = highly decayed

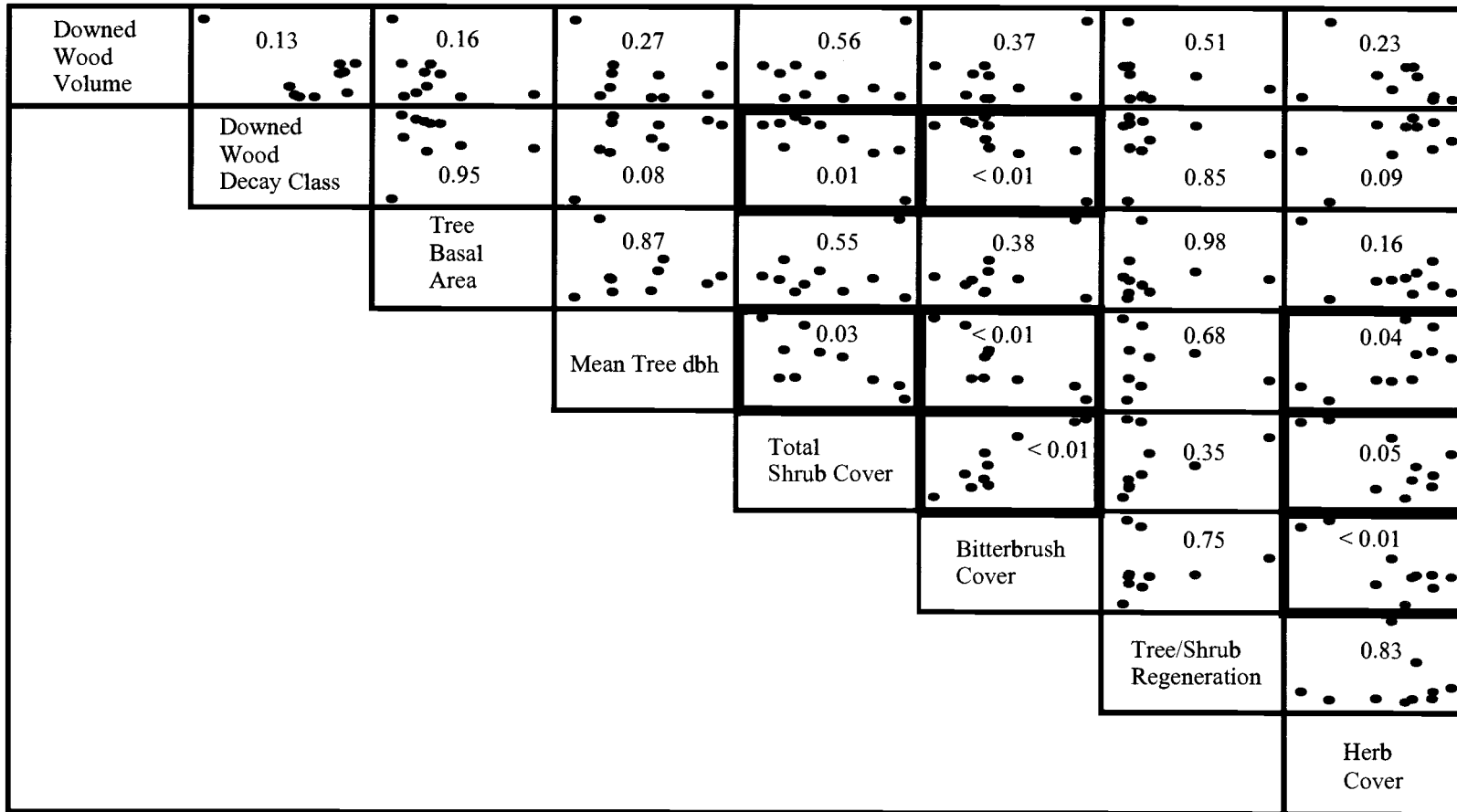


Figure 2.3. Correlations among habitat variables on 10 study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon. The p-value for each correlation is noted inside each box. Boxes outlined in bold indicate Pearson correlation coefficients > 0.6. Variables are described in the text and Table 2.2.

Table 2.3. Number of individual small mammals captured in live traps during four sample periods on 10 study units (some animals were captured multiple times within and among sample periods). All small mammal sampling took place in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon. Block 3 was not trapped during fall 2000 due to snow.

Family <i>Scientific Name</i>	Common Name	Early Summer 6/25-7/27, 2000	Late Summer 8/29-9/30, 2000	Fall 10/2-10/28, 2000	Early Summer 7/3-8/4, 2001	Total Individuals <sup>a</sup>
Soricidae						
<i>Sorex spp.</i>	Shrews	0	0	2	0	2
Leporidae						
<i>Sylvilagus nuttallii</i>	Mountain cottontail	2	0	0	0	2
Sciuridae						
<i>Sciurus douglasii</i>	Douglas' squirrel	0	1	0	0	1
<i>Spermophilus lateralis</i>	Golden-mantled ground squirrel	108	92	16	138	275
<i>Tamias amoenus</i>	Yellow-pine chipmunk	422	581	314	533	1139
<i>Tamias senex</i>	Allen's chipmunk	4	5	11	12	26
Heteromyidae						
<i>Perognathus parvus</i>	Great Basin pocket mouse	3	5	0	8	15
Muridae						
<i>Peromyscus maniculatus</i>	Deer mouse	155	193	145	76	450
Mustelidae						
<i>Mustela frenata</i>	Long-tailed weasel	1	0	0	0	1
Total Individuals <sup>b</sup>		695	877	488	767	
Total Captures <sup>c</sup>		2262	3176	1131	2605	
Trap Nights/Sample Period		2895	2811	2228	2881	

<sup>a</sup> – Number of uniquely-identified individual animals captured during the study.

<sup>b</sup> – Number of uniquely-identified individual animals captured during each sample period.

<sup>c</sup> – Number of animals captured during each sample period.

in capture probabilities across most grids, its relative robustness and low absolute bias (Burnham and Overton 1979), and its good population estimation ability when trap occasions are  $< 5$  but capture probabilities are  $> 0.05$  (White et al. 1982, Manning et al. 1995).

Although nine small mammal species were captured during the study, low encounters with six species prohibited statistically analyzing their habitat relationships. Capture patterns for two of these species, however, are worthy of mention. First, Allen's chipmunk (*Tamias senex*) captures were divided between high and low downed wood study units ( $n = 12$  and  $14$  individuals, respectively; Figure 2.4). Conversely, of 15 Great Basin pocket mice (*Perognathus parvus*) encountered, all but one were captured on low downed wood study units (Figure 2.5).

#### Analysis of Variance

Across the four seasonal small mammal sample periods, densities were similar between study units with high and low downed wood volumes for yellow-pine chipmunks ( $p = 0.82$ ), golden-mantled ground squirrels ( $p = 0.11$ ), and deer mice ( $p = 0.52$ ; Table 2.4, Figure 2.6). Seasonal effects on density were found for ground squirrels and mice, but not chipmunks (Figure 2.7). Golden-mantled ground squirrels were least dense during fall 2000 (adjusted  $p$  values  $< 0.01$ ), but densities were similar among all remaining sample period comparisons (adjusted  $p$  values  $> 0.9$ ). Deer mouse densities were lowest in early summer 2001 (adjusted  $p$

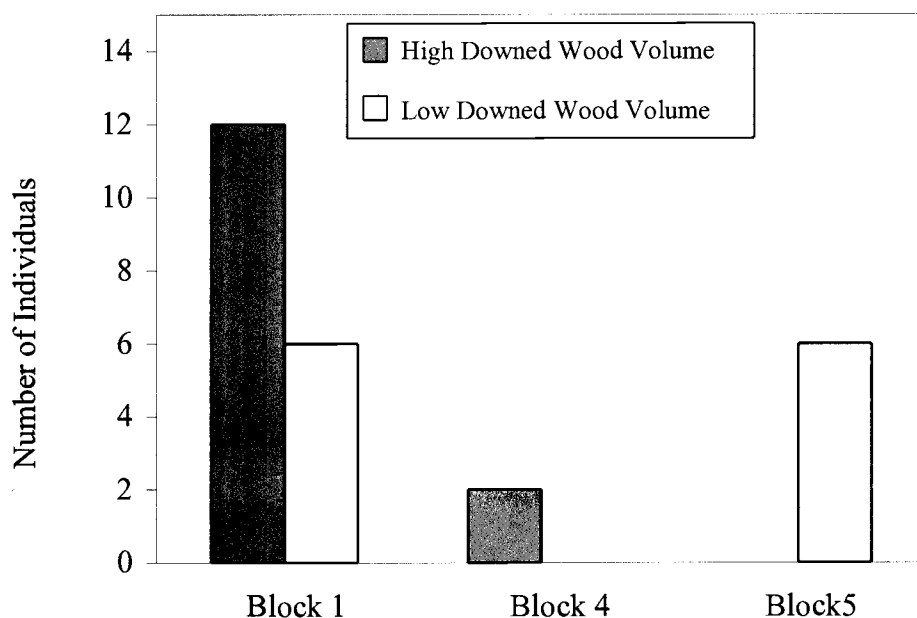


Figure 2.4. The number of Allen's chipmunk (*Tamias senex*) individuals captured on study units with high and low downed wood volumes on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were captured on study units with high (range: 72.8 to 234.2 m<sup>3</sup>/ha) and low (range: 6.3 to 37.2 m<sup>3</sup>/ha) downed wood volumes in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during 10,815 trap nights. Each downed wood volume condition was replicated across five blocks. No individuals were captured on blocks 2 or 3.

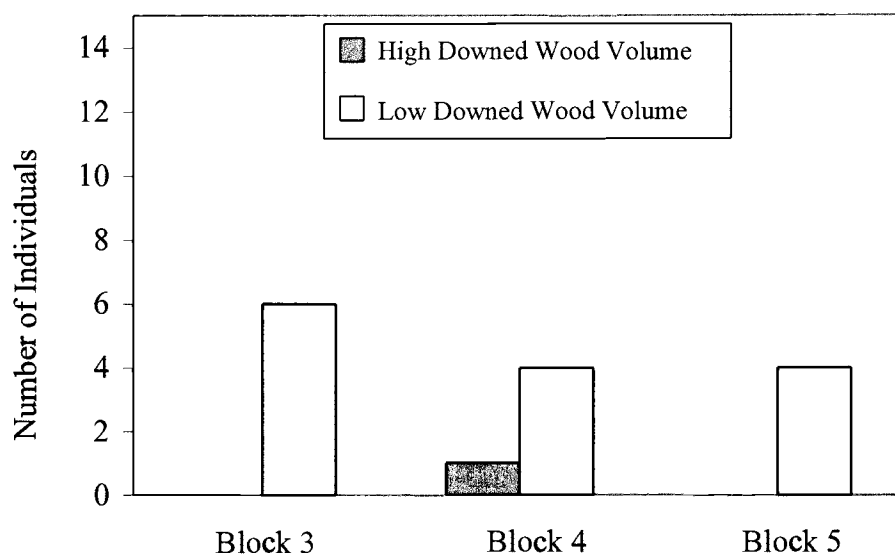


Figure 2.5. The number of Great Basin pocket mouse (*Perognathus parvus*) individuals captured on study units with high and low downed wood volumes on the Deschutes National Forest, Oregon in 2000 and 2001. Pocket mice were captured on study units with high (range: 72.8 to 234.2 m<sup>3</sup>/ha) and low (range: 6.3 to 37.2 m<sup>3</sup>/ha) downed wood volumes in ponderosa pine (*Pinus ponderosa*)/ antelope bitterbrush (*Purshia tridentata*) forests during 10,815 trap nights. Each downed wood volume condition was replicated across five blocks. No individuals were captured on blocks 1 or 2.

Table 2.4. Small mammal population parameter relationships between high (range: 72.8 to 234.2 m<sup>3</sup>/ha) and low (range: 6.3 to 37.2 m<sup>3</sup>/ha) downed wood study units in 2000 and 2001. Yellow-pine chipmunks (*Tamias amoenus*), golden-mantled ground squirrels (*Spermophilus lateralis*), and deer mice (*Peromyscus maniculatus*) were captured on study units in ponderosa pine (*Pinus ponderosa*)/ antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon during four sample periods: early summer, late summer, and fall 2000, and early summer 2001.

Species	ANOVA F	P value	Significant Correlations (p < 0.1)
<b>Yellow-Pine Chipmunk</b>			
Density	F <sub>1,4</sub> = 0.06	0.82	
Season	F <sub>3,22</sub> = 2.39	0.10	
Density x Season	F <sub>3,22</sub> = 0.52	0.68	
Reproductive Condition	F <sub>1,4</sub> = 0.63	0.67	
Year	F <sub>1,8</sub> = 1.22	0.29	
Reproductive Condition x Year	F <sub>1,8</sub> = 1.38	0.21	
Survival	F <sub>2,8</sub> = -0.74	0.69	
<b>Golden-Mantled Ground Squirrel</b>			
Density	F <sub>1,4</sub> = 4.05	0.11	
Season	F <sub>3,22</sub> = 12.63	< 0.001	*
Density x Season	F <sub>3,22</sub> = 2.11	0.13	
Survival	F <sub>2,3</sub> = 3.14	0.09	*
<b>Deer Mouse</b>			
Density	F <sub>1,4</sub> = 0.49	0.52	
Season	F <sub>3,22</sub> = 8.40	< 0.001	*
Density x Season	F <sub>3,22</sub> = 0.24	0.87	
Reproductive Condition	F <sub>1,4</sub> = 0.64	0.47	
Year	F <sub>1,8</sub> = 0.03	0.88	
Reproductive Condition x Year	F <sub>1,8</sub> = 0.23	0.65	

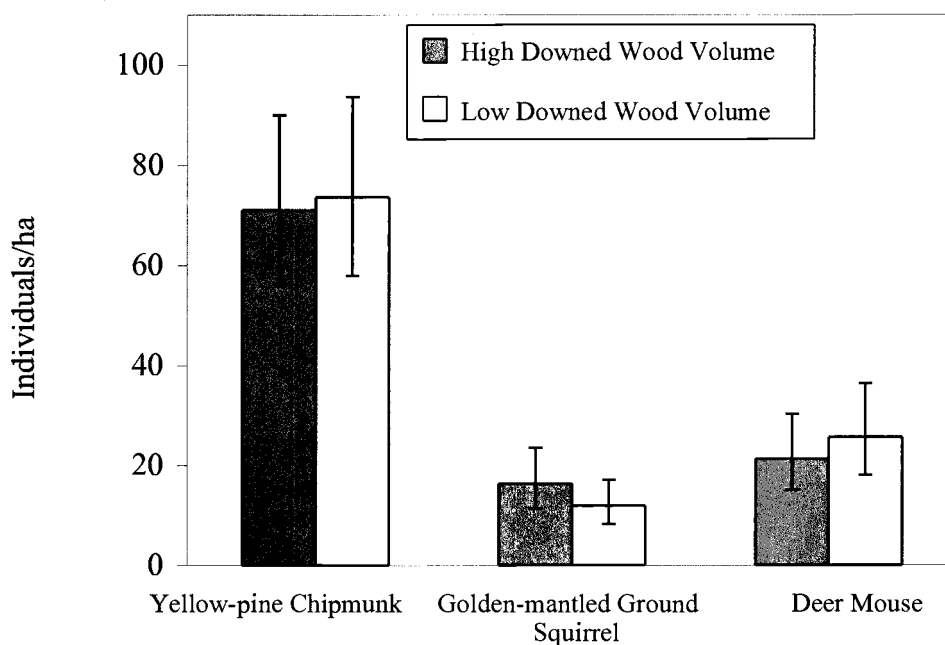


Figure 2.6. Small mammal density estimates on study units with high and low downed wood volumes on the Deschutes National Forest, Oregon in 2000 and 2001. Small mammals were captured on study units with high (range: 72.8 to 234.2 m<sup>3</sup>/ha) and low (range: 6.3 to 37.2 m<sup>3</sup>/ha) downed wood volumes in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during 10,815 trap nights. Each downed wood volume condition was replicated across five blocks. Vertical bars represent 90% confidence intervals. Densities were similar between units with high and low downed wood volumes for all small mammal species.



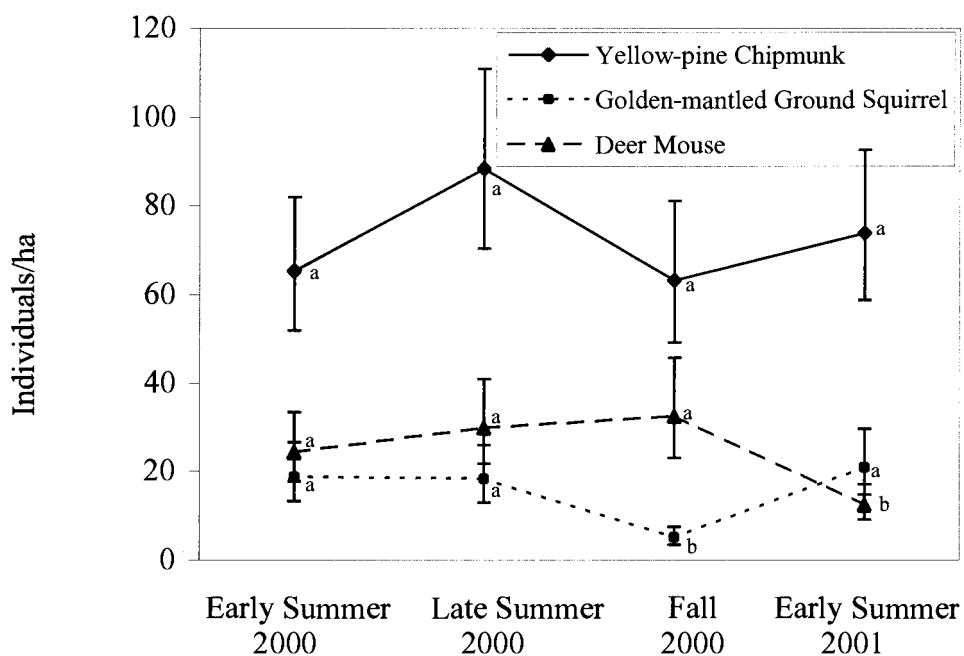


Figure 2.7. Small mammal density estimates on study units on the Deschutes National Forest, Oregon during four sample periods in 2000 and 2001. Small mammals were captured in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during 10,815 trap nights. Each downed wood volume condition was replicated across five blocks. Vertical bars represent 90% confidence intervals. Different letters within a species represent a significant difference ( $p < 0.1$ ) across seasons.

values  $< 0.05$ ), and similar across all remaining sample period comparisons (adjusted  $p$  values  $> 0.64$ ). Yellow-pine chipmunk densities were similar among all seasons (adjusted  $p$  values  $> 0.18$ ). No species demonstrated a significant interaction between season and downed wood volume ( $p$  values  $\geq 0.13$ ; Table 2.4).

