



## AN ABSTRACT OF THE THESIS OF

Chad A. Marks-Fife for the degree of Master of Science in Wildlife Science presented on June 2, 2016.

Title: Estimation of Population Age Structure, Detection Probability, and Density of Red Tree Voles in Oregon.

Abstract approved: \_\_\_\_\_

Katie M. Dugger

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Red tree voles (*Arborimus longicaudus*) are a unique species of Arvicoline rodent found in western Oregon and northwest California. Their preferred habitat is mature and old-growth coniferous forest dominated by Douglas-fir (*Pseudotsuga menziesii*). Tree voles are an important prey item for northern spotted owls and many other predators, but are extremely difficult to sample. As a result, little is known about their abundance or population dynamics. We used several methods to describe tree vole detectability, density, and population age structure. We verified a relationship between molar tooth development and age in red tree voles, allowing us to estimate the age of voles recovered in pellets regurgitated by spotted owls in Oregon. We found that the age distribution of tree voles in spotted owl pellets varied from year to year but not from region to region within the species range. We found evidence for a positive relationship between annual precipitation and the proportion of juvenile tree voles in owl pellets on one of two study areas.

We conducted modified line-transect surveys at 31 locations representing three forest stand age classes (young, mature, old) in the Oregon Coast Range to visually detect potential red tree vole nests. We climbed trees where potential nests were detected from the ground in order to determine the species and the occupancy status of nests. We used the transect and climbing data and distance sampling techniques to estimate detection probabilities and density of active tree vole nest trees in relation to forest age class. Our

surveys suggested that density of tree vole nest trees increased with forest age, whereas detection probability of nest trees decreased with forest age. Regardless of forest age, mean detection probability of nest trees was low ( $< 30\%$ ). We used estimates of nest tree density on our study area to estimate the minimum density of adult tree voles ( $\sim 1.91/\text{ha}$ ) and the density of individual tree vole home ranges ( $\sim 4.2/\text{ha}$ ). These estimates of detection probability and density suggest that only a small proportion of nest trees are detected and buffered against disturbance using methods described in the survey protocol used by federal agencies in Oregon and California. We recommend methods to improve detection rates of nest trees, including application of our density estimates to occupied stands, modification of stand-specific data using our estimates of detection probability, performing full-tree nest searches in every tree climbed, performing a 100 m search radius around confirmed nest trees, and targeting larger-than-average trees (with respect to stand-specific data) for spot searches.

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Estimation of Population Age Structure, Detection Probability, and Density of  
Red Tree Voles in Oregon

by  
Chad A. Marks-Fife

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Chad A. Marks-Fife, Author

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too many ways to fully address here. Bill's enthusiasm for climbing was a big part of my early climbing experience, and his love for the outdoors will be with me for a lifetime.

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## AUTHOR CONTRIBUTIONS

Eric Forsman and Katie M. Dugger contributed to this project at most stages, including acquiring funding, assisting with study design and development, and editorial review of all chapters.

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# CHAPTER 1

## GENERAL INTRODUCTION

Chad A. Marks-Fife

Red tree voles (*Arborimus longicaudus*) are small Arvicoline rodents endemic to coniferous forests of western Oregon and northwestern California (Bailey 1936, Hayes 1996). They live almost exclusively in the forest canopy and feed on the needles, cambium, and bark from conifer branches (Maser 1966, Forsman et al. 2009). Red tree voles are found primarily in Douglas-fir (*Pseudotsuga menziesii*) forest where they consume Douglas-fir needles, though in some areas they also consume needles from western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), grand fir (*Abies grandis*), and other conifers (True 1890, Taylor 1915, Walker 1928, Benson and Borell 1931). Data from pitfall traps and nest surveys indicate that tree voles are most abundant in older forests (Corn and Bury 1986, Raphael 1988, Gilbert and Allwine 1991, Gillesberg and Carey 1991, Meiselman and Doyle 1996, Gomez and Anthony 1998, Manning and Maguire 1999, Martin and McComb 2002, Dunk and Hawley 2009), and it is thought that tree vole abundance is declining as their preferred habitat becomes increasingly fragmented and reduced in extent by logging, forest fires, and conversion of forest lands to non-forest uses (Huff et al. 1992, Smith et al. 2003, Forsman et al. 2004a, Forsman et al. 2016). Recent surveys indicate that tree voles have become uncommon in the northern Coast Range of Oregon where most old forests have been harvested or burned and converted to young, intensively managed forests (Forsman et al. 2004a, Price et al. 2015, Forsman et al. 2016). A status review in 2011 by the U.S. Fish and Wildlife Service concluded that the red tree vole warranted listing as a threatened or endangered distinct population segment in the Oregon Coast Range north of the Siuslaw River, but the listing was precluded because other species had higher priority (USFWS 2011).

Red tree voles are important food items for many forest birds and mammals in Oregon, including the northern spotted owl (*Strix occidentalis caurina*; Forsman et al. 2004a, 2004b, Graham and Mires 2005, Swingle et al. 2010). In addition, barred owls (*Strix varia*) have recently expanded into the Pacific Northwest and are a relatively new predator of tree voles (Wiens et al. 2014, Wiens and Dugger *unpubl. data*). Whether predation pressure on tree voles has increased as a result of the growing number of barred owls is unknown, but seems likely. The evolving interaction between tree voles, spotted owls, and barred owls is in need of more study.