Across the two early summer sample periods, the proportion of reproductive females in each adult population was similar between high and low downed wood study units for yellow-pine chipmunks ( $p = 0.67$ ) and deer mice ( $p = 0.47$ ; Table 2.4, Figure 2.8). Female reproductive condition was also similar between years for yellow-pine chipmunks ( $p = 0.29$ ) and deer mice ( $p = 0.88$ ). There was no significant interaction between year and downed wood volume for reproductive condition of either species ( $p$  values  $\geq 0.21$ ; Table 2.4).

Yellow-pine chipmunk survival was similar between high and low downed wood study units (adjusted  $p = 0.69$ ), but golden-mantled ground squirrel survival was greater (adjusted  $p = 0.09$ ) on units with high volumes of downed wood (Table 2.4, Figure 2.9). The odds for golden-mantled ground squirrel survival were 4.2 times higher (90% CI range: 1.1 to 15.8) on study units with high versus low downed wood volumes.

### Model Selection

Across seasons, tree basal area best explained yellow-pine chipmunk density (Table 2.5). Each  $3.6 \text{ m}^2/\text{ha}$  increase in tree basal area was associated with a 10% increase in chipmunk density (90% CI range: 4% to 16% more

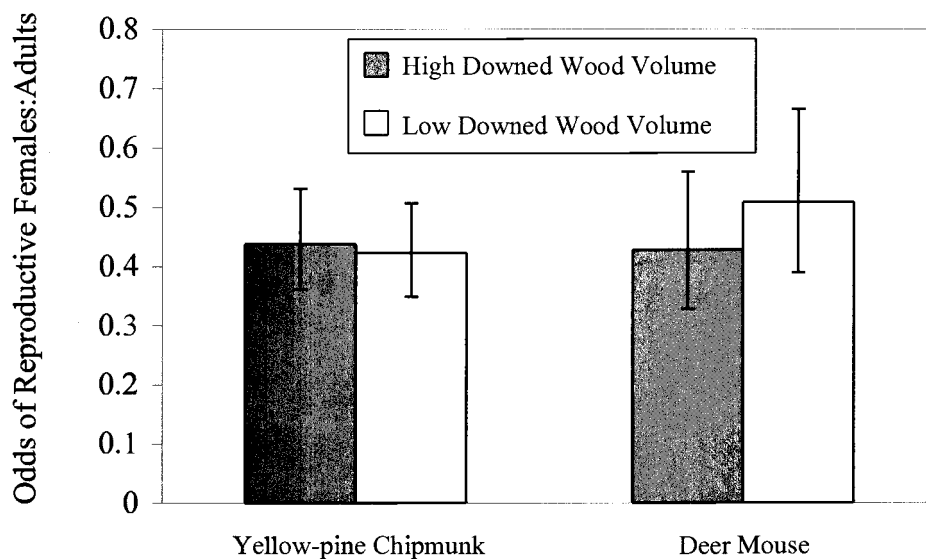


Figure 2.8. The odds of reproductive females in the entire adult population on study units with high and low downed wood volumes on the Deschutes National Forest, Oregon in 2000 and 2001. Small mammals were captured on study units with high (range: 72.8 to 234.2 m<sup>3</sup>/ha) and low (range: 6.3 to 37.2 m<sup>3</sup>/ha) downed wood volumes in ponderosa pine (*Pinus ponderosa*)/ antelope bitterbrush (*Purshia tridentata*) forests during early summer 2000 and 2001. Each downed wood volume condition was replicated across five blocks. Vertical bars represent 90% confidence intervals. The proportion of reproductive females was similar between units with high and low downed wood volume for both yellow-pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*).

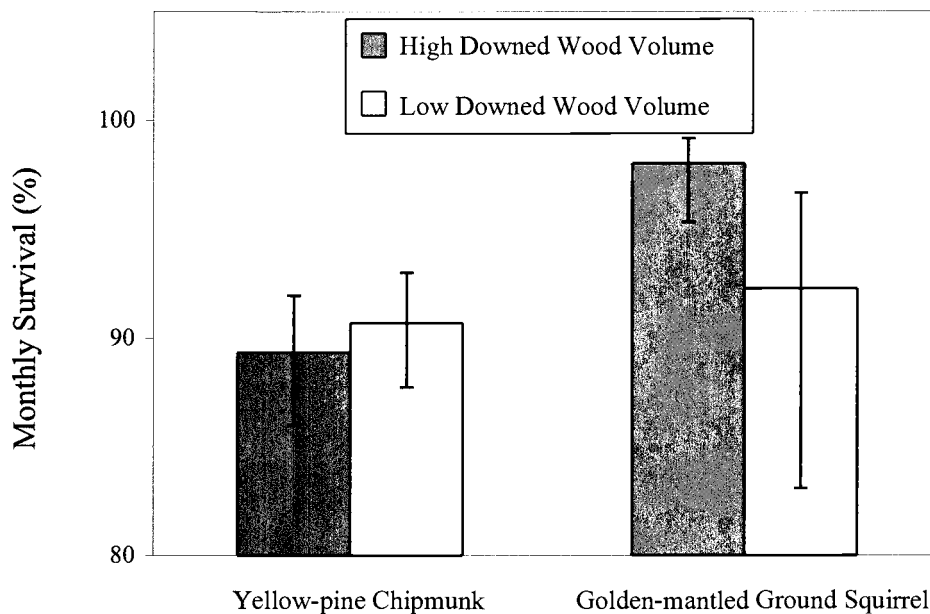


Figure 2.9. Mean monthly survival estimates for yellow-pine chipmunks (*Tamias amoenus*) and golden-mantled ground squirrels (*Spermophilus lateralis*) on study units with high and low downed wood volumes on the Deschutes National Forest, Oregon between 2000 and 2001. Survival estimates were obtained for chipmunks on 10 study units (five replicate blocks) and ground squirrels on seven study units (four replicate blocks) with high (range: 72.8 to 234.2 m<sup>3</sup>/ha) and low (range: 6.3 to 37.2 m<sup>3</sup>/ha) downed wood volumes in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests between early summer 2000 and early summer 2001. Vertical bars represent 90% confidence intervals. Ground squirrel survival was significantly higher on high versus low downed wood units ( $p = 0.09$ ) but chipmunks showed no significant difference.

Table 2.5. Model comparison across seasons using AIC for yellow-pine chipmunk (*Tamias amoenus*) density on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during four sample periods: early summer, late summer, and fall 2000, and early summer 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Tree Basal Area	9	35.27	0.00	0.859	+
Downed Wood Volume	10	41.27	6.00	0.043	
Downed Wood Decay Class	9	41.99	6.72	0.030	
Season (Null Model)	9	42.01	6.73	0.030	
Total Shrub Cover	10	43.79	8.52	0.012	
Tree/Shrub Regeneration	10	44.36	9.09	0.009	
Bitterbrush Cover	10	44.55	9.28	0.008	
Herb Cover	10	45.68	10.41	0.005	
Mean Tree dbh	10	45.73	10.45	0.005	

<sup>a</sup> – Season was analyzed alone and in combination with each habitat variable although not shown (e.g., Season + Tree Basal Area).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

individuals/ha; Figure 2.10). The ratio of Akaike weights for tree basal area versus downed wood volume (the second best habitat variable) indicated 20 times more support for tree basal area as the best explanatory variable for yellow-pine chipmunk density. Furthermore, downed wood decay class poorly predicted chipmunk density relative to tree basal area (Table 2.5).

Year in combination with herb cover, and year alone were the two best models explaining yellow-pine chipmunk reproductive condition (Table 2.6). However, because year alone was among the set of best explanatory variables for chipmunk reproductive condition, the strength of evidence that herb cover adequately explains reproductive condition better than annual variation is weak. There was little statistical evidence that downed wood volume or decay class were good explanatory variables for chipmunk reproductive condition (Table 2.6).

Multiple variables had strong relationships with yellow-pine chipmunk survival. Tree basal area, block alone, mean tree dbh, herb cover, downed wood volume, and downed wood decay class all had strong support for explaining yellow-pine chipmunk survival according to their  $\Delta$  values and Akaike weights (Table 2.7). Because block alone was among the set of best explanatory variables for chipmunk survival, the strength of evidence that any single habitat variable adequately explains survival better than blocking variation is minimal.

Across seasons, golden-mantled ground squirrel density was best explained by mean tree dbh and downed wood volume (Table 2.8). Each 3.3 cm increase in mean tree dbh was associated with a 10% increase in ground squirrel density (90%

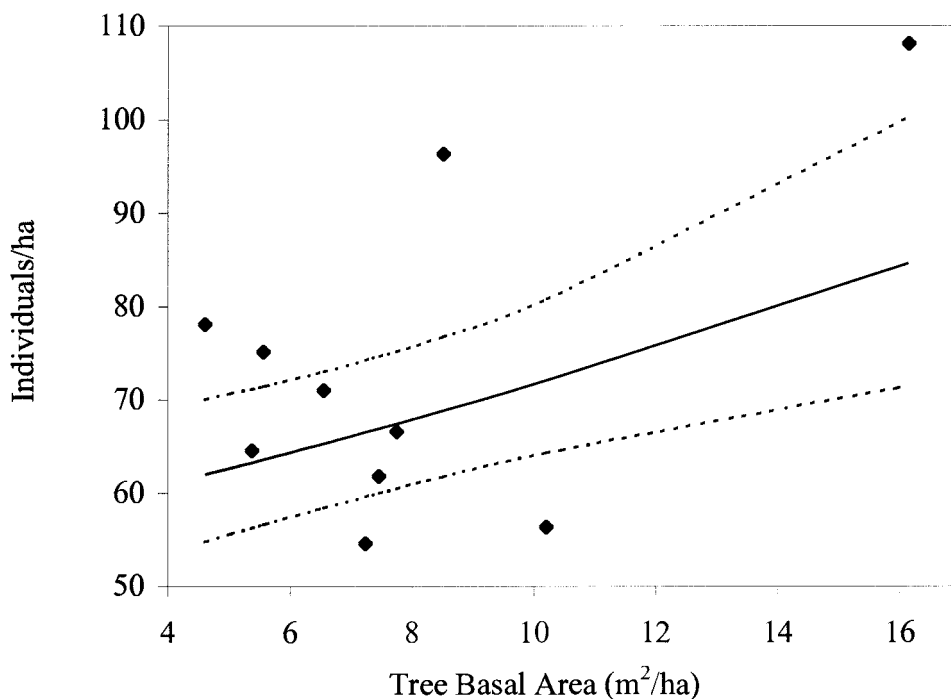


Figure 2.10. Yellow-pine chipmunk (*Tamias amoenus*) density estimates relative to tree basal area on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests. The dashed lines represent 90% confidence intervals around the regression line. Points represent the mean density estimate for each study unit for four sample periods: early summer, late summer, and fall 2000, and early summer 2001. The relationship between chipmunk density and tree basal area was significant ( $p = 0.002$ ).

Table 2.6. Model comparison across years using AIC for the proportion of reproductively active yellow-pine chipmunk (*Tamias amoenus*) females on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were captured on study units in ponderosa pine (*Pinus ponderosa*)/ antelope bitterbrush (*Purshia tridentata*) forests during two sample periods: early summer 2000 and 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Herb Cover	6	2.25	0.00	0.424	
Year (Null Model)	5	2.31	0.06	0.412	0
Total Shrub Cover	6	6.09	3.84	0.062	
Downed Wood Decay Class	7	6.63	4.38	0.047	
Bitterbrush Cover	7	8.87	5.62	0.015	
Downed Wood Volume	7	8.96	6.71	0.015	
Mean Tree dbh	7	9.17	6.92	0.013	
Tree Basal Area	7	10.90	8.65	0.006	
Tree/Shrub Regeneration	7	10.99	8.74	0.005	

<sup>a</sup> – Year was analyzed alone and in combination with each habitat variable although not shown (e.g., Year + Herb Cover).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .



Table 2.7. Model comparison across blocks using AIC for yellow-pine chipmunk (*Tamias amoenus*) survival on 10 study units on the Deschutes National Forest, Oregon between 2000 and 2001. Chipmunks were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests from early summer 2000 to early summer 2001.

Model <sup>a</sup>	K <sup>b</sup>	QAIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Tree Basal Area	7	956.03	0.00	0.230	
Block (Null Model)	6	956.70	0.67	0.165	0
Mean Tree dbh	7	957.28	1.24	0.123	
Herb Cover	7	957.62	1.58	0.104	
Downed Wood Volume	7	957.78	1.75	0.096	
Downed Wood Decay Class	7	958.02	1.99	0.085	
Tree/Shrub Regeneration	7	958.32	2.29	0.073	
Total Shrub Cover	7	958.68	2.64	0.061	
Bitterbrush Cover	7	958.73	2.70	0.059	

<sup>a</sup> – Block was analyzed alone and in combination with each habitat variable although not shown (e.g., Block + Tree Basal Area).

<sup>b</sup> – Number of model parameters including the intercept and re-encounter parameter.

<sup>c</sup> – Model QAIC<sub>c</sub> value.

<sup>d</sup> – Difference between model QAIC<sub>c</sub> value and minimum QAIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model QAIC<sub>c</sub> value – model QAIC<sub>c</sub> value  $\geq 2$ .

Table 2.8. Model comparison across seasons using AIC for golden-mantled ground squirrel (*Spermophilus lateralis*) density on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Ground squirrels were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during four sample periods: early summer, late summer, and fall 2000, and early summer 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Mean Tree dbh	8	81.48	0.00	0.472	+
Downed Wood Volume	8	81.84	0.36	0.394	+
Season (Null Model)	8	86.11	4.62	0.047	
Total Shrub Cover	9	87.60	6.11	0.022	
Tree Basal Area	9	87.82	6.33	0.020	
Bitterbrush Cover	9	88.00	6.51	0.020	
Herb Cover	9	89.28	7.80	0.010	
Tree/Shrub Regeneration	9	89.32	7.84	0.010	
Downed Wood Decay Class	9	89.57	8.08	0.010	

<sup>a</sup> – Season was analyzed alone and in combination with each habitat variable although not shown (e.g., Season + Mean Tree dbh).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

CI range: 3% to 17% more individuals/ha; Figure 2.11). Similarly, each 35.1 m<sup>3</sup>/ha increase in downed wood volume coincided with a 10% ground squirrel density increase (90% CI range: 3% to 17% more individuals/ha; Figure 2.12). Downed wood decay class poorly explained golden-mantled ground squirrel density (Table 2.8).

Out of the nine potential predictor variables for golden-mantled ground squirrel survival, only tree/shrub regeneration and downed wood decay class failed, albeit narrowly, the  $\Delta = 2.0$  criterion for inclusion in the set of best predictor variables ( $\Delta = 2.01$  and  $2.02$ , respectively; Table 2.9). The remaining variables had similar predictive merit as evidenced by their  $\Delta$  values and Akaike weights. Similar to yellow-pine chipmunk survival, because block alone was among the set of best explanatory variables, the strength of evidence that a single habitat variable explains survival better than blocking variation is weakened.

Three models best-explained deer mouse density: season alone, season and tree basal area, and season and total shrub cover (Table 2.10). Due to season alone having strong support for explaining deer mouse density, the strength of evidence that tree basal area or total shrub cover explains density better than seasonal variation is minimal. Neither downed wood volume nor decay class strongly explained deer mouse density (Table 2.10).

Year was the best predictor of deer mouse reproductive condition (Table 2.11). Downed wood volume and decay class did not contribute significantly to

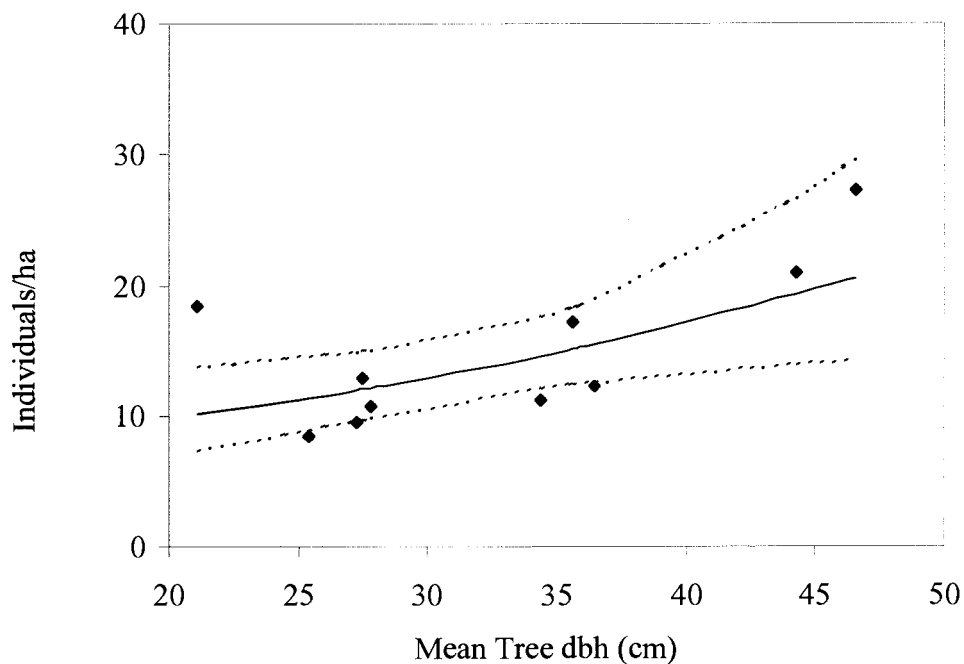


Figure 2.11. Golden-mantled ground squirrel (*Spermophilus lateralis*) density estimates relative to mean tree dbh on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Ground squirrels were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests. The dashed lines represent 90% confidence intervals around the regression line. Points represent the mean density estimate for each study unit for four sample periods: early summer, late summer, and fall 2000, and early summer 2001. The relationship between ground squirrel density and mean tree dbh across the four sample periods was significant ( $p = 0.02$ ).