Red tree voles in Oregon and California are included in the “Survey and Manage” program under the Northwest Forest Plan (USDA 2007). In federally-managed forests of western Oregon, the USDA Forest Service (USFS) and the USDI Bureau of Land Management (BLM) are required to perform pre-disturbance surveys before engaging in management activities that are likely to have a significant negative impact on the habitat, life cycle, microclimate, or life support requirements of tree voles (Huff et al. 2012). Because it is difficult to sample tree vole populations using conventional small mammal trapping methods, tree voles are surveyed primarily by detection of their nests, which are located in the live crowns of trees (Maser 1966, Gillesberg and Carey 1991, Meiselman and Doyle 1996, Thompson and Diller 2002). Their nests are identified based on the presence of multiple signs, including resin ducts removed from needles during feeding, conifer cuttings, small twigs, accumulations of fecal pellets, and variable amounts of moss and lichen (Clifton 1960, Maser 1966, Gillesberg and Carey 1991, Meiselman and Doyle 1996, Swingle 2005). From the ground, these nests can often be confused with the nests of birds or other arboreal mammals such as Douglas squirrels (*Tamiasciurus douglasii*), northern flying squirrels (*Glaucomys sabrinus*), and woodrats (*Neotoma spp.*). Thus, tree climbing is a time-intensive, but necessary part of the identification and documentation of tree vole presence.

Tree voles are not colonial and are distributed sparsely across the landscape (Howell 1926, Clifton 1960, Meiselman 1992). They are difficult to detect and nearly impossible to trap, eliminating mark-recapture as a method for studying population dynamics. Thus, reliable data regarding population demographics have not been recorded for tree voles. Evolving practices for tree vole habitat management will depend on the development of methods to study population structure, abundance, and habitat selection, as well as ecological interactions with other species. Our objective was to investigate alternative methods for studying population demographics in this perplexing species.

## CHAPTER 2

### AGE STRUCTURE OF RED TREE VOLES IN SPOTTED OWL PELLETS ESTIMATED WITH REGRESSION MODELS OF MOLAR TOOTH DEVELOPMENT

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## ABSTRACT

We used dental measurements from a sample of 136 known-age red tree voles (*Arborimus longicaudus*) to develop a regression model that could be used to estimate vole age. We then used the regression model to estimate the age of tree voles from the remains of 1,717 individuals found in northern spotted owl (*Strix occidentalis caurina*) pellets collected in Oregon during 1970-2009. The best regression equation included the quadratic structure of the ratio between two molar measurements (crown height and anterior length) and the natural log of vole age in days. This equation predicted that molar roots begin to develop at ~40 days of age, and that molar crowns wear completely away at ~1,177 days of age.

Based on the best regression equation, the age distribution of tree voles in spotted owl pellets was dominated by young animals. Forty-seven percent of individuals were  $\leq 6$  months old and only 0.5% were older than two years. The sample of tree vole remains from pellets was not a random sample of the population, but included an unknown amount of sampling bias (by owls) and seasonal collection bias (by researchers). However, we believe these data represent the age distribution of tree voles as it relates to predator-prey relationships with spotted owls.

We found evidence for relationships between annual variation in the mean number of young produced by spotted owls and annual variation in the proportion of juvenile tree voles in owl pellets, but the results were contrary to our predictions and not consistent among study areas. All of the top or competitive models in the Tyee spotted owl demographic study area included a positive effect of annual or seasonal precipitation on the proportion of juvenile voles in owl pellets. We suggest that annual variation in tree vole breeding performance is influenced primarily by climate and weather factors, with secondary effects from predation, and not by density-dependent causes.

## INTRODUCTION

Although the red tree vole (*Arborimus longicaudus*) was first described as a unique species over a century ago, relatively little is known about its population ecology or long-term population trends (Clifton 1960, Hamilton 1962, Verts and Carraway 1998, Swingle 2005). Research in recent years has shed some light on tree vole genetics and taxonomy (Murray 1995, Bellinger et al. 2005) and geographic distribution (Forsman et al. 2004b, Forsman et al. 2016), but demographic parameters such as population age structure and density have always been difficult to estimate because the arboreal lifestyle and specialized diet of tree voles make them nearly impossible to sample using traditional trapping methods (Swingle et al. 2004). Collections of tree vole specimens have generally been opportunistic and localized, or limited to small numbers of specimens captured in pitfall traps (Clifton 1960, Hamilton 1962, Corn & Bury 1986, Johnson 1973, Johnson & George 1991, Swingle and Forsman 2009). Surveys of occupied nests have indicated that tree voles are unevenly distributed and occur at low densities compared to most other Arvicolines (Swingle and Forsman 2009). In addition, the unique biological characteristics and behaviors of tree voles make it impossible to infer their population-ecology based on information from studies of other vole species. For these reasons, our understanding of tree vole population demography is limited.

Red tree voles exhibit several biological characteristics that are uncommon among Arvicolines. They have a long gestation period (28 days), small litters (2-4 young), and a long period of natal dependency (47-60 days; Clifton 1960, Hamilton 1962, Forsman et al. 2009). Their diet, which consists almost entirely of conifer needles, is arguably the least varied diet of any North American mammal (Hamilton 1962). They obtain nearly all of their water from their food (Forsman and Price 2011), but have also been observed licking water off the surface of conifer needles (Howell 1926, Maser 1966). They are solitary in nature with no documented colonial behavior (Swingle 2005, Forsman et al. 2009). Swingle and Forsman (2009) found that adult female tree voles occupied individual home ranges that averaged  $1,732 \pm 366 \text{ m}^2$  in size (range = 36-10,308  $\text{m}^2$ ) and typically included a central nest tree and up to six adjacent trees that often contained secondary nests. Infringement on nest trees by neighboring females was most often met

with aggression, and the brief act of copulation appeared to be the only non-antagonistic interaction between males and females (Forsman et al. 2009).

Population dynamics of Arvicoline rodents has long been a topic of interest to ecologists because these species frequently exhibit multi-annual fluctuations in abundance and population structure that often appear to be cyclic (Tamarin 1978, Negus et al. 1986, Boonstra 1994). Cycles typically occur over 3-5 year periods and are observable as changes in demographic, reproductive, behavioral, and genetic conditions (Tamarin 1978, Tkadlec and Zejda 1998). The underlying mechanisms that drive these patterns appear to vary among species (Boonstra 1994). Indicator variables in analyses of cyclic population fluctuations include litter size, timing of reproduction, age of first reproduction among cohorts, length of the reproductive season, and the age structure of the population (Negus et al. 1986, Boonstra 1994).

Multi-annual fluctuations in the abundance and population structure of Arvicolid populations are generally divided into two categories indicating whether the primary influential factors are intrinsic or extrinsic to the species (Negus et al. 1986, Boonstra 1994). Cyclic patterns that are caused by intraspecific (intrinsic) factors (e.g., density-dependent shifts in population structure) remain relatively constant over time and are not interrupted by temporal heterogeneity in the environment (Negus et al. 1986, Boonstra 1994). In many other Arvicolids, multi-annual fluctuations are correlated with extrinsic factors such as climate regimes and resource abundance (Negus et al. 1986, Boonstra 1994). Alternatively, multi-annual fluctuations may be correlated with interspecific interactions (e.g., predation pressure) if annual variation in the predator species is not driven by annual variation in the Arvicoline prey species (Tamarin 1978, Negus et al. 1986). These fluctuations are not considered “cyclic” since they are inherently unpredictable (Garsd and Howard 1981). Regardless of whether the underlying causes are intrinsic or extrinsic to the species, understanding the population age structure in Arvicoline populations is a critical component of investigations into multi-annual fluctuations.

In Arvicoline species that can be studied with traditional sampling methods, analyses of population age structure have depended upon the development of methods to

estimate specific ages of individuals in the sample based on biological characteristics such as eye lens weight (Askaner and Hansson 1967, Kozakiewicz 1976, Janova et al. 2003) and length of the molar roots (Koshkina 1955, Zejda 1961, 1977, Bergstedt 1965, Tupikova et al. 1968, Lowe 1971, Viro 1974, Hansson 1983, Tkadlec and Zejda 1998). At present, no such method has been developed to estimate age in red tree voles. Although it is possible to classify tree voles into broad age categories (e.g., juvenile, subadult, adult) based on mass and pelage color, these attributes become relatively static once tree voles reach adult size at around 100-120 days (Clifton 1960, Hamilton 1962, Maser and Storm 1970, Swingle 2005). Thus, there are two constraints to investigating population age structure in tree voles. First, difficulty in obtaining a robust sample of individuals from wild populations, and second, absence of a method to accurately estimate the age of individuals. In this study we address both issues.

In the last 40 years there have been numerous long-term studies addressing the life history and demography of northern spotted owls (*Strix occidentalis caurina*) in Oregon, Washington, and California (Gould 1977, Forsman et al. 1984, 2011, Miller et al. 1997, Anthony et al. 2006, Dugger et al. 2016). Many of these studies involved collection of regurgitated pellets that have been used to describe various aspects of the spotted owl diet (Forsman 1975, Barrows 1980, Forsman et al. 1984, 2004a, 2004b, Ward 1990, Zabel et al. 1995). During 1996-2003, Forsman et al. (2004a) compiled and analyzed all the available spotted owl pellet data from studies in western Oregon. Over 24,000 prey items were identified from more than 1,100 owl territories, and additional pellets continue to be collected (Forsman et al. 2004a, Forsman et al. 2016). Red tree voles are an important prey species in spotted owl diets in western Oregon, and the remains of approximately 3,000 tree voles were identified in pellets collected during 1970-2012 (Forsman et al. 2004a). This is the largest sample of red tree vole remains in existence, but it cannot necessarily be used to infer demographic information about wild populations. Every tree vole in this sample was predated by a spotted owl and the majority of pellets were collected during the spotted owl breeding season (March – August). Thus, this sample of tree vole remains from pellets is not a random sample of the population, but includes an unknown amount of sampling bias (by owls) and seasonal

collection bias (by researchers). However, we believe these data can be used to describe the age distribution of tree voles as it relates to predator-prey relationships with northern spotted owls. Predation is often an influential factor in the multi-annual fluctuation patterns of Arvicolids (Negus et al. 1986, Boonstra 1994) and an analysis of tree vole remains in spotted owl pellets might document attributes of local, annual, and seasonal foraging behavior of owls with regards to this important prey item.

Any analysis of red tree vole age distribution in owl pellets requires the development of a method to age tree voles from skeletal remains. Fortunately, tree voles belong to a genus of Arvicoline rodents that has rooted hypsodont molars (True 1890, Johnson 1973). The molar roots begin to appear sometime between 30-60 days after birth and elongate with age (Figure 2.1). In addition, the high crowns of the molars wear down over time. Our visual examination of molar development in museum specimens suggested that tree vole age could be estimated as a function of root development and crown wear in the molars, as in other Arvicolines with rooted molars (e.g., Koshkina 1955, Zejda 1961, 1977, Bergstedt 1965, Tupikova et al. 1968, Lowe 1971, Viro 1974, Hansson 1983, Tkadlec and Zejda 1998).

Our primary objective in this chapter was to develop a regression equation that could be used to estimate age of tree voles from remains in spotted owl pellets based on measurements of lower M1 molars. We used this regression equation to evaluate the age distribution of tree voles found in the pellets of northern spotted owls, and to evaluate the data for evidence of multi-annual fluctuations in tree vole population age structure from an examination of among-year differences in age ratios of tree voles in owl pellets. We also examined temporal variation in the age distribution of tree voles in owl pellets for correlation with climate and weather variables.

## METHODS

### **Molar Measurements**

To estimate the age distribution of red tree voles in spotted owl pellets we first developed an equation that quantified relationships between vole age and measurements

of the lower M1 molar. To do this, we obtained measurements of molars from known-age tree voles from two independent sources. The first sample included 96 known-age specimens located in natural history museums. The second sample included 61 known-age individuals that we bred and raised in captivity at Oregon State University during 2013-2014.