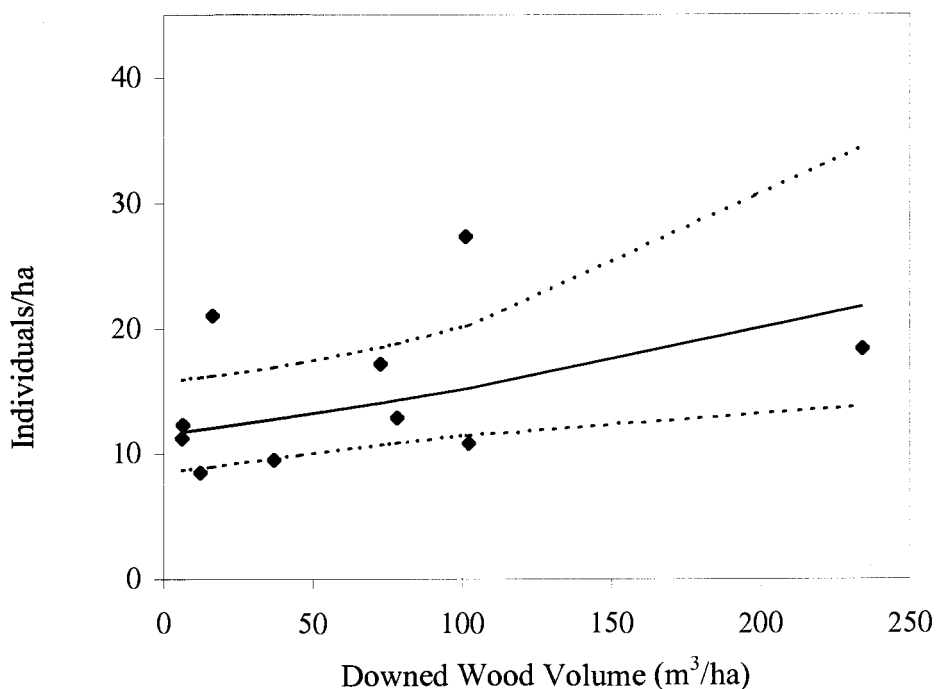


Figure 2.12. Golden-mantled ground squirrel (*Spermophilus lateralis*) density estimates relative to downed wood volume on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Ground squirrels were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests. The dashed lines represent 90% confidence intervals around the regression line. Points represent the mean density estimate for each study unit for four sample periods: early summer, late summer, and fall 2000, and early summer 2001. The relationship between ground squirrel density and downed wood volume was significant ( $p = 0.02$ ).

Table 2.9. Model comparison across blocks using AIC for golden-mantled ground squirrel (*Spermophilus lateralis*) survival on seven study units on the Deschutes National Forest, Oregon between 2000 and 2001. Ground squirrels were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests from early summer 2000 to early summer 2001. Survival could only be modeled on seven study units (low downed wood volume – block 2, block 3, block 4, block 5; high downed wood volume – block 3, block 4, block 5).

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Block (Null Model)	5	179.87	0.00	0.192	0
Mean Tree dbh	6	180.64	0.77	0.131	
Bitterbrush Cover	6	180.70	0.83	0.127	
Downed Wood Volume	6	180.83	0.96	0.119	
Total Shrub Cover	6	181.01	1.14	0.109	
Herb Cover	6	181.17	1.30	0.100	
Tree Basal Area	6	181.68	1.81	0.078	
Tree/Shrub Regeneration	6	181.88	2.01	0.070	
Downed Wood Decay Class	6	181.89	2.02	0.070	

<sup>a</sup> – Block was analyzed alone and in combination with each habitat variable although not shown (e.g., Block + Mean Tree dbh).

<sup>b</sup> – Number of model parameters including the intercept and re-encounter parameter.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

Table 2.10. Model comparison across seasons using AIC for deer mouse (*Peromyscus maniculatus*) density on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Mice were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during four sample periods: early summer, late summer, and fall 2000, and early summer 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Season (Null Model)	6	67.33	0	0.291	0
Tree Basal Area	7	69.10	1.78	0.119	
Total Shrub Cover	7	69.13	1.80	0.118	
Tree/Shrub Regeneration	7	69.44	2.12	0.101	
Herb Cover	7	69.65	2.33	0.091	
Downed Wood Volume	7	69.98	2.66	0.077	
Downed Wood Decay Class	7	70.18	2.85	0.070	
Mean Tree dbh	7	70.24	2.92	0.068	
Bitterbrush Cover	7	70.33	3.00	0.065	

<sup>a</sup> – Season was analyzed alone and in combination with each habitat variable although not shown (e.g., Season + Tree Basal Area).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

Table 2.11. Model comparison across years using AIC for the proportion of reproductively active deer mouse (*Peromyscus maniculatus*) females on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Mice were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during two sample periods: early summer 2000 and 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Year (Null Model)	6	103.46	0	0.447	0
Downed Wood Decay Class	7	106.27	2.81	0.109	
Tree Basal Area	7	106.28	2.82	0.109	
Downed Wood Volume	7	106.74	3.29	0.086	
Herb Cover	7	107.33	3.87	0.065	
Bitterbrush Cover	7	107.67	4.22	0.054	
Tree/Shrub Regeneration	7	108.03	4.57	0.046	
Mean Tree dbh	7	108.18	4.73	0.042	
Total Shrub Cover	7	108.21	4.76	0.041	

<sup>a</sup> – Year was analyzed alone and in combination with each habitat variable although not shown (e.g., Year + Downed Wood Decay Class).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .



explaining mouse reproductive condition (Table 2.11). A correlation summary of the model selection analyses is presented in Table 2.12.

## DISCUSSION

### Downed Wood Volume

Of the three small mammal species of interest, only the golden-mantled ground squirrel exhibited significant relationships with downed wood. Ground squirrel survival was greater on study units with high versus low downed wood volumes, and densities of this species increased with increasing downed wood volume. Although little, if any, past research has quantified the use of downed wood by golden-mantled ground squirrels, studies have qualitatively described these ground squirrels using logs and stumps for sunning and lookout sites (Grinnell et al. 1930, Maser et al. 1979), and logs are important structures for cover, feeding, breeding, and resting (Thomas 1979, Brown 1985, Bartels and Thompson 1993). In their description of golden-mantled ground squirrel burrows, Bihl and Smith (1998) noted that rocks were used frequently to conceal entrances and provide structural support. In the absence of prevalent rocky outcrops, as in this study, downed wood may serve compensatory structural functions in burrows, thus improving habitat and promoting increases in ground squirrel abundance and survival.

Table 2.12. Correlative relationships between population parameters and AIC model variables for yellow-pine chipmunks (*Tamias amoenus*), golden-mantled ground squirrels (*Spermophilus lateralis*), and deer mice (*Peromyscus maniculatus*) captured on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Small mammals were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests. Correlations are noted as 0, +, or – for variables of models when  $\Delta_i < 2$ , and the null model AIC value – model AIC value  $\geq 2$ .

Species	Population Parameter	Season <sup>a</sup> , Year <sup>b</sup> , or Block <sup>c</sup>	Downed Wood Volume (m <sup>3</sup> /ha)	Downed Wood Decay Class (1 – 3)	Tree Basal Area (m <sup>2</sup> /ha)	Mean Tree dbh (cm)	Total Shrub Cover (%)	Bitterbrush Cover (%)	Tree/Shrub Regeneration (#/ha)	Herb Cover (%)
Yellow-pine chipmunks	Density	a				+				
	Reproductive Condition	0 <sup>b</sup>								
	Survival	0 <sup>c</sup>								
Golden-mantled ground squirrels	Density	a	+				+			
	Survival	0 <sup>c</sup>								
Deer mice	Density	0 <sup>a</sup>								
	Reproductive Condition	0 <sup>b</sup>								

<sup>a</sup> – Density: early summer 2000, late summer 2000, fall 2000, and early summer 2001

<sup>b</sup> – Reproductive condition: early summer 2000 and 2001.

<sup>c</sup> – Survival: five geographically separated blocks.

Downed wood may also provide a foraging benefit, in that fungi are often associated with dead wood, and ground squirrels consume fungi. In mixed coniferous forests of the Sierra Nevada, Tevis (1952, 1953) found that in autumn, during years of low conifer seed production, golden-mantled ground squirrel stomachs contained up to 93 percent fungi by volume relative to other food sources. In these same forests, Pyare and Longland (2001) found hypogeous fungal spores in 100 percent of the golden-mantled ground squirrel stomachs examined, while in coniferous forests of Oregon, Maser et al. (1978) identified fungi as 44 percent of the stomach contents. Although downed wood frequently provides favorable substrate and cool, moist microclimates for the growth of hypogeous fungi (Maser et al. 1979, Hagan and Grove 1999), these fungi are likely to be less abundant in xeric versus mesic forests (States and Gaud 1997), as in this study. Consequently, fungi may be an unreliable food source for golden-mantled ground squirrels in the ponderosa pine forests of central Oregon, and they may be consumed only opportunistically (Pyare and Longland 2001).

In this study, neither yellow-pine chipmunks nor deer mice exhibited significant relationships with downed wood volume. Few studies have quantified the use of downed wood by yellow-pine chipmunks or deer mice for refugia, travel/escape routes, or lookout points (e.g., States 1976, Carter 1993, McMillan and Kaufman 1995, McCay 2000), and much of the data remains descriptive and qualitative (Grinnell et al. 1930, Broadbooks 1958, Maser et al. 1979, Thomas 1979). Further, no studies, to my knowledge, have quantified yellow-pine

chipmunk population-level relationships with downed wood, and the few studies that focused on deer mice have obtained differing results. For example, in coniferous forests of Canada, Bowman et al. (2000) found minimal relation between the abundance of deer mice and downed wood (diameter > 8 cm, length > 1 m), while Carter (1993) observed positive relationships between deer mice and downed wood (diameter > 1 cm, unspecified length).

Because yellow-pine chipmunks and deer mice do not rely heavily on fungi for their diet, potential increases in the fungal community with increases in downed wood volume may not greatly impact populations of these small mammals. In coniferous forests of the Sierra Nevada, yellow-pine chipmunk stomachs contained less than 50 percent fungi by volume (Tevis 1952, 1953, Maser et al. 1978, Maser and Maser 1987), and stomachs of deer mice from Wyoming, Colorado, and California contained  $\leq$  12 percent fungi (Jameson 1952, Williams 1959). In addition, stomachs of deer mice from coniferous forests of Oregon and Nevada seldom contained fungal spores (Maser et al. 1978, Pyare and Longland 2001). These data, coupled with the hypothesized low abundance of hypogeous fungi in semi-arid forest habitats with open canopies (States and Gaud 1997, Pyare and Longland 2001), likely reduces the dependence of these small mammals on fungi in the ponderosa pine forests of this study.

The weak chipmunk and mouse population relationships with downed wood in this study, suggest that downed wood is not the most significant habitat component for at least some small mammal species in central Oregon forests. For

yellow-pine chipmunks, basal area of ponderosa pine trees was an important habitat element. Likewise, in ponderosa pine forests of central Oregon under conditions of varying shrub cover, yellow-pine chipmunk densities were positively correlated with total shrub cover and bitterbrush cover (Chapter 3). Increasing tree basal area often corresponds with increasing canopy cover, resulting in cooler stand temperatures (Smith et al. 1997). Shrub cover also helps moderate soil temperatures in hot environments, and it provides small mammals with cover for predator avoidance (Wight et al. 1992, Brown et al. 1988). Thus, chipmunks in the semi-arid ponderosa pine forests studied here may gravitate toward trees and shrubs to minimize heat loading and their exposure to high daytime temperatures (Chappell 1978, States 1976). Logs probably did not provide sufficient and consistent levels of cover across the spatial scales utilized by this rather mobile diurnal rodent.

Deer mice, on the other hand, are one of the most versatile vertebrates in Oregon and Washington (Brown 1985). Because they are habitat generalists, and persist and thrive under wide ranging habitat conditions (Baker 1968, Verts and Carraway 1998), the influence of individual habitat features such as downed wood on mouse populations may be minimal, and instead, this species may be responding to a combination of resource availability and intraspecific competition (Van Horne 1982). Although only indirectly comparable with this research, numerous studies have identified similar deer mouse populations under conditions of differing forest structure resulting from timber harvesting, prescribed burning, and herbicide

application (e.g., Runciman and Sullivan 1996, Sullivan and Boateng 1996, Waters and Zabel 1998). Such research corroborates with the observations in this study of similar mouse populations across conditions of varying downed wood volume.

The low number of Allen's chipmunk and Great Basin pocket mouse encounters during this study necessitates further investigation before solid conclusions about their relationships with downed wood are justified, but I provide the following information to stimulate further research examining the relationships between these species and downed wood. First, although Allen's chipmunks have been descriptively documented using logs and stumps for refuge (Grinnell et al. 1930), similar captures within high and low downed wood units in this study suggest that numbers of these chipmunks may not be substantially influenced by downed wood volume. Instead, evidence indicates that this chipmunk is closely tied to increasing canopy cover in forested habitats (Sharpley 1983). Conversely, Great Basin pocket mice were only captured on units with low downed wood volume. Downed wood may inhibit over-ground movement of pocket mice, just as cheatgrass (*Bromus tectorum*), an often densely occurring grass in arid habitats, has been hypothesized to do in a bitterbrush-cheatgrass community (Gano and Rickard 1982). To my knowledge, no studies have quantified the relationships between these two small mammal species and downed wood, and the above information may help illustrate research opportunities. It should also be noted that the rather dry and open ponderosa pine forests of this study probably represent marginal habitat for both species; Allen's chipmunks are more commonly associated with

closed-canopy conifer forest or chaparral habitats (Grinnell et al. 1930, Tevis 1956, Sharples 1983), while Great Basin pocket mice tend to occur more often in arid sagebrush (*Artemesia* spp.) communities (Verts and Kirkland 1988, Verts and Carraway 1998). Downed wood is undoubtedly less abundant in arid sagebrush habitats, and may help explain the weak association with pocket mice in these forests.

### Downed Wood Decay

Downed wood decay did not emerge as an important habitat component for any of the small mammals examined. Although decayed downed wood may be important for highly insectivorous and mycophagous small mammals as habitat for insect and fungi food sources (Gilbert and Allwine 1991, Tallmon and Mills 1994, Carey and Johnson 1995), the three small mammal species of interest in this study are omnivorous, and they consume seeds and vegetation, in addition to fungi and invertebrates (Verts and Carraway 1998). Further, the invertebrate prey of yellow-pine chipmunks and golden-mantled ground squirrels appears to lean toward defoliating arthropods, not species associated with decaying logs. Tevis (1952, 1953) found the stomach contents of yellow-pine chipmunks and golden-mantled ground squirrels from coniferous forests of the Sierra Nevada, California, to contain from 13 to 64 and 0 to 16 percent insects by volume, respectively, and these quantities were heavily weighted toward arboreal and shrub inhabiting caterpillars. In ponderosa pine/antelope bitterbrush forests of central Oregon, these

chipmunks and ground squirrels have the ability to forage opportunistically on bitterbrush-defoliating invertebrates. For example, the western tent caterpillar (*Malacosoma californicum*), experiences periodic outbreaks (Mitchell 1990) and was abundant on many units during this study.

Deer mice, with their high diet plasticity, forage on the most abundant foods available. In the western Cascade Mountains of Washington, deer mice fed on a combination of seeds, fungi, vegetation, and invertebrates in forested and clearcut sites, but a lone individual encountered in a burned clearcut had consumed only invertebrates (Gunther et al. 1983). In coniferous forests of Arizona, California, Colorado, and Wyoming, deer mouse stomachs contained from 8 to 80 percent invertebrates by volume and 14 to 81 percent seeds by volume (Jameson 1952, Williams 1959, Goodwin and Hungerford 1979). As a result, given the variable diet and high seed consumption potential for deer mice inhabiting ponderosa pine and antelope bitterbrush forests, these mice are not likely to depend on food sources provided primarily by decayed logs.

Yellow-pine chipmunks, golden-mantled ground squirrels, and deer mice also may have failed to show significant relationships with downed wood decay because the full range of decay possibilities was not available across the study units. Sound downed wood was uncommon in these pine forests, thus possible functions provided by intact downed wood, including feeding stations, travel routes, and lookout sites, could not be weighed against functions provided by highly decayed wood.



## Temporal and Spatial Variation

In addition to the relationships between small mammal populations and habitat features, several responses were strongly influenced by temporal or spatial (blocking) variation. Temporal and spatial trends in seed production, predation, intra- or inter-specific competition, climate, and other habitat components may all influence small mammal population fluctuations through changes in reproduction, survival, and abundance (Jameson 1953, Terman 1968, Van Horne 1981, Fryxell et al. 1998, Maguire 1999, Bowman et al. 2001). Further, high levels of intra-specific variation among population responses may result from tradeoffs between density, reproduction, and survival (Van Horne 1983, Pulliam 1988) or a failure to examine habitat features having critical links to specific population parameters. As a result, more clearly understanding changes in small mammal populations may require examining not only their relationships with habitat components, but also the temporal variability of the resources provided by the habitat components.

## Conclusions

Results from this study suggest that golden-mantled ground squirrel density and survival are positively correlated with downed wood volume, whereas, yellow-pine chipmunk and deer mouse populations appear minimally affected by downed wood. Thus, managing ponderosa pine forests east of the Cascade Mountains in Oregon to emulate pre-European conditions through reductions in downed wood volume may negatively impact golden-mantled ground squirrel populations.

Conversely, although yellow-pine chipmunks and deer mice could be substantially influenced by other changes in forest structure during attempts to create primeval forests, alterations in downed wood volume alone appear minimally influential on their populations. Such postulation, however, requires caution, as attempts to truly emulate historical forest conditions will alter not only downed wood, but also a myriad of additional forest structures, and perhaps alter the utility and importance of downed wood for these small mammals.

The results also suggest that under current forest conditions, downed wood is a less critical habitat component for small mammals in the relatively xeric ponderosa pine forests of central Oregon than in more mesic forests west of the Cascade crest, where downed wood may be generally more abundant (Spies et al. 1988, Robertson and Bowser 1999). Thus west side forests may provide more opportunities for small mammals to use downed wood for nesting, foraging, and travel, especially, for highly insectivorous and mycophagous species. Even so, downed wood probably serves golden-mantled ground squirrels via structural functions related to burrow construction and foraging opportunities associated with hypogeous fungi. Conversely, yellow-pine chipmunk and deer mouse behavioral and physiological strategies probably reduce the value of downed wood as a habitat component. Likewise, other habitat features such as antelope bitterbrush cover, and the size, and abundance of ponderosa pine appear important for these eastside small mammal communities, as these habitat elements may largely replace food and cover functions provided by downed wood in more mesic forests.

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## CHAPTER 3

SMALL MAMMAL RELATIONSHIPS WITH ANTELOPE BITTERBRUSH IN  
CENTRAL OREGON

## ABSTRACT

Antelope bitterbrush (*Purshia tridentata*) is an important component of many ponderosa pine (*Pinus ponderosa*) forests in central Oregon because of the role it plays in forest wildfires, its potential benefit to forest productivity through Nitrogen fixation, and its importance as a seed source for small mammals and browse for mule deer (*Odocoileus hemionus*). Although much is understood regarding the importance of small mammal scatter-hoarding activities for bitterbrush seed dispersal and germination, little is known about bitterbrush impacts on small mammal populations. This study examines relationships between small mammal populations and various habitat features, with emphasis on antelope bitterbrush. Small mammals were live trapped during four sample periods from June through October 2000, and July and August 2001 in ponderosa pine/antelope bitterbrush forests on the Deschutes National Forest in central Oregon. Density, reproductive condition, and survival of the three most abundant small mammal species [yellow-pine chipmunk (*Tamias amoenus*), golden-mantled ground squirrel (*Spermophilus lateralis*), and deer mouse (*Peromyscus maniculatus*)] were estimated on five study units with high ( $\bar{x} = 31.2\%$ ) and five units with low ( $\bar{x} = 9.2\%$ ) shrub cover. Analysis of Variance tests indicated that only yellow-pine

chipmunk densities were significantly impacted by shrub cover ( $p = 0.05$ ). Chipmunk densities were 57% higher on study units with high versus low shrub cover. Likewise, regression modeling suggested that, relative to other habitat variables examined, total shrub cover and bitterbrush cover were important for yellow-pine chipmunk densities. Each 4.4% increase in total shrub cover and each 2.3% increase in bitterbrush cover coincided with 10% increases in chipmunk density. Finally, temporal and spatial variability were important for many of the population parameters examined, indicating considerable population variability among seasons, years, and locations.

## INTRODUCTION

Ponderosa pine (*Pinus ponderosa*) forests of the western United States have undergone major alterations since settlement by Europeans in the mid- to late-1800's, primarily due to land management activities such as grazing, logging, and fire suppression (Cooper 1960, Agee 1994, Harrod et al. 1999, Moore et al. 1999). In contrast to present day ponderosa pine forests of central Oregon, pre-European forests often experienced frequent fires burning every 4 to 24 years (Bork 1985), which resulted in reduced shrub cover, higher forb and ground cover, and temporally and spatially aggregated cohorts of ponderosa pine (Morrow 1985).

Antelope bitterbrush (*Purshia tridentata*) is a dominant shrub in many ponderosa pine forests east of the crest of the Cascade Mountains and has become established at higher than historical densities, while simultaneously increasing in

decadence and senescence (Clements and Young 1997). These altered shrub conditions affect other components of the forest ecosystem. For instance, shrubs constitute 35 to 84% of the mule deer (*Odocoileus hemionus*) diet during summer and fall (Gay 1998), and antelope bitterbrush can average up to 53% of the mule deer winter diet (Guenther et al. 1993), but the reduced nutritive quality of decadent and senescent bitterbrush requires greater consumption for the same nutritive return. Further, bitterbrush can help maintain and increase site productivity in ponderosa pine forests through soil Nitrogen accretion (Busse et al. 1996, Busse 2000), while decadent and/or live bitterbrush with needle drape poses considerable wildfire risk. Wildlife managers and researchers have begun investigating the implications of emulating historical forest conditions, including reductions in bitterbrush cover, on potentially catastrophic wildfires, forest productivity, and wildlife habitat (Moore et al. 1999, Busse et al. 2000, Tiedemann et al. 2000).

The response of bitterbrush to natural and prescribed fire, as well as mowing, to reduce standing biomass and increase shrub vigor is often variable and can be influenced by plant genetics, geographic location, soil type, moisture condition, and plant age. These interacting factors make sprouting success following disturbance difficult to predict (Blaisdell and Mueggler 1956, Nord 1965, Cook et al. 1994, Busse et al. 2000, Jabbes 2000). For example, in central Oregon, moderate bitterbrush sprouting occurred following spring underburns, which contradicts other studies in the region, and emphasizes the site-specific response of bitterbrush to fire (Busse et al. 2000). Generally, however, antelope bitterbrush

sprouts poorly following natural or prescribed fire, and successful regeneration is often most effectively achieved through new seedlings (Driscoll 1963, West 1968, Sherman and Chilcote 1972, Martin 1983). Alternatively, although the short-term response of antelope bitterbrush to mowing appears more positive, resulting in increased leader growth (Jones 1983), the long-term and large-scale effects of mowing are largely unknown (Blaisdell and Mueggler 1956, Ferguson and Basile 1966, Clark et al. 1982).

Bitterbrush seedling regeneration following fire is significantly impacted by seed dispersal and seedling establishment accomplished through small mammal foraging activities (West 1968, Sherman and Chilcote 1972, Vander Wall 1994). The yellow-pine chipmunk (*Tamias amoenus*), for example, harvests bitterbrush and pine seeds during the late summer and early fall, and deposits them as caches in the soil. Cached seeds are often located in favorable microsites (e.g., mineral soil) some distance from the parent plant, and they possess a higher probability of survival than seeds not cached (West 1968, Sherman and Chilcote 1972, Vander Wall 1992, 1994, 1995). Conversely, impacts on bitterbrush by small mammal species that cache seeds, such as the golden-mantled ground squirrel (*Spermophilus lateralis*) and deer mouse (*Peromyscus maniculatus*), are poorly understood (Vander Wall 1992), although they are largely regarded as important seed and seedling predators (McKeever 1964, Sullivan 1979).

In ponderosa pine forests of central Oregon, yellow-pine chipmunks, golden-mantled ground squirrels, and deer mice dominate the small mammal



community. In addition to the ecological roles these animals fill as consumers and dispersers of seed (Tevis 1952, Vander Wall 1992, 1994), they also consume and disperse hypogeous fungi (Tevis 1952, 1953, Maser et al. 1978, Pyare and Longland 2001) and serve as prey for avian and mammalian predators (Sutton 1992, Bartels and Thompson 1993, Verts and Carraway 1998). Currently, however, we have sparse data on the relationships of these small mammals with antelope bitterbrush and other habitat components in semi-arid ponderosa pine forests.

The objectives of this study, therefore, were: 1) to test for differences in yellow-pine chipmunk, golden-mantled ground squirrel, and deer mouse density, reproductive condition, and survival between forested areas with high and low shrub cover; 2) to identify associations of small mammal population parameters with different habitat features, with an emphasis on shrub and live bitterbrush cover; and 3) to quantify habitat relationships across different seasons and years to assess temporal variability in small mammal population trends. Results from this study will contribute to our knowledge of eastside forest ecology and can be applied to the development of forest management plans that consider small mammal habitat needs.

## METHODS

### Study Area

This study took place on the Bend/Fort Rock Ranger District of the Deschutes National Forest in central Oregon in areas supporting the ponderosa pine/antelope bitterbrush (*Purshia tridentata*)/Idaho fescue (*Festuca idahoensis*) plant association which typically occurs on pumice soils (Franklin and Dyrness 1988, Volland 1988). Across the study area, annual precipitation ranges from approximately 300 to 540 mm, mostly in the form of snow (National Weather Service recording stations near Bend and Wickiup Dam, Oregon; USDC 2002).

Initially, I located forested areas on the Deschutes National Forest based on the plant association and stand age from GIS maps, and then visually assessed the areas according to homogeneity of the plant community, the estimated number of trees per hectare, mean tree diameter, and downed wood volume. I then selected paired study units (blocks) based on a visual assessment of total shrub cover; one study unit possessed relatively low (range: 4.5 to 13.1%) and the other high (range: 21.0 to 41.8%) shrub cover (Figure 3.1). Subsequently, I will refer to these study unit conditions as “low” and “high” shrub, respectively. Due to logistical limitations in small mammal sampling and to ensure that animals could not move among blocks, only five geographically scattered blocks (separation of each block > 16 km) were included in the research.

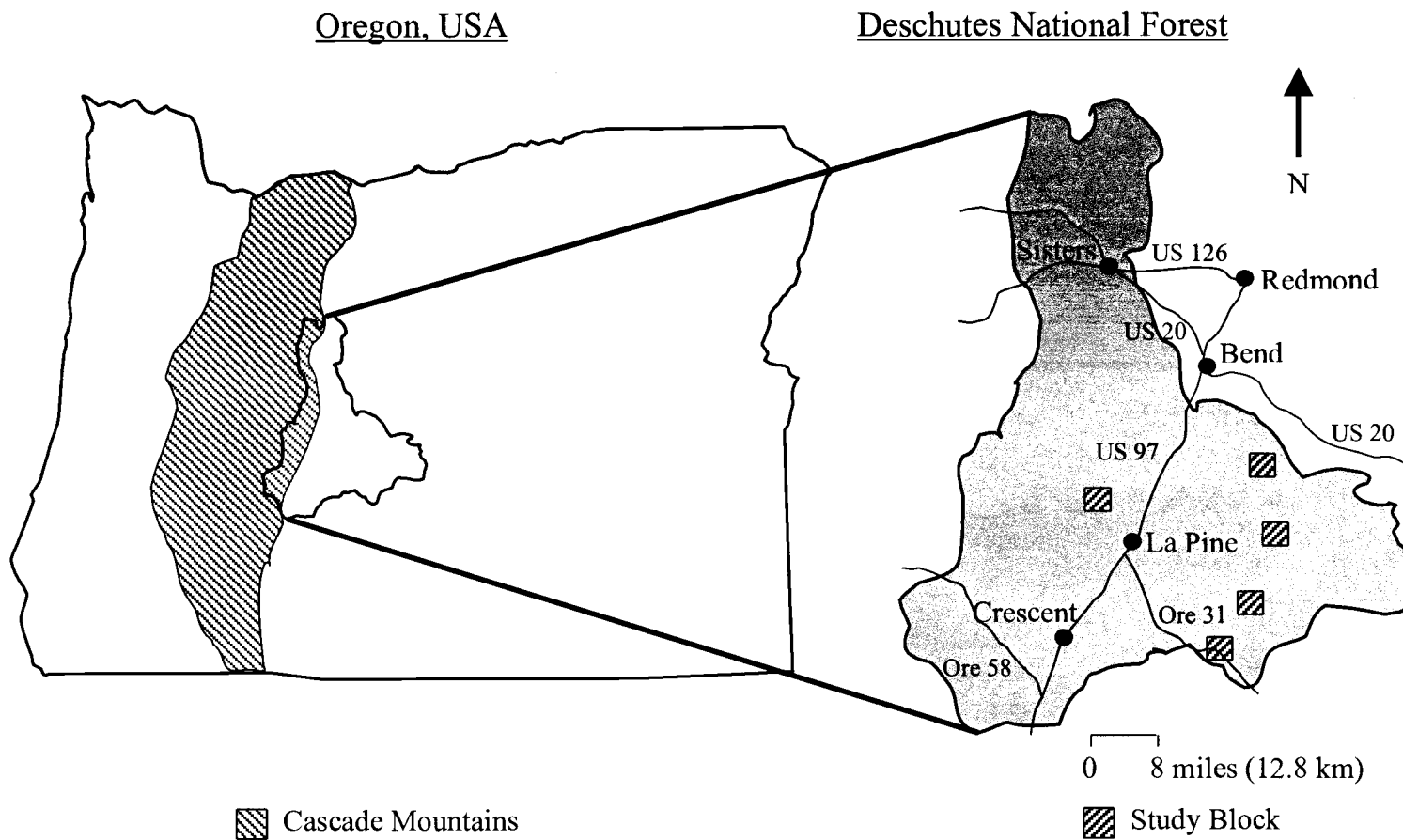


Figure 3.1. The locations of five study blocks in ponderosa pine (*Pinus ponderosa*) forests on the Deschutes National Forest, east of the Cascade crest, Oregon. Each block is comprised of one study unit with one high shrub cover ( $\bar{x} = 31.2\%$ ) and one study unit with low shrub cover ( $\bar{x} = 9.2\%$ ).

The 10 study units selected range in elevation from 1285 to 1505 m and were characterized by discontinuous overstory canopies with medium to large ponderosa pines dominating the overstory (USDA 1995); a small number of lodgepole pines (*Pinus contorta*) were found on three of the study units. The mean diameter of ponderosa pines on the 10 units ranged from 25 to 62 cm, mean density ranged from 33 to 137 trees/ha, and canopy cover was 16 to 42%. Antelope bitterbrush comprised 69 to 99% of the shrub cover on the 10 units, while rabbitbrush (*Ericameria bloomeri*), rubber rabbitbrush (*E. nauseosus*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*) were less common. Idaho fescue, western needle grass (*Achnatherum occidentale*), and squirreltail (*Elymus elymoides*) were common grasses. Three of the five low shrub units received underburn treatments by the U.S.D.A. Forest Service between 1995 and 1999, and the remaining two units were machine mowed in 1998 and 1999. The burned and mowed areas ranged in size from approximately 27 to 171 ha (M. Drapeau, Deschutes National Forest, pers. com.). Two of the five high shrub units underwent shelterwood harvest in the early 1980's, and all 10 units were probably railroad logged between 1920 and 1950 (M. Deppmeier, Deschutes National Forest, pers. com.). The five high shrub units were also used in a concurrent study examining small mammal relationships with varying downed wood volumes (identified as low downed wood units in Chapter 2).

## Habitat Sampling

On each 0.64-ha study unit I established one 8- x 8-sampling grid with 10-m spacing between grid points (Figure 3.2). On each unit, I measured eight habitat features with potential for influencing small mammal abundance, reproduction, and survival based on previous life history and habitat relationship studies. Percent total shrub cover was quantified using the line-intercept method (Bonham 1989) along eight 80-m parallel transects passing over each grid point. Shrub cover was measured in centimeters as the continual distance of all shrub components separated by  $< 5.0$  cm that crossed the vertical plane of the horizontal transect. Additionally, I visually estimated the percent of live antelope bitterbrush cover crossing each transect as an index of plant vigor and potential seed production. Hereafter, the term “bitterbrush cover” will be used when discussing live bitterbrush cover.

I calculated tree basal area ( $\text{m}^2/\text{ha}$ ) from the diameter at breast height (dbh) of all ponderosa pine trees  $> 4$ -cm dbh within 3 m either side of each transect (i.e., 80- x 6-m strip plots). Mean tree dbh for each unit was calculated as the sum of all ponderosa pine dbh values divided by the total number of ponderosa pine trees on that unit. Because the major perceived benefit of trees for small mammals is a combination of seeds for forage and shade from large canopies, lodgepole pines were excluded from the analyses due to their low frequency among and within study units, and their small size relative to ponderosa pines on the study units (mean dbh: lodgepole = 19.8 cm, ponderosa = 38.0 cm).

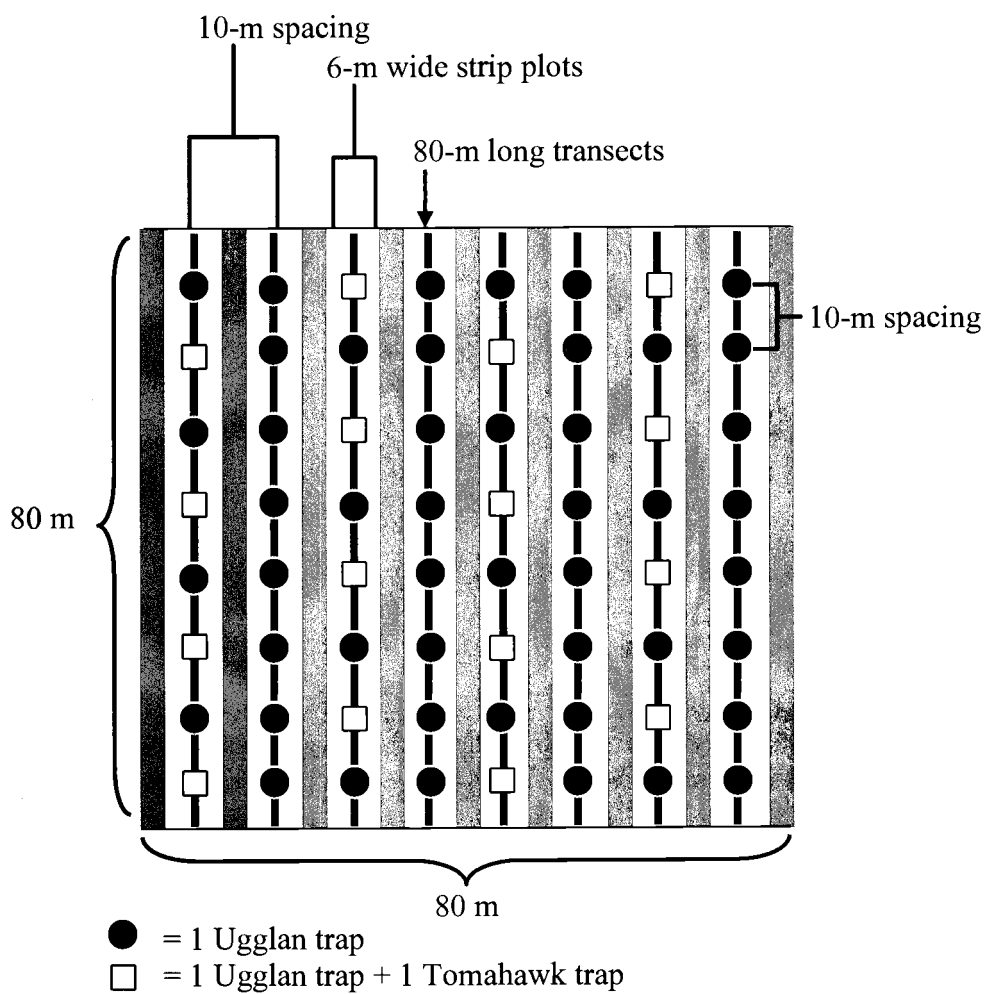


Figure 3.2. Study unit sampling design. Downed wood volume and char were sampled by complete census within each 80- x 80-m study unit. Additional habitat features were measured on the eight 80-m transects and within the 6-m wide strip plots. Small mammal traps were placed every 10 m in an 8- x 8-grid.

Tree and shrub regeneration were combined into the single category “tree/shrub regeneration” as a measure of live shoots available for consumption by small mammals. I measured regeneration as seedlings per hectare in 0.5- x 0.5-m plots at 2-m intervals along each transect. Tree regeneration included seedlings < 1.4-m tall, and shrub regeneration included seedlings < 2-yr old based on height, typically < 7.5-cm tall, and absence of branching (Hormay 1943). Percent herb cover was estimated using point intercepts along each transect at 0.5- and 1-m intervals and was defined as the percent of ground cover on each unit that consisted of broad-leafed and non-woody plants, grasses, or sedges.