We collected measurements of lower M1 molars in known-age voles and voles in owl pellets by photographing molars with a digital camera (Leica DFC425) mounted on a Leica S6D binocular scope. Magnification was set at 2.0 and images were taken on the buccal side of the molar (lingual side in special cases) and measured to the nearest  $\mu\text{m}$  using the linear measurement tool in program IMAGE PRO™ PLUS. Sampling priority was given to the right side lower M1 molar. In cases where the right molar was missing, the left molar was measured in its place. Four primary measurements were taken on each molar (Fig. 2.1). Anterior length (AL) was the vertical distance from the tip of the anterior root to the occlusal surface, measured along the 2<sup>nd</sup> columnar cusp, parallel with the longest portion of the root. Posterior length (PL) was the vertical distance from the tip of the posterior root to the occlusal surface, measured along the 5<sup>th</sup> columnar cusp, parallel with the longest portion of the root. Crown height (CH) was the vertical distance along the 4<sup>th</sup> columnar cusp from the occlusal surface down to the high point of the crutch between the roots. Crown length (CL) was the distance between the anterior and posterior occlusal edges of the crown.

Although M1 molar roots in tree voles did not begin to appear until 30-60 days of age, the base of the tooth began to develop in other ways shortly after birth. At 12 days old, the molar consisted of a developed crown with the base still open and unformed. At this stage the reentrant grooves ran the entire length of the tooth from the occlusal surface to the open base, sometimes referred to as the “dentine crutch” (Lowe 1971). As the vole aged, the base of the molar closed and expanded downward to create a smooth cementum “neck” below the reentrant grooves (Fig. 2.2; Gustafsson et al. 1982, Meri et al. 2008). The development of the molar neck ultimately terminated at the crutch peak and roots began to form on either side. As a secondary measurement, we recorded neck height (NECK) in the OSU lab sample of tree voles, defined here as the vertical distance along

the 4<sup>th</sup> columnar cusp from the dentine crutch (point parallel to the bottom of the reentrant grooves) down to the bottom of the tooth at the anticipated location of the crutch peak (Fig. 2.2).

### **Museum Sample**

Molars from known-age tree voles at the Burke Museum of Natural History, University of Washington, Seattle WA (n = 23), and Slater Natural History Museum, University of Puget Sound, Tacoma WA (n = 73), were measured in 2012. The majority of these specimens were captive-reared animals from studies conducted by Clifton (1960), Hamilton (1962) and M.L. Johnson (*unpubl. data*). With museum permission, the lower M1 molar in each right mandible was examined by using a diamond-tipped Dremel Tool<sup>®</sup> to remove the bone around the buccal side of the tooth to expose the roots. This permitted measurement of molars under a microscope without removing the molar from the jaw, avoiding accidental breakage of the roots and leaving specimens intact for future studies (Figs. 2.1, 2.2).

### **OSU Laboratory Sample**

Preliminary analysis of molar measurements in the sample of known-age tree voles from museums showed strong associations between root development and age but revealed the need for additional data, particularly in the first year of life. We augmented the museum molar sample by raising a colony of known-age tree voles. We captured ten wild adult tree voles (one male, nine females) and bred them in captivity to produce a sample of molars from known-age animals representing age classes in 60-day increments from 60-480 days. Our objective was to raise 5-7 individuals in each of the eight age classes. Protocols for care and maintenance of the captive colony were approved by OSU's Institutional Animal Care and Use Committee.

Founder voles for the OSU captive colony were captured during February-July 2013 in coastal conifer forests near Harlan, Benton County, OR. Nest structures were located by driving or walking through the woods while searching the forest canopy for nests. When we detected a nest that exhibited signs of tree vole occupancy from the

ground, we climbed the tree and gently probed the nest with a stiff piece of wire, capturing the vole when it evacuated the nest (Swingle et al. 2004). We determined the sex and reproductive condition of individuals in the field using multiple external cues including mass and urogenital distance (Clifton 1960, Hamilton 1962, Maser and Storm 1970, Swingle 2005). Females were often pregnant at the time of capture. If an adult female was captured and exhibited signs of lactation, the climber searched the nest for juveniles by carefully digging into the nest until the main chamber was discovered. If we found juveniles in the nest we collected them along with their mother. Age of pre-dispersed juveniles was estimated based on mass and morphological features (Clifton 1960, Hamilton 1962, Maser and Storm 1970).

We housed the captive colony of tree voles at the Research Animal Isolation Laboratory at OSU from February 2013 – July 2014. Each adult vole was kept in a separate enclosure with an information card that displayed the vole's identification number, parentage, birthdate, and intended harvest date. Breeding in the lab was facilitated by running a length of 1.5" diameter vacuum hose between two cages to allow a male tree vole access to a female overnight. Although the lab began with only the one wild adult male breeder, several juvenile males obtained from the field or from mothers that were pregnant at capture were used as breeders when they reached sexual maturity. Females in the breeding population were weighed at regular intervals to observe a sudden increase in mass that could signal pregnancy ( $> 2\text{g/wk}$ ). A projected birth date for the litter was estimated from an assessment of female mass, the probable date of conception, and an average gestation time of 28 days (Clifton 1960, Hamilton 1962). For 48 hours leading up to the projected birth date, we listened closely to the maternal cages for high pitched begging calls made by newborn young. If no calls were detected for 48 hours after the projected birth date, the nest was carefully inspected by hand. The majority of captive birth dates were considered accurate to within  $\pm 48$  hours. Juvenile voles remained with their mothers through weaning ( $56 \pm 4$  days), after which they were transferred to individual enclosures.

To meet the objective of 5-7 individuals in each age class, each known-age vole in the laboratory was given a pre-assigned date to be euthanized. To avoid potential

genetic effects on the molar-age regression, we separated siblings into different age classes and mixed the parentage of each age class as much as possible. The earliest known-age voles imported or produced in the lab were assigned to the oldest age classes so that the complete sample could be collected in the shortest possible time. On a known-age vole's scheduled harvest day, the individual was euthanized (AVMA 2013) and standard body measurements were recorded. Specimens were then prepared as museum skins. Skeletons were cleaned in a Dermestid beetle colony, degreased in 1% ammonia, rinsed in fresh water, and allowed to dry.