I quantified downed wood volume ( $\text{m}^3/\text{ha}$ ) by complete census on each study unit and measured the large-end (LED) and small-end diameters (SED) and total length for each wood piece > 0.5-m long with LED > 10 cm and SED > 1 cm. I calculated the volume for each wood piece using the formula for a frustrum of a cone (Harmon and Sexton 1996),

$$V = L(\text{LED} + (\text{LED} \times \text{SED})^{0.5} + \text{SED})/3 \quad (1)$$

where, V = volume ( $\text{m}^3$ )

L = piece length (m)

LED = large-end diameter (m)

SED = small-end diameter (m).

Finally, because observations suggest that logs charred by fire are differentially used by wildlife (Maser et al. 1979), the amount of downed wood char was

estimated using two categories. Class-0 logs were charred on  $\leq 50\%$  of their surface area; class-1 logs were charred  $> 50\%$ .

### Small Mammal Sampling

An 8- x 8-trapping grid was overlain on the sampling grid of each study unit (Figure 3.2). At each grid point, I placed one multi-capture Ugglan® model 3 (250 x 78 x 65 mm) wire-mesh live-trap (64 traps/study unit). Additionally, one Tomahawk® model 102 (406 x 127 x 127 mm) wire-mesh live-trap was placed at alternating grid points on alternating rows (16 traps/study unit). All traps were placed in protective cardboard containers and thoroughly covered with available bark pieces, wood, or vegetation to minimize animal exposure to heat and precipitation. Each trap was locked open and pre-baited with sunflower seeds four days prior to trapping. While live trapping, each trap was baited with one grape and several black-oil sunflower seeds, and provided with cotton or wool for thermal insulation.

I simultaneously trapped small mammals on both study units in one block for four consecutive days (24-hour periods). I randomly trapped each of the five blocks consecutively, one per week, for five weeks within a sample period. All blocks were trapped a total of four sample periods in 2000 and 2001, with the exception that block 3 was not trapped in fall 2000 due to unexpected snow in October 2000, precluding access to the block. Small mammal trapping spanned 14 months and included: early summer 2000 (June 25 to July 27), late summer 2000



(August 29 to September 30), fall 2000 (October 2 to October 28), and early summer 2001 (July 3 to August 4). Hereafter, the terms “season” and “year” will be used when discussing different sample periods within and between years, respectively.

Each captured animal received two uniquely numbered ear tags, one in each ear. I also recorded the capture status (new or recapture), species, weight, sex, and female reproductive condition (reproductive or nonreproductive) of each individual captured. Females with distended abdomens (pregnant), large fleshy mammae, and visible lactation were recorded as reproductively active. Minimum weights from known adult yellow-pine chipmunks ( $> 35$  g) and golden-mantled ground squirrels ( $> 113$  g), based on their capture histories (i.e., captured in both 2000 and 2001;  $n = 75$  and 16, respectively), were used to classify the remaining individuals as adults or juveniles. Because only one deer mouse was captured in both 2000 and 2001, adult mice ( $> 15$  g) were separated from juveniles based on the lowest weight of reproductively active individuals.

Because of the difficulty in distinguishing the yellow-pine chipmunk from its congener, the least chipmunk (*Tamias minimus*), in the field (Carraway and Verts 1995) coupled with the previously cited rarity of the least chipmunk within tree lines (States 1976, Chappell 1978), I assumed that all captured chipmunks were yellow-pine chipmunks. If least chipmunks were captured, their infrequent encounters should not have significantly influenced the results.

The Institutional Animal Care and Use Committee at Oregon State University approved all mammal-sampling methods (permit no. 2419). All animals were captured under Oregon Department of Fish and Wildlife Scientific Taking Permit nos. 097-00 and 113-01.

### Density

Because enumeration methods (e.g., number of individuals captured) may be negatively biased and potentially inappropriate for interspecific or habitat comparisons due to possible violation of the assumption of equal capture probabilities (Nichols and Pollock 1983, Nichols 1986), I used closed population models in the population estimation program, CAPTURE (Otis et al. 1978; Rexstad and Burnham 1991), to estimate population size on each study unit for each sample period. CAPTURE adjusts population estimates according to differing capture probabilities due to influences of time, behavior, and heterogeneity. As a result, population comparison among habitats and species should be more accurate (Nichols and Pollock 1983, Nichols 1986, Slade and Blair 2000). I independently selected a single population size estimator for each small mammal species to minimize estimation differences of population size due to biases among estimators.

For each species I calculated the mean maximum distance moved (MMDM) in CAPTURE to estimate the effective trapping area on each study unit (Wilson and Anderson 1985). This distance was used to calculate the boundary strip width (W) where,

$$W = 0.5 \times \text{MMDM}, \quad (2)$$

and this width was added to all sides of the respective study unit. Population estimates were divided by the effective trapping area for each species on each unit to obtain density estimates (individuals/ha).

### Reproductive Condition

As expected, the majority of females exhibiting signs of reproductive activity were captured during the two early summer sample periods (Jameson 1953, Broadbooks 1958, McKeever 1964). Consequently, only data from these periods in 2000 and 2001 were used to estimate the proportion of reproductively active females in the entire adult population for each species on each study unit. I used these proportions as an index of adult reproductive potential. Due to problematic data (e.g., low observer certainty), golden-mantle ground squirrel reproductive condition was not analyzed.

### Survival

I used program MARK (Version 2.0; White and Burnham 1999) to calculate a single estimate of monthly apparent survival on each study unit over the period of study. MARK provides estimates of apparent survival for marked animals based on re-encounter histories and performs model comparisons using Akaike's Information Criterion (AIC) involving time, group, and habitat effects to evaluate their relative importance (White and Burnham 1999). The term apparent

survival is the probability that an animal is alive and available for recapture when death and emigration cannot be differentiated (White and Burnham 1999).

Hereafter, the term “survival” will be used when discussing apparent survival.

Only adult individuals were used in the survival analyses to reflect longevity in the territorial breeding population rather than mobility of immigrating and emigrating juveniles. Due to insufficient adult recaptures among sample periods that would affect the reliability of survival estimates, not all study units or species were analyzed. Survival was estimated for yellow-pine chipmunks on all 10 study units, golden-mantled ground squirrel survival was estimated on seven units, and deer mouse survival was not estimated.

#### Analysis of Variance

A blocked Analysis of Variance (ANOVA) was performed for each species to test for differences in small mammal density, reproductive condition, and survival between study units with high and low shrub cover. Density and reproductive condition analyses included repeated measures to account for the repeated population sampling and interaction terms for season or year and shrub cover. Because a single mean monthly survival estimate was calculated for each study unit, survival tests did not include repeated measures or interactions. Due to problematic data, differences in golden-mantled ground squirrel reproductive condition (e.g., low observer certainty) and deer mouse survival (e.g., infrequent adult captures and recaptures) were not tested. Because real differences can be

masked by natural variability in observational field studies, ANOVA results were tested at  $\alpha = 0.1$  to increase the ability to detect small mammal population differences. In addition, Tukey-Kramer adjustments and Dunnett's tests (Ramsey and Schafer 1997) were used to calculate confidence intervals around means reflective of multiple comparisons among sample periods and studies (i.e., high shrub units were also used in a companion downed wood study: see Chapter 2), and the resulting p-values are denoted as "adjusted p." All ANOVA analyses were performed in SAS, Version 8 (SAS Institute, Inc. 1999).

### Model Selection

AIC, and multiple linear and logistic regression were used to examine small mammal density, reproductive condition, and survival relationships with habitat features (Burnham and Anderson 1998). This approach engages the concept of model selection and uncertainty, best inference given the data, and a priori model development (Anderson et al. 2000). In practice, I utilized the second order criterion,  $AIC_c$  (Anderson et al. 2001),

$$AIC_c = -2\log(\mathcal{L}(\hat{\theta}|y)) + 2K + (2K(K+1))/(n-K-1) \quad (3)$$

where,  $(\mathcal{L}(\hat{\theta}|y))$  = maximized log-likelihood value

K = number of parameters in a model

n = sample size when  $n/K < 40$ .

Additionally, I checked the data for overdispersion (Ramsey and Schafer 1997) and when present, used the quasi-likelihood model selection (Burnham and Anderson 1998), QAIC<sub>c</sub>,

$$\text{QAIC}_c = [-2\log(\hat{f}(\hat{\theta}|y))]/\hat{c} + 2K + (2K(K+1)/(n-K-1)) \quad (4)$$

where,  $\hat{c}$  = variance inflation factor.

Models were ranked according to the difference between the AIC value for a given model and the lowest AIC value in the candidate set,

$$\Delta_i = \text{AIC value} - \text{AIC min} \quad (5)$$

where, AIC min = the smallest value in the candidate set.

The value,  $\Delta_i$ , allows a strength of evidence comparison among models, where increasing  $\Delta_i$  values correspond with decreasing plausibility of the fitted model being a “best” approximating model(s) in the set (Anderson et al. 2000). I interpreted only those models with  $\Delta_i < 2$ , as having substantial support for explaining variation in the data (Burnham and Anderson 1998). Alternatively, models were interpreted as having weak support when their  $\Delta_i \geq 2$  or their AIC values were within 2 units of a null model (e.g., a model that does not include a habitat variable). Finally, I examined Akaike weights ( $w_i$ ), which represent the relative likelihood for a model ( $i$ ) being a best model relative to another ( $j$ ) in the same set as  $w_i/w_j$  (Anderson et al. 2000).

For analyzing density and reproductive condition data, I created nine a priori explanatory models that included time and habitat variables of interest (Table 3.1). Null models only estimated variation among seasons (density analyses) or

Table 3.1. Variable descriptions for models examined as predictors of small mammal density, reproductive condition, and survival. The models were used for small mammals captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon in 2000 and 2001. For measurement descriptions and criteria see the Methods section of this chapter.

Variable	Description
Season <sup>a</sup>	Null model. Time effects associated with repeat sampling across multiple seasons
Year <sup>b</sup>	Null model. Time effects associated with repeat sampling across multiple years
Block <sup>c</sup>	Null model. Spatial and/or temporal effects associated with sampling different blocks
Total Shrub Cover	Total ground cover of shrubs (%)
Bitterbrush Cover	Ground cover of live bitterbrush (%)
Tree Basal Area	Ponderosa pine basal area (m <sup>2</sup> /ha)
Mean Tree dbh	Mean diameter at breast height for ponderosa pine (cm; dbh > 4 cm)
Tree/Shrub Regeneration	Tree and shrub seedlings (#/ha)
Herb Cover	Combined ground cover of grasses, sedges, and broad-leafed forbs (%)
Downed Wood Volume	Downed wood volume (m <sup>3</sup> /ha; large end diameter > 10 cm, small end diameter > 1 cm, and length > 0.5 m)
Downed Wood Char	State of charring on downed wood (0 – ≤ 50% char, 1 – > 50% char)

<sup>a</sup> – Early summer 2000, late summer 2000, fall 2000, and early summer 2001; used for density analyses.

<sup>b</sup> – Early summer 2000 and 2001; used for reproductive condition analyses.

<sup>c</sup> – Five geographically separated blocks; used for survival analyses.

years (reproductive condition analyses). Density models were examined using multiple linear regression, and I assessed the assumptions of normality and constant variance and performed natural log ( $\log_{(n)}$ ) transformations on all small mammal density estimates to meet these assumptions. Female reproductive condition models were examined using multiple linear regression with logit transformations of the proportion of reproductively active females among each adult population. All models for density and reproductive condition using AIC were calculated using maximum likelihood estimators, included blocks, incorporated repeated measures to account for repeated population sampling, and were performed in SAS, Version 8 (SAS Institute, Inc. 1999).

For analyzing survival data, I created nine a priori explanatory models (Table 3.1); null models only estimated variation among blocks. I then utilized logistic regression and the design matrix in MARK (White and Burnham 1999) to compare monthly survival estimates for each species. All models for survival were calculated using maximum likelihood estimators, included blocks, and all re-encounter probabilities were modeled as constant. All survival analyses using AIC were performed in MARK (Version 2.0; White and Burnham 1999).

In all analyses using AIC, I limited the number of models examined to nine to minimize situations where the number of models exceeded the sample size (Anderson et al. 2001). All analyses possessed a larger sample size ( $n = 10$ ) than the number of models ( $n = 9$ ) except for ground squirrel survival, which could only be reliably estimated on seven study units ( $n = 7$ ). Additionally, to reduce the



likelihood of over-fitting models, I limited each model to a single time (or block) and/or habitat variable and avoided interaction terms, trading the ability to identify more complex model effects for curtailing the likelihood of obtaining spurious results (Burnham and Anderson 1998). Finally, some models in the density and female reproductive condition analyses included two variables (i.e., time and one habitat variable) but possessed different numbers of model parameters (K) due to different correlation structures associated with repeated measures analyses and/or lack of variance among blocks.

## RESULTS

Mean total shrub cover was 9.2% (SD = 3.8%) and 31.2% (SD = 8.5%) for the five low and high shrub units, respectively. Similarly, mean bitterbrush cover was 2.8% (SD = 2.0%) and 13.5% (SD = 5.2%). Values for additional habitat features measured during the study, and a correlation matrix for habitat variables, are presented in Table 3.2 and Figure 3.3, respectively.

During the four small mammal sample periods, 1,705 individuals from seven small mammal species were captured and marked. Yellow-pine chipmunks, golden-mantled ground squirrels, and deer mice made up 98% of the captures (Table 3.3). Capture probabilities across sample periods for chipmunks, ground squirrels, and mice ranged between 0.85 to 0.99, 0.43 to 0.99, and 0.61 to 0.99, respectively. The jackknife population estimator ( $M_h$ ; Burnham and Overton 1978, 1979) was ultimately selected for all three species based on apparent heterogeneity

Table 3.2. Values for the eight habitat features measured on 10 study units on five blocks in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon.

Study Unit	Total Shrub Cover (%)	Bitterbrush Cover (%)	Tree Basal Area (m <sup>2</sup> /ha)	Mean Tree dbh (cm)	Tree/Shrub Regeneration (seedlings/ha)	Herb Cover (%)	Downed Wood Char (0 – 1) <sup>a</sup>	Downed Wood Volume (m <sup>3</sup> /ha)
<i>Low Shrub Cover</i>								
Block 1	12.34	1.57	17.96	62.37	1404.00	14.76	0.81	20.37
Block 2	5.98	2.54	12.81	31.52	748.80	32.89	0.69	8.92
Block 3	13.10	6.05	6.37	41.37	1341.60	27.50	0.06	19.53
Block 4	9.85	3.07	11.31	30.26	936.00	17.26	0.45	8.66
Block 5	4.50	0.80	11.98	47.14	655.20	27.29	0.87	5.44
Mean	9.15	2.81	12.08	42.53	1017.12	23.94	0.58	12.58
SD	3.81	2.02	4.13	13.11	340.78	7.63	0.33	6.87
<i>High Shrub Cover</i>								
Block 1	41.77	21.86	16.14	25.42	1872.00	3.71	0.36	12.54
Block 2	21.00	11.39	10.21	36.47	998.40	31.49	0.44	6.66
Block 3	31.57	10.90	5.57	34.38	2464.80	35.61	0.29	6.32
Block 4	24.68	8.54	6.56	44.28	1934.40	31.75	0.15	16.48
Block 5	37.00	14.94	7.46	27.24	11169.60	22.92	0.08	37.17
Mean	31.20	13.52	9.19	33.56	3687.84	25.09	0.26	15.84
SD	8.54	5.19	4.25	7.59	4215.37	12.82	0.15	12.66
Total Mean	20.18	8.16	10.64	38.05	2352.48	24.52	0.42	14.21
Total SD	13.19	6.76	4.24	11.15	3151.26	9.97	0.29	9.75

<sup>a</sup> – 0 ≤ 50% charred, 1 ≥ 50% charred

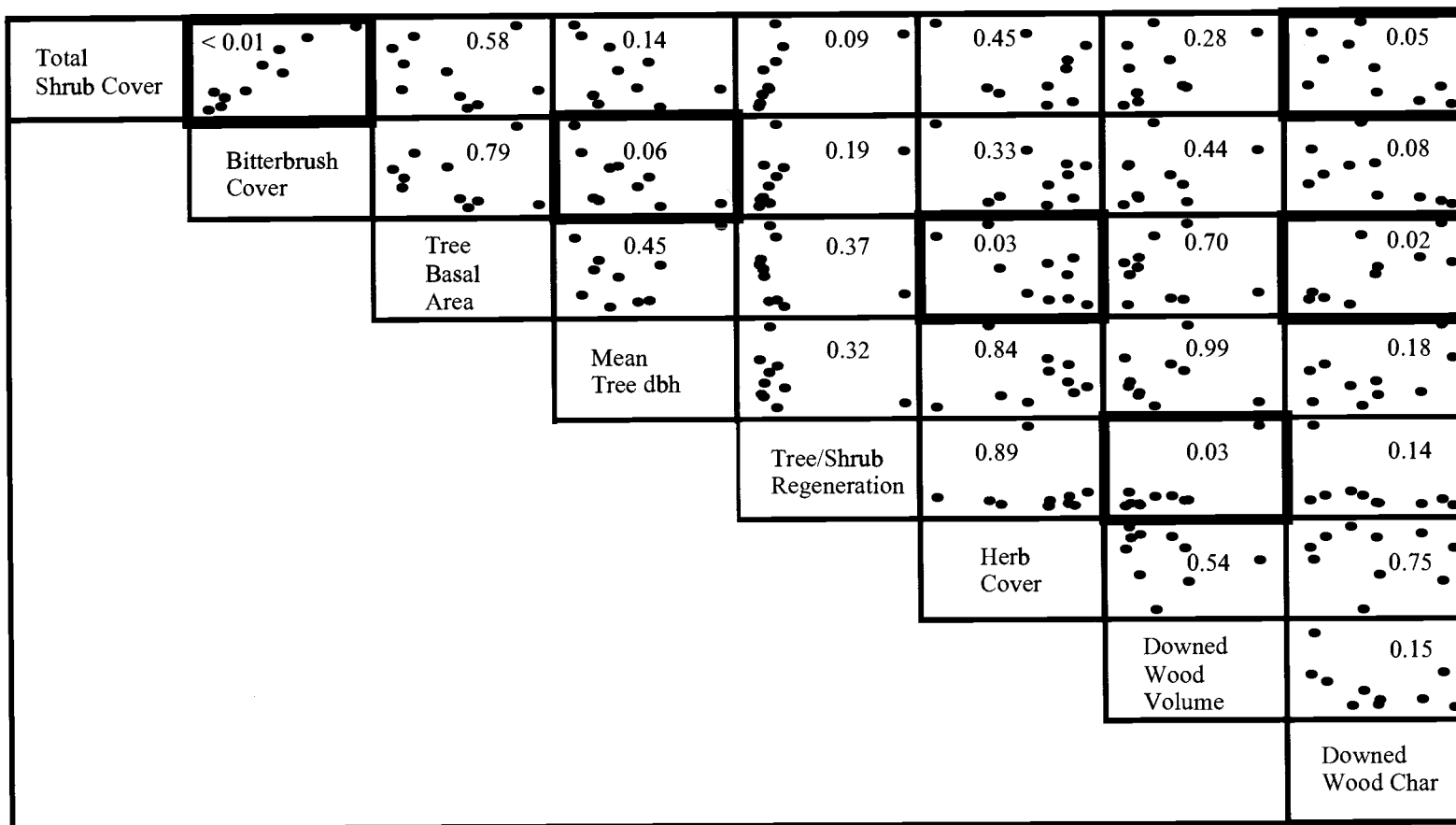


Figure 3.3. Correlations among habitat variables on 10 study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon. The p-value for each correlation is noted inside each box. Boxes outlined in bold indicate Pearson correlation coefficients > 0.6. Variables are described in the text and Table 3.2.