The procedure used to measure the lower M1 molars from our laboratory sample of tree voles was identical to the procedure used to measure the molars in the museum sample. The buccal side of the right side lower M1 molar was targeted in every case. Photographs of teeth from all samples were archived for future reference. The museum skins and skeletons were divided and donated to the Oregon State University Fisheries and Wildlife mammal collection and the Burke Museum of Natural History at the University of Washington.

### **Molar-Age Regression**

The data from all known-age tree voles in the museum and OSU laboratory samples were combined for analysis. The two data sets were distinguished by a categorical covariate (SAMPLE) which was later used to test for differences in sample source. In several very young individuals there was no measurable root development, and the bottom of the molar was convexly rounded, creating a scenario where crown height was slightly longer than the anterior or posterior lengths ( $CH \geq AL$ ). Molars from these individuals were excluded from the analysis. We also excluded nine individuals from the museum sample whose teeth were either broken or maloccluded, resulting in abnormal measurements.

We believed that the explanatory variable in the molar-age regression needed to account for potential calibration bias in the measuring phase of data collection. Our main concern was that measurements from museum and captive specimens might differ slightly compared to specimens from owl pellets because molars from owl pellets were

extracted from the jaw and placed directly on the microscope stage plate, whereas molars of museum and captive voles were measured in the jaw, where they were elevated slightly above the stage plate. To compensate for this potential bias we based all comparisons between samples on 17 ratios generated from two or more of the four primary measurements recorded for each molar (Table 2.1). The use of ratios resulted in relative measurements that standardized the data and eliminated any problems associated with calibration bias.

We used an information-theoretic approach to determine which ratio of lower M1 molar measurements most accurately predicted age (in days) of tree voles. All statistics were generated using Program R (R Development Core Team 2012). Residual scatterplots for all models were generated using the R package “ggplot2” (Wickham 2009) to test the assumptions of homogeneity of variance, linearity, and normality. Non-linearity in the molar-age relationship revealed the need for data transformation, so we performed a natural log (ln) transformation of the dependent variable (age) before continuing the analysis. We evaluated model likelihood using Akaike’s Information Criterion corrected for small sample sizes ( $AIC_c$ ) and Akaike weights. Models with  $\Delta AIC_c < 2$  were considered competitive with the top model (Burnham and Anderson 2002). We used R-squared values to determine how well variation in tooth measurements predicted vole age. We further examined the molar-age relationship by fitting a scatterplot of the data with a locally-weighted smoothing (LOESS) line and a regression line from the top model.

To reduce bias from over-fitting, we conducted k-fold cross validation on our top model using the Data Analysis and Graphing (DAAG) package in program R (Maindonald & Braun 2011). We used the ‘cv.lm’ function with the 10-fold application (Harrell 1998), which randomly removes 10 folds from the data and uses them to test the predictive value of the regression. We used the overall sum of squares across folds to estimate prediction error.

### **Effects of Sex and Sample Source**

We developed four models to evaluate the effects of sex (SEX) and sample source (SAMPLE) on tree vole age estimates using the best-supported tooth measurement ratio (Table 2.2). We evaluated model likelihood using an information-theoretic approach and  $AIC_c$  values. The SAMPLE covariate tested for differences in the molar-age relationship between molars in the museum sample and the OSU laboratory sample. Voles of unknown sex were excluded from this analysis. Both covariates were tested as interaction effects because neither would be expected to predict tree vole age independently from molar development. The model set also contained an additive model that included both effects and an intercept-only model to test the null hypothesis that neither SEX nor SAMPLE had interaction effects on the molar-age relationship.

### **Spotted Owl Pellet Sample**

The sample of spotted owl pellets from western Oregon was collected in 1970-2009 and included at least one lower M1 molar from 1,717 red tree voles. Collection information for each tree vole specimen was compiled from the owl pellet database and sorted by year and geographic location (Table 2.3). This allowed us to associate 1,712 of the individuals in the sample with eight geographic subregions that were delineated by Forsman et al. (2004a, 2004b). These subregions corresponded with major mountain ranges or subdivisions of major mountain ranges within the distribution of northern spotted owls in Oregon, including the North Coast, Central Coast, South Coast, Willamette Valley, North Cascades, Central Cascades, Interior Southwest, and Eastern Cascades (Fig. 2.3). Tree vole remains were identified in pellets from each of the geographic subregions except for the Willamette Valley and Eastern Cascades.

We also assigned 1,707 of the molar samples from owl pellets to long-term spotted owl demographic study areas in which the pellets were collected. There were five of these study areas in western Oregon, and data collection on all of them was initiated between 1987-1990 and continued through the present (Dugger et al. 2016). The five study areas included in this analysis were: Coast Ranges, HJ Andrews, Tyee, Klamath, and South Cascades (Fig. 2.3). These study areas overlapped with the geographic

subregions mentioned earlier and were not mutually exclusive, so the majority of tree vole remains in the pellet data had associations with units from both spatial delineations. For example, there was a strong similarity in the “South Coast” and “Tyee” columns of Table 2.3 because those two areas overlapped and shared many of the same tree vole observations.

Sample sizes of tree vole remains in the pellet data varied by location and year. Because the largest accumulations of continuous data occurred in the Central Coast, South Coast, and Central Cascades geographic subregions and the Coast Ranges and Tyee demographic study areas, we focused on comparisons using pellet data from those areas (Table 2.3). We assumed that all pellets were collected in the same year that they were produced, a reasonable assumption because the majority of pellets were collected at owl nest sites after recent regurgitation, and any pellets left overwinter deteriorated rapidly and were rarely available for collection in subsequent years.

### **Age Distribution of Tree Voles in Spotted Owl Pellets**

We used the best molar-age regression model from the analysis of known-age tree voles to estimate individual age (in days) of 1,717 tree voles in the owl pellet sample. The data were binned into 30-day age classes beginning at day 16. We used the ratio of juvenile voles ( $\leq 75$  days old) relative to total voles in a given annual sample ( $Pr_{75}$ ) as an index of annual tree vole productivity. To examine annual variation in  $Pr_{75}$  within individual spatial units, we calculated  $Pr_{75}$  for all spatial unit \* year combinations in the owl pellet data that included  $\geq 10$  tree vole specimens (Table 2.3). We then calculated mean  $Pr_{75}$  estimates (across years) for each spatial unit that included  $\geq 10$  years with  $\geq 10$  tree vole specimens per year ( $\overline{Pr_{75}}$ ). We examined the standard errors and 95% confidence intervals of  $\overline{Pr_{75}}$  estimates as measures of variation in annual tree vole productivity. Some spatial units included enough data to derive  $\geq 10$  estimates of variation in  $Pr_{75}$  between consecutive years ( $\Delta Pr_{75}$ ). We used these data to calculate spatially-stratified mean estimates of the difference in  $Pr_{75}$  from year<sub>(t-1)</sub> to year<sub>(t)</sub> ( $\overline{\Delta Pr_{75}}$ ).

### **Relationship Between Tree Vole Productivity and Spotted Owl Productivity**

We used multi-model linear regression to examine correlations between the mean annual number of young produced by female northern spotted owls (NYF; Dugger et al. 2016) and our index of annual red tree vole productivity (Pr75) on three of the spotted owl demographic study areas (Coast Ranges, HJ Andrews, and Tyee). Estimates of Pr75 were spatially stratified by demographic study area and geographic subregion. In some cases we pooled the data from the Central Coast and South Coast subregions to examine potential relationships with annual spotted owl productivity at a larger scale.

Because data from owl pellets were sparse from 1970-1989, we limited our analysis of the relationship between tree vole productivity and spotted owl productivity to the years 1990-2009 (Table 2.3). Using regional owl productivity estimates as dependent variables, we developed nine models to compare NYF and Pr75 values in regions of spatial overlap (Table 2.4). We included an additional nine models that predicted a one-year lag between Pr75 in year<sub>(t-1)</sub> and NYF in year<sub>(t)</sub>, reasoning that variation in the population of a prey species might not manifest effects in the predator species until the following year. Two of the spatial units also included  $\geq 10$  estimates of difference in Pr75 between consecutive years ( $\Delta$ Pr75), which were converted into two-factor categorical variables representing annual net increase/decrease in tree vole productivity from year<sub>(t-1)</sub> to year<sub>(t)</sub> (Table 2.4). The NYF values in these models were similarly converted to categorical annual net increase/decrease variables ( $\Delta$ NYF) and the relationships were compared using linear regression. Models testing one-year lag effects on the annual net increase/decrease relationship between tree vole productivity and spotted owl productivity were included. All models in the analysis were evaluated using *P*-values and *R*<sup>2</sup> values because an information theoretic approach could not be used to evaluate models developed using data sets associated with different spatial units and time series.

## **Relationship Between Tree Vole Productivity and Regional Climate and Weather Factors**

We used an information-theoretic approach to evaluate correlations between Pr75 and annual climate and weather variables in two of the northern spotted owl demographic study areas (Coast Ranges and Tyee). Geographic subregions were not considered in this analysis because the climate and weather data we had available were calculated locally based on spotted owl study area boundaries (Dugger et al. 2016). Temperature and precipitation data for each study area were obtained from Parameter Elevation Regression on Independent Slope Models (PRISM) maps using weather station data and digital elevation models (Oregon Climate Service 2008). Temperature and precipitation estimates were subdivided into an annual period (1 Jul – 30 Jun) and three seasonal periods: early nesting season (Mar – Apr), late nesting season (May - Jun), and winter (Nov - Feb). The Palmer Drought Severity Index (PDSI) represented the annual deviation of moisture conditions from the 30-year mean of 1970-2000 (NOAA 2008a). The Southern Oscillation/el Niño Index (SOI; NOAA 2008b) and the Pacific Decadal Oscillation (PDO; University of Washington 2008) represented annual measures of region-wide climate patterns. Regressions were run using two model sets with Pr75 as the dependent variable in study areas that included  $\geq 10$  years that each included  $\geq 10$  tree vole specimens (Table 2.3) during 1990-2009 (Table 2.5). Covariates were tested in individual models and evaluated using  $\Delta AIC_c$ , Akaike weights,  $R^2$  values, and standardized beta coefficients. Both model sets included an intercept-only model to test the null hypothesis that annual tree vole productivity was not correlated with annual climate factors.

## **RESULTS**

### **Molar-Age Regression**

The known-age molar sample used in our analysis contained molars from 52 tree voles raised in the OSU lab (age range = 38-480 days) and 84 museum specimens (age range = 39-1052 days). The model that best described the relationship between molar

measurements and tree vole age ( $\ln(\text{age})$ ) was a regression of the ratio of crown height over anterior length (CH/AL; Table 2.6). Hereafter, we will refer to this ratio as the best tooth ratio (BTR). A scatterplot of the data overlaid with a LOESS line suggested that the rate of change in BTR increased with age to a point but then slowed (Fig. 2.4), so we fit an additional model using a quadratic regression of BTR on  $\ln(\text{age})$ . The quadratic model, which will hereafter be referred to as BTRQ, was strongly supported, receiving almost 100% of the Akaike weight (Table 2.6). The exponentiated form of the regression from BTRQ was:

$$\text{age in days} = 1176.619 * \exp\left(-1.0097 * \left[\frac{CH}{AL}\right]\right) * \exp\left(-2.3696 * \left[\frac{CH}{AL}\right]^2\right)$$

The amount of variation in the molar-age relationship explained by BTRQ was high ( $R^2 = 0.912$ ; Table 2.6). The estimated overall sum of squares from 10-fold cross validation of BTRQ was low (0.0624), indicating low prediction error across folds (Fig. 2.5). Ten of the models in our model set exhibited  $R^2 \geq 0.824$ , indicating that while these models were less efficient at explaining variance than the top model, they nonetheless did predict tree vole age reasonably well.