Table 3.3. Number of individual small mammals captured in live traps during four sample periods on 10 study units (some animals were captured multiple times within and among sample periods). All small mammal sampling took place in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon. Block 3 was not trapped during fall 2000 due to snow.

Family <i>Scientific Name</i>	Common Name	Early Summer 6/25-7/27, 2000	Late Summer 8/29-9/30, 2000	Fall 10/2-10/28, 2000	Early Summer 7/3-8/4, 2001	Total Individuals <sup>a</sup>
Sciuridae						
<i>Sciurus douglasii</i>	Douglas' squirrel	1	0	0	0	1
<i>Sciurus griseus</i>	Western gray squirrel	1	0	0	0	1
<i>Spermophilus lateralis</i>	Golden-mantled ground squirrel	98	99	29	127	272
<i>Tamias amoenus</i>	Yellow-pine chipmunk	323	512	270	477	982
<i>Tamias senex</i>	Allen's chipmunk	0	1	9	3	12
Heteromyidae						
<i>Perognathus parvus</i>	Great Basin pocket mouse	3	6	0	13	20
Muridae						
<i>Peromyscus maniculatus</i>	Deer mouse	144	177	142	67	417
Total Individuals <sup>b</sup>		577	795	450	687	
Total Captures <sup>c</sup>		1830	2877	1087	2332	
Trap Nights/Sample Period		2908	2823	2253	2903	

<sup>a</sup> – Number of uniquely-identified individual animals captured during the study.

<sup>b</sup> – Number of uniquely-identified individual animals captured during each sample period.

<sup>c</sup> – Number of animals captured during each sample period.

in capture probabilities across most grids, its relative robustness and low absolute bias (Burnham and Overton 1979), and its good population estimation ability when trap occasions are  $< 5$  but capture probabilities are  $> 0.05$  (White et al. 1982, Manning et al. 1995).

Although seven small mammal species were captured during the study, low encounters with four species prohibited statistically analyzing their habitat relationships. Capture patterns for two species, however, are worthy of mention: all Allen's chipmunk (*Tamias senex*) encounters were on high shrub units ( $n = 12$ ; Figure 3.4), and Great Basin pocket mice (*Perognathus parvus*) captures were two times more abundant on high versus low shrub units ( $n = 14$  and 6 individuals, respectively; Figure 3.5).

#### Analysis of Variance

Yellow-pine chipmunk densities were higher on study units with high versus low shrub cover ( $p = 0.05$ ), but densities were similar between study units for golden-mantled ground squirrels ( $p = 0.31$ ) and deer mice ( $p = 0.27$ ; Table 3.4, Figure 3.6). Yellow-pine chipmunk densities were 57% higher (90% CI range: 10% to 124% more individuals/ha) on high versus low shrub units. All three small mammal species displayed seasonal differences in density (Table 3.4, Figure 3.7). Yellow-pine chipmunk densities were lower during early versus late summer 2000 (adjusted  $p = 0.06$ ), but chipmunk densities were similar among all remaining sample period comparisons (adjusted  $p$  values  $> 0.29$ ). Golden-mantled ground

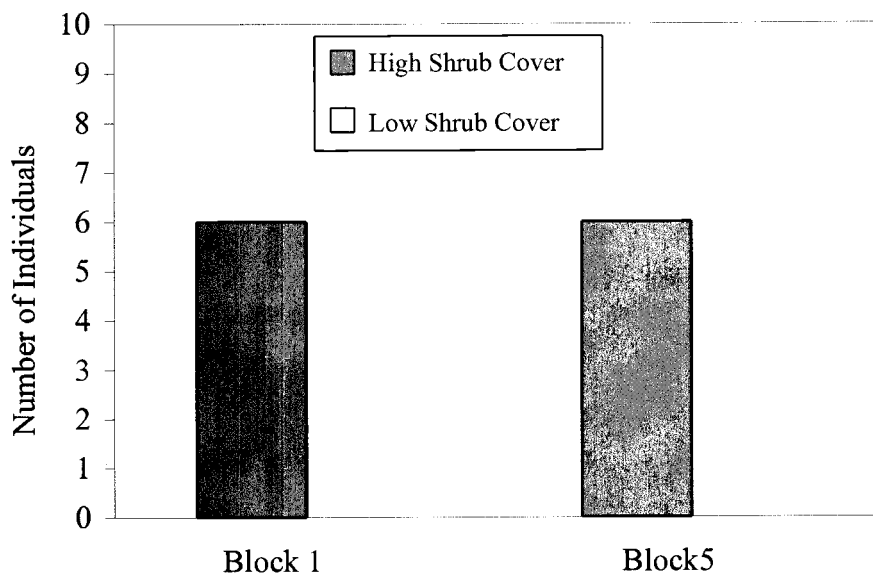


Figure 3.4. The number of Allen's chipmunk (*Tamias senex*) individuals captured on study units with high and low shrub cover on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were captured on study units with high (range: 21.0 to 41.8%) and low (range: 4.5 to 13.1%) shrub cover in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during 10,887 trap nights. Each shrub cover condition was replicated across five blocks. No individuals were captured on blocks 2, 3, or 4.

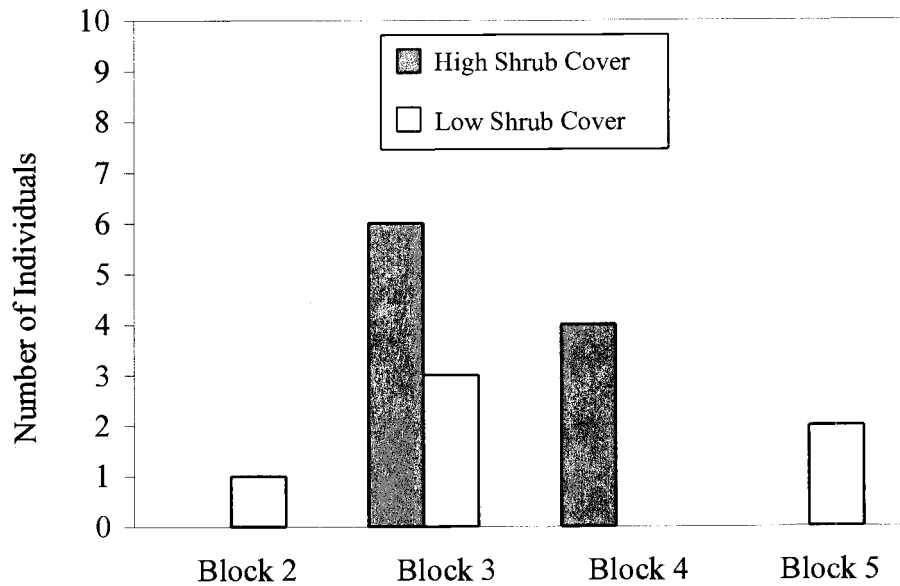


Figure 3.5. The number of Great Basin pocket mouse (*Perognathus parvus*) individuals captured on study units with high and low shrub cover on the Deschutes National Forest, Oregon in 2000 and 2001. Pocket mice were captured on study units with high (range: 21.0 to 41.8%) and low (range: 4.5 to 13.1%) shrub cover in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during 10,887 trap nights in 2000 and 2001. Each shrub cover condition was replicated across five blocks. No individuals were captured on block 1.

Table 3.4. Small mammal population parameter relationships between high (range: 21.0 to 41.8%) and low (range: 4.5 to 13.1%) shrub study units in 2000 and 2001. Yellow-pine chipmunks (*Tamias amoenus*), golden-mantled ground squirrels (*Spermophilus lateralis*), and deer mice (*Peromyscus maniculatus*) were captured in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon during four sample periods: early summer, late summer, and fall 2000, and early summer 2001.

Species	ANOVA F	p value	Significant Correlations (p < 0.1)
<b>Yellow-Pine Chipmunk</b>			
Density	F <sub>1,4</sub> = 7.39	0.05	*
Season	F <sub>3,22</sub> = 3.03	0.05	*
Density x Season	F <sub>3,22</sub> = 0.42	0.74	
Reproductive Condition	F <sub>1,4</sub> = 0.26	0.64	
Year	F <sub>1,8</sub> = 5.13	0.05	*
Reproductive Condition x Year	F <sub>1,8</sub> = 0.00	0.97	
Survival	F <sub>2,8</sub> = 0.49	0.84	
<b>Golden-Mantled Ground Squirrel</b>			
Density	F <sub>1,4</sub> = 1.36	0.31	
Season	F <sub>3,22</sub> = 10.48	< 0.001	*
Density x Season	F <sub>3,22</sub> = 1.51	0.24	
Survival	F <sub>2,3</sub> = -1.30	0.43	
<b>Deer Mouse</b>			
Density	F <sub>1,4</sub> = 1.65	0.27	
Season	F <sub>3,22</sub> = 15.02	< 0.001	*
Density x Season	F <sub>3,22</sub> = 0.76	0.53	
Reproductive Condition	F <sub>1,4</sub> = 0.49	0.52	
Year	F <sub>1,8</sub> = 0.14	0.72	
Reproductive Condition x Year	F <sub>1,8</sub> = 0.28	0.61	



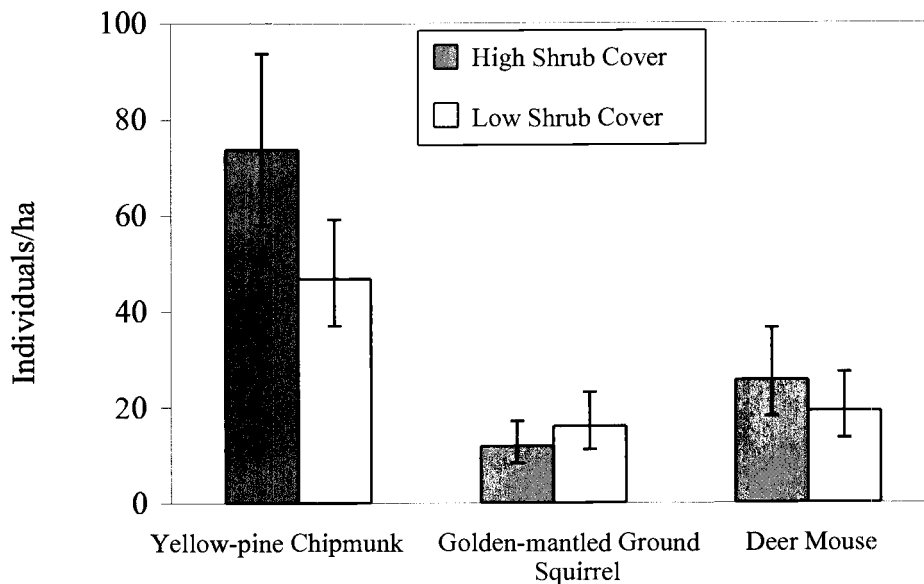


Figure 3.6. Small mammal density estimates on study units with high and low shrub cover on the Deschutes National Forest, Oregon in 2000 and 2001. Small mammals were captured on study units with high (range: 21.0 to 41.8%) and low (range: 4.5 to 13.1%) shrub cover in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during 10,887 trap nights. Each shrub cover condition was replicated across five blocks. Vertical bars represent 90% confidence intervals. Chipmunk density was significantly higher on high versus low shrub units ( $p = 0.05$ ) but ground squirrel and mouse densities were not different between shrub cover types.

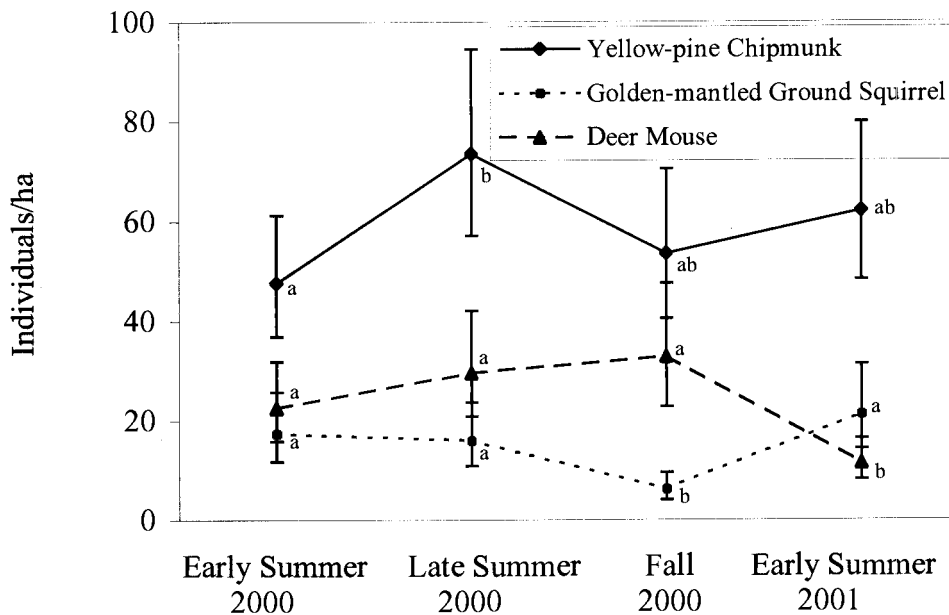


Figure 3.7. Small mammal density estimates on study units on the Deschutes National Forest, Oregon during four sample periods in 2000 and 2001. Small mammals were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during 10,887 trap nights. Each shrub cover condition was replicated across five blocks. Vertical bars represent 90% confidence intervals. Different letters within a species represent a significant difference ( $p < 0.1$ ) across seasons.

squirrel densities were lowest during fall 2000 (adjusted  $p$  values  $< 0.01$ ), while ground squirrel densities were similar among all remaining sample period comparisons (adjusted  $p$  values  $> 0.72$ ). Deer mouse densities were lowest during early summer 2001 (adjusted  $p$  values  $< 0.01$ ) and similar across all remaining sample period comparisons (adjusted  $p$  values  $> 0.25$ ). The analyses showed no evidence of interaction between season and shrub cover for any species ( $p$  values  $\geq 0.24$ ; Table 3.4).

Across the two early summer sample periods, the proportion of reproductive females in each adult population was similar between high and low shrub units for yellow-pine chipmunks ( $p = 0.64$ ) and deer mice ( $p = 0.52$ ; Table 3.4, Figure 3.8). A larger proportion of chipmunk females were reproductively active ( $p = 0.05$ ) during early summer 2001 versus early summer 2000, but deer mice did not show a difference ( $p = 0.72$ ). There was no significant interaction between year and shrub cover in the analyses for either species ( $p$  values  $\geq 0.61$ ; Table 3.4). Survival was similar between high and low shrub units for yellow-pine chipmunks (adjusted  $p = 0.84$ ) and golden-mantled ground squirrels (adjusted  $p = 0.43$ ; Table 3.4, Figure 3.9).

### Model Selection

Across seasons, total shrub cover and bitterbrush cover best-explained yellow-pine chipmunk density (Table 3.5). Each 4.4% increase in total shrub cover corresponded with a 10% increase in chipmunk density (90% CI range: 6% to 15%

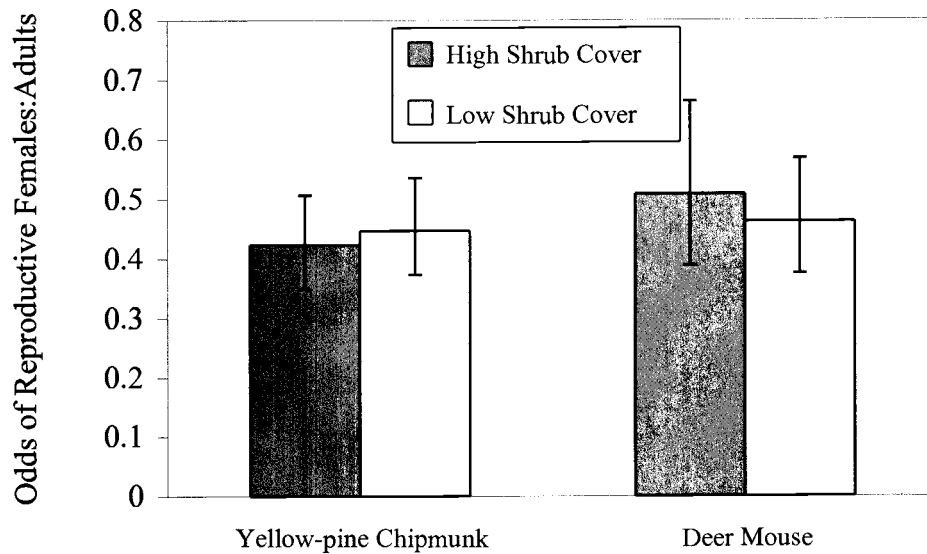


Figure 3.8. The odds of reproductive females in the entire adult population on study units with high and low shrub cover on the Deschutes National Forest, Oregon in 2000 and 2001. Small mammals were captured on study units with high (range: 21.0 to 41.8%) and low (range: 4.5 to 13.1%) shrub cover in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during early summer 2000 and 2001. Each shrub cover condition was replicated across five blocks. Vertical bars represent 90% confidence intervals. The proportion of reproductive females was similar between units with high and low shrub cover for both yellow-pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*).