The BTR covered a range of values from 1-0, where “1” represented a young animal lacking discernable roots (CH = AL) and “0” represented an extremely old individual with a crown that was worn completely away. The predicted intercept representing the beginning of root development occurred at ~40 days old. This estimate was consistent with our observations, because the earliest observed root development in the pooled sample of known-age tree voles occurred in an individual ~39 days old. The predicted intercept when the molar crown wore completely away occurred at ~1,177 days. This estimate is probably underestimated (though not drastically), because a few tree voles in captivity have survived beyond 1,177 days without their molar crowns wearing completely away (Johnson field notes on file at UWBM, Clifton 1960, Forsman *unpubl. data*).

The highest ranking model that did not use measurements of root length included the ratio of crown height over crown length (CH/CL; Table 2.6). We examined the quadratic form of this ratio and found that it did not improve the accuracy of age prediction over the non-quadratic model, so we present the non-quadratic model below. This model may be a useful alternative for predicting tree vole age in specimens where measurements of the molar roots are confounded by breakage or other factors.

$$\text{age in days} = 1922.708 * \exp\left(-2.54347 * \left[\frac{CH}{CL}\right]\right)$$

Although we had only a small sample of tree voles younger than 39 days (pre-root development) for whom measurements of neck height (NECK) were recorded ( $n = 8$ ), we hypothesized that NECK might be of some use calculating age in young tree voles lacking developed molar roots. Measurement of NECK had a mean of  $0.222 \pm 0.018$  mm (NECK/CH =  $0.068 \pm 0.004$ ) in our youngest known-age tree voles (12 days;  $n = 2$ ) and a mean of  $0.809 \pm 0.037$  mm (NECK/CH =  $0.253 \pm 0.01$ ) in the 60-day-old age class ( $n = 6$ ). The mean NECK measurement for voles  $\geq 60$  days ( $n = 52$ ) was  $0.912 \pm 0.023$  mm. We regressed the ratio of NECK/CH on tree vole age (not transformed), but the small sample size made it impossible to derive a strong regression ( $P = 0.11$ ). Regardless, the linear regression of the NECK/CH ratio on age in tree voles  $< 39$  days old may be helpful assigning age estimates to very young specimens.

$$\text{age in days} = 5.1 + 101.5 \left(\frac{NECK}{CH}\right)$$

### **Effects of Sex and Sample Source**

The highest ranking model in our analysis of the effects of sample source (SAMPLE) and sex (SEX) on the relationship between BTRQ and age included an interaction between SAMPLE and BTRQ (Table 2.7). No other models were competitive and the top model received almost three times the Akaike weight of the next closest model, which included additive interactions of SAMPLE and SEX. However, the model

including the SEX interaction alone was  $> 18 \Delta AIC_c$  from the top model and  $> 6 AIC_c$  from the null model (Table 2.7). Thus, we concluded that there was much stronger evidence for the effect of the SAMPLE\*BTRQ interaction than there was for the SEX\*BTRQ interaction.

Based on these results we calculated separate regressions for the samples from the OSU lab and museums. The exponentiated form of the equation for tree vole age in the OSU molar sample was:

$$\text{age in days}_{[\text{lab}]} = 572.951 * \exp\left(1.8442 * \left[\frac{CH}{AL}\right]\right) * \exp\left(-4.9187 * \left[\frac{CH}{AL}\right]^2\right)$$

The exponentiated form of the equation for tree vole age in the museum molar sample was:

$$\text{age in days}_{[\text{museum}]} = 1522.486 * \exp\left(-2.195 * \left[\frac{CH}{AL}\right]\right) * \exp\left(-1.2581 * \left[\frac{CH}{AL}\right]^2\right)$$

The regression curves from the separate models intersected at 146 and 590 days of age (Fig. 2.6). Within this range, age estimates were slightly higher for the OSU lab sample than for the museum sample. Outside this range the age estimates from the museum regression were higher, only becoming significantly divergent in very young and very old specimens. Given the small difference between the two models we used the combined regression to predict tree vole age for the remaining analyses.

### **Age Distribution of Tree Voles in Spotted Owl Pellets**

Of the tree voles found in spotted owl pellets, 19% were  $\leq 75$  days old, 47% were  $\leq 6$  months old, 82% were  $\leq 1$  year old, and 99.5% were  $\leq 2$  years old (Fig. 2.7). The 25<sup>th</sup>, 50<sup>th</sup>, and 75<sup>th</sup> percentiles occurred at 87 days, 197 days, and 317 days, respectively. The estimated age of the oldest tree vole in the pellet sample was almost three years (1088 days). We grouped the seven oldest individuals into a single age class ( $\geq 736$  days

[2 years]) since regression estimates on molars at this advanced stage of development probably have an increased margin of error. There were only 14 individuals in which lower M1 molar roots had not yet begun to appear ( $AL \leq CH$ ), indicating that predation on the youngest cohort of voles (16-39 days) was limited. These individuals were assumed to be > 15 days old because tree voles in the first two weeks of life are blind and virtually never venture outside the maternal nest (Forsman et al. 2009), and their cartilaginous skeletons are often too small and delicate to be recovered from owl pellets (Eric Forsman personal comm.).

Spatially-stratified mean estimates of the annual proportion of juvenile tree voles in owl pellets ( $\overline{Pr75}$ ) ranged from 0.159-0.223, with the highest estimate occurring in the South Coast geographic subregion (Table 2.8; Fig. 2.8-2.9). Estimates for all spatial units had overlapping 95% confidence intervals, suggesting that annual tree vole productivity did not vary significantly among regions (Figure 2.8). The widest set of 95% confidence intervals occurred in the Central Cascades geographic subregion (0.137-0.251), meaning that juvenile tree voles accounted for anywhere between 14-25% of the population in that region in any given year (Table 2.8). This suggested that annual tree vole productivity was highly variable within spatial units across time.