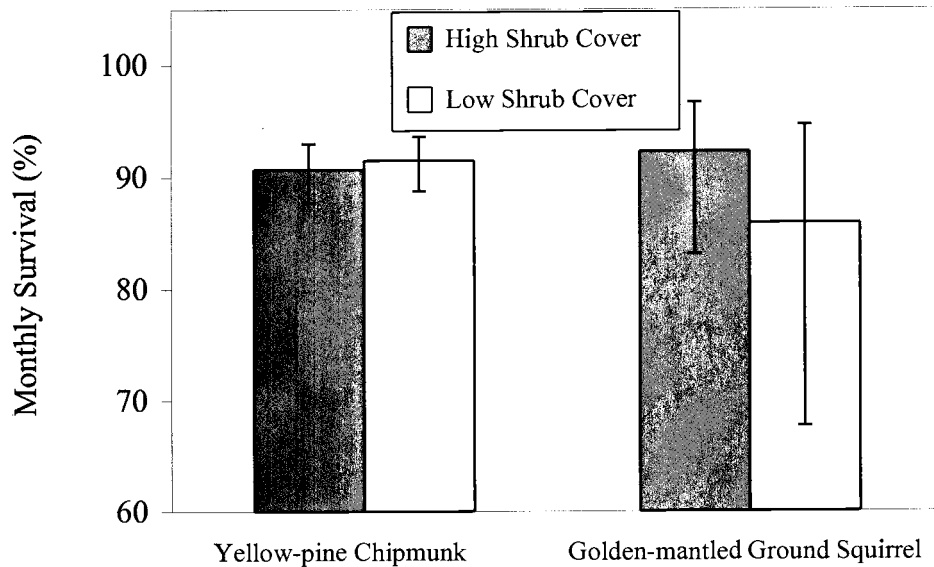


Figure 3.9. Mean monthly survival estimates for yellow-pine chipmunks (*Tamias amoenus*) and golden-mantled ground squirrels (*Spermophilus lateralis*) on study units with high and low shrub cover on the Deschutes National Forest, Oregon between 2000 and 2001. Survival estimates were obtained for chipmunks on 10 study units (five replicate blocks) and ground squirrels on seven study units (four replicate blocks) with high (range: 21.0 to 41.8%) and low (range: 4.5 to 13.1%) shrub cover in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests between early summer 2000 and early summer 2001. Vertical bars represent 90% confidence intervals. Chipmunk and ground squirrel survival were similar on high versus low shrub units.

Table 3.5. Model comparison across seasons using AIC for yellow-pine chipmunk (*Tamias amoenus*) density on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during four sample periods: early summer, late summer, and fall 2000, and early summer 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Total Shrub Cover	8	52.41	0.00	0.492	+
Bitterbrush Cover	8	52.70	0.28	0.426	+
Downed Wood Char	8	56.62	4.22	0.060	
Season (Null Model)	7	60.09	7.68	0.011	
Herb Cover	8	62.84	10.43	0.003	
Downed Wood Volume	8	62.88	10.47	0.003	
Tree Basal Area	8	63.00	10.59	0.002	
Tree/shrub Regeneration	8	63.09	10.68	0.002	
Mean Tree dbh	9	63.75	11.34	0.002	

<sup>a</sup> – Season was analyzed alone and in combination with each habitat variable although not shown (e.g., Season + Total Shrub Cover).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

more individuals/ha; Figure 3.10). Similarly, each 2.3% increase in bitterbrush cover was associated with a 10% chipmunk density increase (90% CI range: 6% to 13% more individuals/ha; Figure 3.11). No additional habitat features had strong evidence for explaining yellow-pine chipmunk density (Table 3.5).

Year, in combination with mean tree dbh, best explained yellow-pine chipmunk reproductive condition (Table 3.6). Each 8.2 cm increase in mean tree dbh reflected a 1.1 times greater odds (90% CI range: 1.05 to 1.15 increase) of encountering reproductive female chipmunks in a population (Figure 3.12). There was little evidence to suggest bitterbrush cover or total shrub cover were good explanatory variables for chipmunk reproductive condition (Table 3.6).

All variables examined had strong relationships with yellow-pine chipmunk survival during the study (Table 3.7). Further, because block alone was among the set of best explanatory variables, the strength of evidence that any single habitat variable explains survival better than blocking variation is weak.

Golden-mantled ground squirrel density was best explained by season alone, season in combination with bitterbrush cover, and season in combination with total shrub cover (Table 3.8). However, because season alone had strong support for explaining ground squirrel densities, strength of evidence that any single habitat variable explains density better than seasonal variation is minimal.

Block, mean tree dbh, herb cover, tree/shrub regeneration, and tree basal area all had similar predictive value for golden-mantled ground squirrel survival (Table 3.9). There was no strong evidence that either total shrub cover or

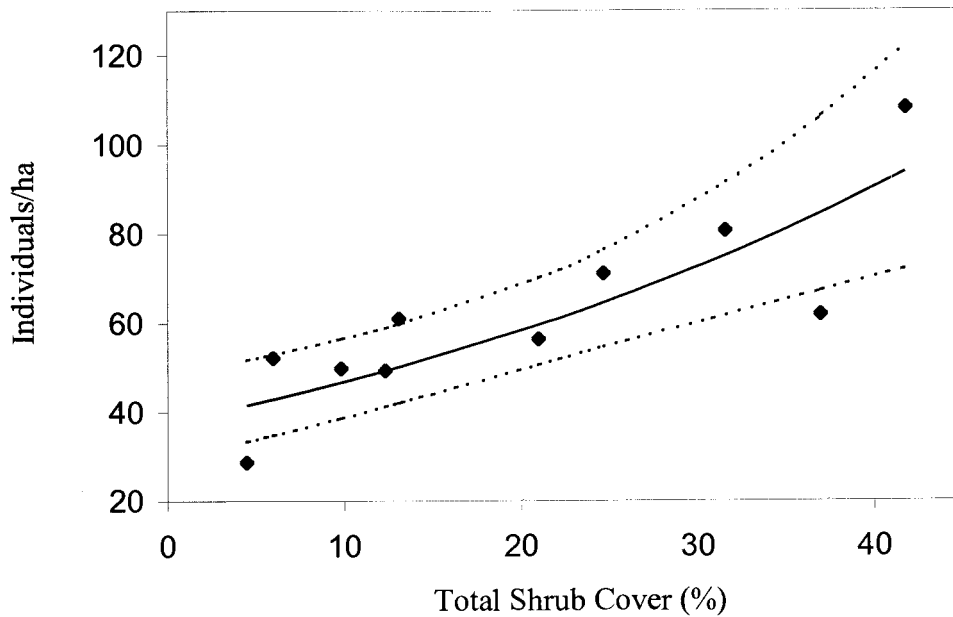


Figure 3.10. Yellow-pine chipmunk (*Tamias amoenus*) density estimates relative to total shrub cover on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests. The dashed lines represent 90% confidence intervals around the regression line. Points represent the mean density estimate for each study unit for four sample periods: early summer, late summer, and fall 2000, and early summer 2001. The relationship between chipmunk density and total shrub cover was significant ( $p < 0.001$ ).



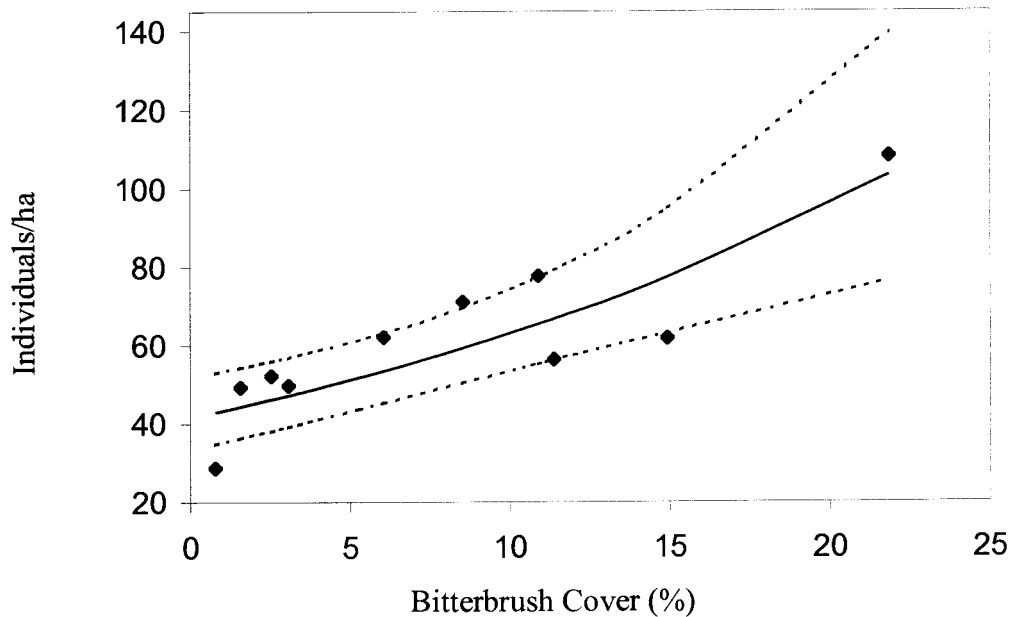


Figure 3.11. Yellow-pine chipmunk (*Tamias amoenus*) density estimates relative to bitterbrush (*Purshia tridentata*) cover on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were capture on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush forests. The dashed lines represent 90% confidence intervals around the regression line. Points represent the mean density estimate for each study unit for four sample periods: early summer, late summer, and fall 2000, and early summer 2001. The relationship between chipmunk density and bitterbrush cover was significant ( $p < 0.001$ ).

Table 3.6. Model comparison across years using AIC for the proportion of reproductively active yellow-pine chipmunk (*Tamias amoenus*) females on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during two sample periods: early summer 2000 and 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Mean Tree dbh	6	1.14	0.00	0.713	+
Year (Null Model)	5	5.20	4.06	0.094	
Tree Basal Area	6	6.10	4.96	0.060	
Downed Wood Char	6	6.13	4.99	0.060	
Bitterbrush Cover	6	8.30	7.16	0.020	
Total Shrub Cover	6	8.73	7.59	0.020	
Downed Wood Volume	6	8.89	7.75	0.015	
Tree/Shrub Regeneration	6	9.33	8.19	0.012	
Herb Cover	6	9.34	8.20	0.012	

<sup>a</sup> – Year was analyzed alone and in combination with each habitat variable although not shown (e.g., Year + Mean Tree dbh).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

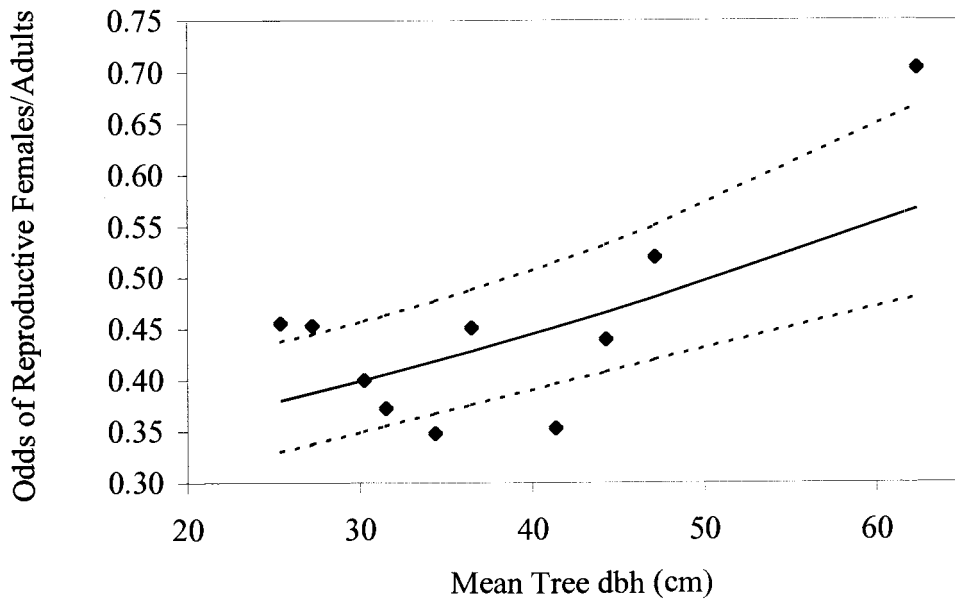


Figure 3.12. The odds of reproductive yellow-pine chipmunk (*Tamias amoenus*) females relative to mean tree dbh on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Chipmunks were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests. The dashed lines represent 90% confidence intervals around the regression line. Points represent the odds for each study unit for two sample periods: early summer 2000 and early summer 2001. The relationship between chipmunk reproductive condition and mean tree dbh was significant ( $p < 0.001$ ).

Table 3.7. Model comparison across blocks using AIC for yellow-pine chipmunk (*Tamias amoenus*) survival on 10 study units on the Deschutes National Forest, Oregon between 2000 and 2001. Chipmunks were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forest from early summer 2000 to early summer 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Block (Null Model)	6	966.69	0.00	0.210	0
Bitterbrush Cover	7	967.51	0.82	0.140	
Downed Wood Char	7	968.00	1.31	0.109	
Herb Cover	7	968.05	1.36	0.107	
Total Shrub Cover	7	968.28	1.59	0.095	
Tree Basal Area	7	968.35	1.66	0.092	
Mean Tree dbh	7	968.51	1.81	0.085	
Downed Wood Volume	7	968.59	1.90	0.081	
Tree/Shrub Regeneration	7	968.61	1.92	0.081	

<sup>a</sup> – Block was analyzed alone and in combination with each habitat variable although not shown (e.g., Block + Bitterbrush Cover).

<sup>b</sup> – Number of model parameters including the intercept and re-encounter parameter.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

Table 3.8. Model comparison across seasons using AIC for golden-mantled ground squirrel (*Spermophilus lateralis*) density on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Ground squirrels were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during four sample periods: early summer, late summer, and fall 2000, and early summer 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Season (Null Model)	7	88.11	0.00	0.322	0
Bitterbrush Cover	8	89.08	0.97	0.198	
Total Shrub Cover	8	89.61	1.50	0.152	
Mean Tree dbh	8	90.77	2.66	0.085	
Downed Wood Volume	8	90.87	2.76	0.081	
Tree Basal Area	8	91.14	3.03	0.071	
Herb Cover	8	91.24	3.14	0.067	
Downed Wood Char	9	94.46	6.36	0.013	
Tree/Shrub Regeneration	9	94.76	6.65	0.012	

<sup>a</sup> – Season was analyzed alone and in combination with each habitat variable although not shown (e.g., Season + Bitterbrush Cover).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

Table 3.9. Model comparison across blocks using AIC for golden-mantled ground squirrel (*Spermophilus lateralis*) survival on seven study units on the Deschutes National Forest, Oregon between 2000 and 2001. Ground squirrels were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests from early summer 2000 to early summer 2001. Survival could only be modeled on seven study units (low shrub cover – block 1, block 3, block 5; high shrub cover – block 2, block 3, block 4, block 5).

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Block (Null Model)	6	182.75	0.00	0.230	0
Mean Tree dbh	7	183.42	0.67	0.165	
Herb Cover	7	184.01	1.26	0.123	
Tree/Shrub Regeneration	7	184.66	1.90	0.089	
Tree Basal Area	7	184.66	1.91	0.089	
Downed Wood Volume	7	184.95	2.20	0.077	
Bitterbrush Cover	7	184.97	2.22	0.076	
Total Shrub Cover	7	184.97	2.22	0.076	
Downed Wood Char	7	184.97	2.22	0.075	

<sup>a</sup> – Block was analyzed alone and in combination with each habitat variable although not shown (e.g., Block + Mean Tree dbh).

<sup>b</sup> – Number of model parameters including the intercept and re-encounter parameter.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

bitterbrush cover explained ground squirrel survival. Similar to yellow-pine chipmunk survival, because block alone was among the set of best explanatory variables, the strength of evidence that a single habitat variable explains survival better than blocking variation is weak.

Deer mouse density was best explained by season in combination with tree basal area (Table 3.10). Each 1.26 m<sup>2</sup>/ha increase in tree basal area was associated with a 10% decrease in mouse density (90% CI range: 5% to 13% fewer individuals/ha; Figure 3.13). Neither total shrub cover nor bitterbrush cover explained deer mouse density well, relative to tree basal area (Table 3.10).

Year alone was the best predictor of deer mouse reproductive condition (Table 3.11). Total shrub and bitterbrush cover were the next best predictors of reproductive condition, but their predictive ability was poor relative to annual variation alone. A correlation summary of the model selection analyses is presented in Table 3.12.

## DISCUSSION

### Shrub/Bitterbrush Cover

Only yellow-pine chipmunks had significant relationships with shrub or bitterbrush cover. Yellow-pine chipmunk densities were higher on high versus low shrub units, and chipmunk densities increased when total shrub or bitterbrush cover increased.

Table 3.10. Model comparison across seasons using AIC for deer mouse (*Peromyscus maniculatus*) density on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Mice were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during four sample periods: early summer, late summer, and fall 2000, and early summer 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Tree Basal Area	7	54.18	0.00	0.937	-
Downed Wood Char	8	61.17	6.99	0.028	
Total Shrub Cover	8	62.77	8.59	0.013	
Mean Tree dbh	8	63.19	9.01	0.010	
Bitterbrush Cover	8	63.63	9.45	0.008	
Season (Null Model)	8	66.86	12.69	0.002	
Herb Cover	9	69.55	15.37	0.000	
Tree/Shrub Regeneration	9	69.89	15.71	0.000	
Downed Wood Volume	9	69.98	15.80	0.000	

<sup>a</sup> – Season was analyzed alone and in combination with each habitat variable although not shown (e.g., Season + Tree Basal Area).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .



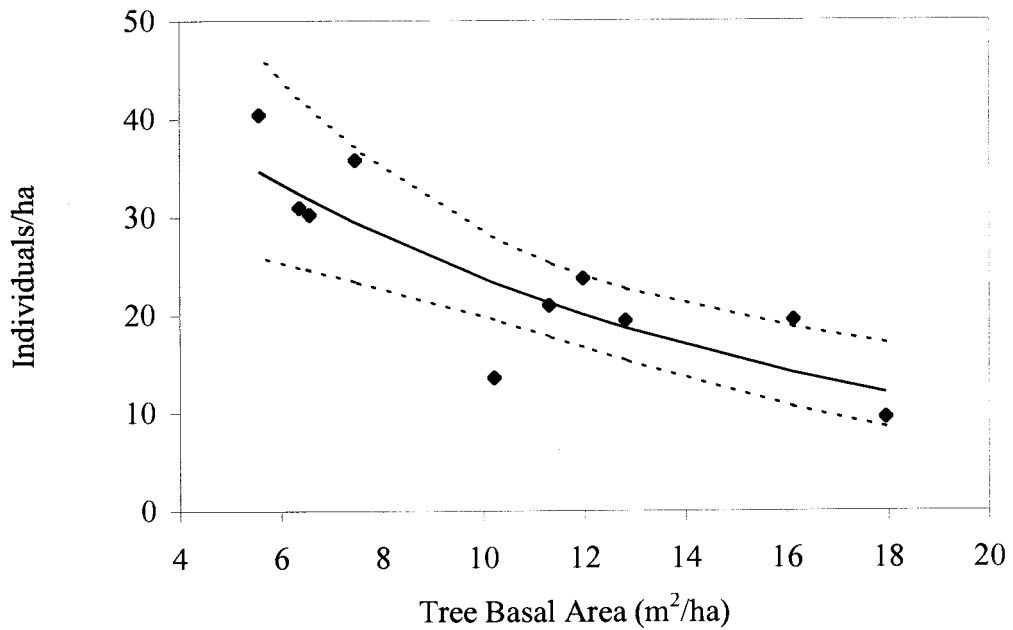


Figure 3.13. Deer mouse (*Peromyscus maniculatus*) density estimates relative to tree basal area on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Mice were captured on study units in ponderosa pine (*Pinus ponderosa*)/ antelope bitterbrush (*Purshia tridentata*) forests. The dashed lines represent 90% confidence intervals around the regression line. Points represent the mean density estimate for each study unit for four sample periods: early summer, late summer, and fall 2000, and early summer 2001. The relationship between mouse density and tree basal area was significant ( $p < 0.001$ ).

Table 3.11. Model comparison across years using AIC for the proportion of reproductively active deer mouse (*Peromyscus maniculatus*) females on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Mice were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests during two sample periods: early summer 2000 and 2001.

Model <sup>a</sup>	K <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	$\Delta_i$ <sup>d</sup>	$w_i$ <sup>e</sup>	+/- <sup>f</sup>
Year (Null Model)	5	31.56	0.00	0.377	0
Total Shrub Cover	6	33.69	2.13	0.130	
Bitterbrush Cover	6	33.70	2.14	0.130	
Herb Cover	6	34.07	2.51	0.107	
Downed Wood Char	6	35.12	3.55	0.064	
Basal Area	6	35.52	3.95	0.052	
Mean Tree dbh	6	35.73	4.17	0.047	
Downed Wood Volume	6	35.73	4.17	0.047	
Tree/Shrub Regeneration	6	35.74	4.18	0.047	

<sup>a</sup> – Year was analyzed alone and in combination with each habitat variable although not shown (e.g., Year + Total Shrub Cover).

<sup>b</sup> – Number of model parameters including the intercept, variance, and covariance parameters.

<sup>c</sup> – Model AIC<sub>c</sub> value.

<sup>d</sup> – Difference between model AIC<sub>c</sub> value and minimum AIC<sub>c</sub> value.

<sup>e</sup> – Approximate probability that a model is the best in the set.

<sup>f</sup> – Correlation between the population parameter and the habitat variable of competing models with  $\Delta_i < 2$ , and null model AIC<sub>c</sub> value – model AIC<sub>c</sub> value  $\geq 2$ .

Table 3.12. Correlative relationships between population parameters and AIC model variables for yellow-pine chipmunks (*Tamias amoenus*), golden-mantled ground squirrels (*Spermophilus lateralis*), and deer mice (*Peromyscus maniculatus*) captured on 10 study units on the Deschutes National Forest, Oregon in 2000 and 2001. Small mammals were captured on study units in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests. Correlations are noted as 0, +, or – for variables of models when  $\Delta_i < 2$ , and the null model AIC value – model AIC value  $\geq 2$ .

Species	Population Response	Season <sup>a</sup> , Year <sup>b</sup> , or Block <sup>c</sup>	Total Shrub Cover (%)	Bitterbrush Cover (%)	Tree Basal Area (m <sup>2</sup> /ha)	Tree dbh (cm)	Tree/Shrub Regeneration (seedlings/ha)	Herb Cover (%)	Downed Wood Volume (m <sup>3</sup> /ha)	Downed Wood Char (0 – 1)
Yellow-pine chipmunk	Density	a	+	+						
	Reproductive Condition	b				+				
	Survival	0 <sup>c</sup>								
Golden-mantled ground squirrel	Density	0 <sup>a</sup>								
	Survival	0 <sup>c</sup>								
Deer mouse	Density	a					-			
	Reproductive Condition	0 <sup>b</sup>								

<sup>a</sup> – Density: early summer 2000, late summer 2000, fall 2000, and early summer 2001

<sup>b</sup> – Reproductive condition: early summer 2000 and 2001.

<sup>c</sup> – Survival: five geographically separated blocks.

The positive relationship between yellow-pine chipmunk density and shrub/bitterbrush cover may reflect the foraging habits and physiological constraints of these animals. Yellow-pine chipmunks are omnivorous, but they consume and disperse large quantities of seed, including those of antelope bitterbrush and ponderosa pine (Tevis 1952, 1953, Broadbooks 1958, Vander Wall 1994, 1995, Verts and Carraway 1998). In coniferous forests of the Sierra Nevada, California, yellow-pine chipmunk stomachs contained 31% seed by volume during September and October (Tevis 1952), and 35, 33, and 56% seed during spring, summer, and autumn, respectively (Tevis 1953). Additionally, antelope bitterbrush may provide invertebrate prey, as chipmunks are known to consume shrub-defoliating caterpillars (Tevis 1952, 1953), such as western tent caterpillars (*Malacosoma californicum*), which were prevalent on many of the study units (pers. obs.). Similarly, yellow-pine chipmunks have been seen intensively foraging on pupae of the pandora moth (*Coloradia pandora*) following a prescribed burn (K. Cromack, Jr., Oregon State University, pers. com.), but this invertebrate is, perhaps, only be available as chipmunk forage immediately following fires when caterpillar or pupae abundances are also high.

Yellow-pine chipmunk densities may be limited in areas with low shrub cover, not only because forage availability could be reduced, but also because shrubs, as refugia, will be compromised. Chipmunks utilize shrubs and tree trunks as predator avoidance structures when escaping via terrestrial routes (Sharples 1983). Additionally, chipmunks often place burrow entrances at the base of

bitterbrush shrubs (pers. obs.), and localize their activity around vegetative structures because shrubs and trees moderate solar radiation and soil temperature (Wight et al. 1992), and they help to minimize animal heat loading and exposure to high daytime temperatures (Chappell 1978, States 1976).

Total shrub and bitterbrush cover were the best predictive habitat features measured for golden-mantled ground squirrel density, but there was a lack of evidence supporting these relationship trends relative to seasonal variation. Although previous research documents the association of golden-mantled ground squirrels with open forests and sparsely shrubby habitats (Bartels and Thompson 1993, Verts and Carraway 1998), this study does not provide convincing corroboratory evidence at the spatial scale examined.

Of the three primary small mammal species investigated in this study, the generalist deer mouse is probably most adaptive to a variety of habitat conditions (Baker 1968, Verts and Carraway 1998), and therefore least likely to respond to shrub manipulations. Previous studies suggest that deer mouse populations do not respond predictably to changes in shrub cover following prescribed burning and herbicide application, but when populations respond, they are often short-term (Gashwiler 1959, Gano and Rickard 1982, Gunther et al. 1983, Sullivan and Boateng 1996, Sullivan et al. 1999). The lack of significant relationships between deer mouse populations and shrub/bitterbrush cover in this study may, in part, reflect the one- to five-year time lapse between burning and mowing, and the initial small mammal sampling, which was likely sufficient for populations to re-occupy

the altered areas. For example, although deer mouse populations in coniferous forests of British Columbia, Canada, and the Cascade Mountains of Oregon were initially reduced following prescribed burns, these depressed populations recovered to pre-burn levels within several months after burning (Gashwiler 1959, Sullivan and Boateng 1996), a considerably shorter time lapse than had passed in this study.

Although Allen's chipmunk (*Tamias senex*) and Great Basin pocket mouse (*Perognathus parvus*) encounters were low during this study, the capture trends provide insight into relationships between these species and shrub cover in ponderosa pine/antelope bitterbrush forests. Allen's chipmunks were never captured on burned or mowed units in this study, suggesting a possible avoidance of open ground or an aversion to disturbance. These results concur with previous research that found this chipmunk in close association with closed canopy coniferous forest and moist chaparral habitats (Grinnell et al. 1930, Tevis 1955, Sharples 1983), neither of which were well-represented in the open ponderosa pine units in this study where most shrub cover was removed by burning and mowing. Conversely, although Great Basin pocket mice were encountered on study units with high and low shrub cover, their increased abundance on high shrub units may indicate better habitat conditions associated with increased protective cover and seed production. Research indicates that a congener, the Arizona pocket mouse (*P. amplus*), often forages in association with shrubs, especially in response to predation risk (Brown et al. 1988). As a result, the granivorous Great Basin pocket mouse probably benefits more from high shrub units by deriving both forage and

cover from abundant bitterbrush shrubs. Low shrub units, in contrast, lacked much of the shrub cover but may have provided some foraging opportunities because herb cover was relatively similar among high and low shrub units.

### Temporal and Spatial Variation

In addition to the relationships between small mammal populations and habitat features, several responses were strongly influenced by temporal or spatial (blocking) variation. Temporal and spatial trends in seed production, predation, intra- or inter-specific competition, climate, and other habitat components may all influence small mammal population fluctuations through changes in reproduction, survival, and abundance (Jameson 1953, Terman 1968, Van Horne 1981, Fryxell et al. 1998, Maguire 1999, Bowman et al. 2001). Further, high levels of intra-specific variation among population responses may result from tradeoffs between density, reproduction, and survival (Van Horne 1983, Pulliam 1988) or a failure to examine habitat features having critical links to specific population parameters. As a result, more clearly understanding changes in small mammal populations may require examining not only their relationships with habitat components, but also the temporal variability of the resources provided by the habitat components.

### Conclusions

This study describes relationships between population parameters of three small mammal species and habitat elements in ponderosa pine/antelope bitterbrush

forests of central Oregon. The results suggest that land management objectives that strive to emulate pre-settlement forest conditions through the reduction of bitterbrush cover by burning and mowing may negatively impact yellow-pine chipmunk densities, but golden-mantled ground squirrel and deer mouse populations appear minimally affected. Managing ponderosa pine forests to appear and function similar to those of historical periods has considerable potential to alter the small mammal community and will likely cascade down to influence other forest elements. That is, in addition to dispersing and caching seeds, yellow-pine chipmunks, golden-mantled ground squirrels, and deer mice consume large quantities of seed and emerging seedlings and, therefore, directly influence bitterbrush regeneration and the corresponding fire potential, forest productivity, and mule deer forage. Consequently, prescribed burning or mowing in temporal and spatial patterns that leave remnant bitterbrush shrubs in close proximity to burned and mowed areas will decrease wildfire potential (Busse et al. 2000), enhance habitat for bitterbrush recruitment, and may provide suitable habitat for yellow-pine chipmunks, leading to more rapid bitterbrush regeneration. Although successful implementation would likely include irregularly and differentially sized, shaped, and spaced patches of remnant bitterbrush as habitat, the response of small mammal populations to such configurations have not been thoroughly investigated in ponderosa pine/antelope bitterbrush forests and were not examined in this study. Further, caution should be taken toward such an approach, as many ecological implications of large scale burning (and mowing) remain poorly understood in



many forests of the interior Pacific Northwest (Tiedemann et al. 2000).

Nevertheless, effective bitterbrush management that addresses broader ecological concerns, such as fire regimes, forest productivity, and ungulate populations must also consider small mammal populations in these forests.

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## CHAPTER 4

### CONCLUSIONS

Of the three small mammal species examined during the study, only golden-mantled ground squirrel (*Spermophilus lateralis*) density and survival were positively correlated with downed wood volume under conditions of varying downed wood volume. Yellow-pine chipmunk (*Tamias amoenus*) and deer mouse (*Peromyscus maniculatus*) populations did not exhibit significant relationships with downed wood volume. Alternatively, only yellow-pine chipmunk density was positively correlated with total shrub cover and bitterbrush cover, while golden-mantled ground squirrel and deer mouse populations did not exhibit significant relationships with total shrub cover or bitterbrush cover. Additionally, population parameters often varied in relation to seasons, years, and locations.

This research shows that in ponderosa pine/antelope bitterbrush forests of central Oregon, management actions that manipulate downed wood volume and antelope bitterbrush cover may significantly influence the small mammal community through changes in golden-mantled ground squirrel and yellow-pine chipmunk populations. Although decreases in downed wood volume may lead to decreased golden-mantled ground squirrel density and survival, a greater change may occur following manipulations of antelope bitterbrush. The decrease in antelope bitterbrush following prescribed burning or mowing may lead to a decrease in yellow-pine chipmunk abundance and thus a reduction in antelope

bitterbrush dispersal and regeneration. The relationships between small mammal populations, downed wood, and antelope bitterbrush that were quantified in this study provide much-needed information to address management questions and effectively manage ponderosa pine forests of central Oregon while including small mammal populations as a management goal.

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APPENDIX A. Total downed wood volume and linear lengths<sup>a</sup> for pieces that qualify as leave logs<sup>b</sup> (USDA 1995), on 10 study units with high and low downed wood volumes in ponderosa pine (*Pinus ponderosa*)/antelope bitterbrush (*Purshia tridentata*) forests on the Deschutes National Forest, Oregon. The USDA requires 3 to 6 logs/ac (7.4 to 14.82 logs/ha), 6 or more feet (1.83 m) long, with a total linear length of 20 to 40 feet/ac (36.6 to 73.2 m/ha) of logs 12 inches (30.5 cm) or greater in small-end diameter remain on site following all timber sale activities in ponderosa pine stands.

Study Unit	Total Log Length (ft/ac)	Total Log Volume (ft <sup>3</sup> /ac)	Total Log Length (m/ha)	Total Log Volume (m <sup>3</sup> /ha)
<i>High Downed Wood Volume</i>				
Block 1	1239.38	893.58	935.67	154.77
Block 2	588.96	383.16	444.63	66.36
Block 3	357.36	301.68	269.79	52.25
Block 4	530.44	456.83	400.45	79.12
Block 5	410.53	326.56	309.93	56.56
Mean	625.33	472.36	472.10	81.81
SD	355.43	242.90	268.33	42.07
<i>Low Downed Wood Volume</i>				
Block 1	56.82	34.31	42.89	5.94
Block 2 <sup>c</sup>	8.31	2.66	6.27	0.46
Block 3 <sup>c</sup>	8.89	16.54	6.71	2.86
Block 4	67.54	25.09	50.99	4.35
Block 5	191.47	163.74	144.55	28.36
Mean	66.60	48.47	50.28	8.39
SD	74.86	65.49	56.52	11.34
Total Mean	345.97	260.41	261.19	45.10
SD	381.25	279.36	287.83	48.39

<sup>a</sup> – The following equation was used to calculate log length for each qualifying log:

Log Length (m) = piece length x [(0.305 – LED)/(SED – LED)], where piece length, LED, and SED are in meters.

<sup>b</sup> – Qualifying pieces have the following minimum dimensions:

piece length > 1.83 m (6 ft)

large-end diameter (LED) > 0.305 m (1 ft)

small-end diameter (SED) > 0.305 m (1 ft) for at least 1.83 m (6 ft) of piece length

<sup>c</sup> – Study units that did not meet minimum log length requirements.

APPENDIX B. Parameter estimates and 90% confidence intervals (in parentheses) for models with  $\Delta_i < 2$ , and null model AIC value – model AIC value  $\geq 2$ . Model selection is described in the text and presented in Tables 2.5 to 2.11 and 3.5 to 3.11.

		Model Parameters					
<b>Chapter 2 Models</b>							
Species	Population Parameter	$B^a$ (sample period 4)	$B^b$ (sample period 1)	$B^c$ (sample period 2)	$B^d$ (sample period 3)	$B^e$ (habitat variable)	Habitat Variable <sup>f</sup>
Yellow-pine chipmunk	Density	4.0484 (3.7838, 4.3129)	-0.1553 (-0.5101, 0.1994)	0.1798 (-0.0998, 0.4594)	-0.137 (-0.3694, 0.0954)	0.02669 (0.0135, 0.0398)	Basal Area (m <sup>2</sup> /ha)
Golden-mantled ground squirrel	Density	2.1077 (1.2518, 2.9636)	-0.09224 (-0.4824, 0.2979)	-0.1042 (-0.4937, 0.2853)	-1.3675 (-1.8244, -0.9107)	0.02804 (0.0091, 0.047)	Mean Tree dbh (cm)
		2.8476 (2.4042, 3.291)	-0.1002 (-0.4845, 0.284)	-0.1036 (-0.4867, 0.2796)	-1.4092 (-1.8654, -0.953)	0.002716 (0.0009, 0.0045)	Downed Wood Volume (m <sup>3</sup> /ha)
<b>Chapter 3 Models</b>							
Yellow-pine chipmunk	Density	3.6899 (3.3596, 4.0201)	-0.2690 (-0.5365, -0.0014)	0.1886 (-0.0792, 0.4565)	-0.1698 (-0.4570, 0.1175)	0.02187 (0.014, 0.0298)	Total Shrub Cover (%)
		3.7911 (3.4851, 4.0971)	-0.2687 (-0.539, 0.0016)	0.187 (-0.0829, 0.4568)	-0.1736 (-0.4601, 0.1128)	0.04162 (0.0261, 0.0571)	Bitterbrush Cover (%)
	Reproductive Condition	-1.1561 (-1.4222, -0.8901)	-0.1852 (-0.3178, -0.0527)	-	-	0.01094 (0.0061, 0.0158)	Mean Tree dbh (cm)
Deer mouse	Density	3.3511 (2.7914, 3.9108)	0.6726 (0.355, 0.9903)	0.9483 (0.6476, 1.249)	1.0621 (0.802, 1.3223)	-0.08547 (-0.1216, -0.0494)	Tree Basal Area (m <sup>2</sup> /ha)



## APPENDIX B (CONTINUED)

- <sup>a</sup> – Regression coefficient (intercept) quantifying the effects early summer 2001 (July 3 to August 4) on the population parameter.
- <sup>b</sup> – Regression coefficient quantifying the effects of early summer 2000 (June 25 to July 27) on the population parameter.
- <sup>c</sup> – Regression coefficient quantifying the effects of late summer 2000 (August 29 to September 30) on the population parameter.
- <sup>d</sup> – Regression coefficient quantifying the effects of fall 2000 (October 2 to October 28) on the population parameter.
- <sup>e</sup> – Regression coefficient (slope) quantifying the effects of the habitat variable on the population parameter.
- <sup>f</sup> – Habitat variable included in the model.