Spatially-stratified mean estimates of the difference in the annual proportion of juvenile tree voles in owl pellets between consecutive years ( $\overline{\Delta Pr75}$ ) ranged from 0.077-0.14, with the widest 95% confidence intervals occurring in the Coast Ranges study area (0.09-0.191; Table 2.8; Fig. 2.10). This means that the annual proportion of juvenile voles in the total population changed from 9-19% between consecutive years. Thus, variation in annual tree vole productivity was high between consecutive years, as well as generally variable across longer time spans.

### **Relationship Between Tree Vole Productivity and Spotted Owl Productivity**

We observed few relationships that suggested the annual variation in the number of young produced by spotted owls could be explained by annual variation in tree vole productivity, regardless of the time series or the spatial scale (Tables 2.9-2.10). The one exception occurred in the Coast Ranges demographic study area, where an inverse

relationship between annual net increase/decrease in tree vole productivity from the previous year explained about 34% of annual net increase/decrease in spotted owl productivity in the current year (Table 2.10).

### **Relationship Between Tree Vole Productivity and Regional Climate and Weather Factors**

Annual variation in the productivity of tree voles on the Coast Ranges demographic study area was largely unexplained by climate or weather variables, as the intercept-only model ranked highest in our model set (Table 2.11). Three other models including climate effects were competitive ( $\Delta AIC_c < 2$ ), but none of these models received much  $AIC_c$  model weight and the amount of variation explained by these models was low in all cases ( $R^2 \leq 0.138$ ). For the Tyee study area, the model including a positive effect of mean annual precipitation received the most support, and the two models that included positive effects of early and late breeding season precipitation were also competitive (Table 2.12). All three of the top models explained relatively high amounts of variation in the annual proportion of juvenile tree voles in owl pellets ( $R^2 = 0.442$ - $0.539$ ; Table 2.12), suggesting that increased rainfall during the tree vole breeding season was associated with increased annual productivity of voles. We observed some support for the effect of ocean-atmosphere climate variability, as the 4<sup>th</sup> and 5<sup>th</sup> highest-ranked models ( $\Delta AIC_c < 3$ ) included the Pacific Decadal Oscillation and Southern Oscillation / El Niño Index, which explained 38-41% of the variation in tree vole productivity each year (Table 2.12).

## **DISCUSSION**

### **Molar-Age Regression**

The crown height (CH) measurement was the most important predictor of red tree vole age in our analysis when combined as a ratio with any of the other three primary molar measurements (AL, PL, CL). The best ratio we investigated (CH/AL) could only be used to calculate age estimates for tree voles with visible anterior molar roots, beginning at 39-40 days old. Prior to the development of anterior roots, it is best to

estimate the age of young tree voles using mass and morphological features when possible (Clifton 1960, Hamilton 1962, Maser and Storm 1970), or to observe the developmental stage of the molar neck (NECK; Fig. 2.2) in conjunction with our description of neck development.

We found no evidence for differences in the molar-age relationship between males and females. We did find evidence that the molar-age relationship differed between the known-age specimens raised in the OSU laboratory and the known-age specimens from museums, but the only significant differences in age prediction occurred in the oldest age class ( $> 736$  days). This did not have much effect on our ability to assign tree voles to age categories because voles that were  $> 736$  days old were rare in spotted owl pellets and probably rare in wild populations as well. In addition, the molar-age regression from the pooled data predicted minimum ( $CH/AL = 1$ : beginning of root development) and maximum ( $CH/AL = 0$ : crown worn entirely away) age values that were more consistent with our observations than either of the regressions separately. We concluded that the pooled regression equation was the most accurate predictor of tree vole age.

All of the known-age voles in the OSU lab specimens and most of the known-age specimens obtained from museums were the result of captive rearing, and we cannot discount the possibility that patterns of dental wear differed between captive-raised and wild tree voles. We suspect that these differences, if they exist, were small because all of the OSU lab specimens and most of the captive-reared specimens from museums were fed a natural diet of conifer needles (Clifton 1960, Hamilton 1962, Johnson *unpubl. data*), which should have resulted in comparable amounts of crown wear. The only exceptions included a few museum specimens that were raised by Clifton (1960) on diets that included unspecified amounts of abnormal foods such as apples and potatoes. The fact that we found no evidence of extreme outliers in our data suggested that even the few voles that were fed abnormal diets had tooth wear patterns that were similar to voles fed a normal diet.

### **Age Distribution of Red Tree Voles in Spotted Owl Pellets**

The age distribution of tree voles in spotted owl pellets suggested a prey population dominated by young animals, with only 0.5% of individuals predated at ages > 736 days. This was not surprising given that voles in general tend to be short-lived animals (Tkadlec and Zejda 1998) and that the age record for the oldest tree vole in captivity was a female that lived 1,683 days (4 years, 7 months; Forsman *unpubl. data*). Our analyses also suggested that productivity of tree voles as reflected in owl pellet data varied among years but not among regions. We could not be certain that the age distribution of tree voles in owl pellets accurately reflected the age distribution of tree voles in the wild population, because samples from owl pellets reflect potential preference and sampling bias by owls. It is possible that the high proportion of juvenile voles in owl pellets reflects actual abundance of the juvenile age class in the population, but it is also possible that young animals are more susceptible to predation, regardless of abundance. Conversely, it is also possible that adult voles could be more susceptible to predation than juveniles because adults spend more time out of the nest, foraging for food for their young or searching for mates (Forsman et al. 2009). Another limitation of our analysis was that almost all spotted owl pellets in the sample we examined were collected during the period when owls were roosting at their nest sites (February-August), which corresponded closely with the primary breeding season of tree voles (February-July; Swingle 2005). Thus, any inferences from our data were limited to the tree vole breeding season, and population structure during the non-breeding season would likely be different. We had no way to evaluate these potential sources of bias, and we thus present our results with the caveat that the age distribution that we observed in owl pellets may not accurately reflect the actual age distribution of tree voles in the wild. This topic is in need of more study, but we know of no other method that is likely to produce better estimates of age structure in tree vole populations. All other methods that have been attempted to date have had serious methodological biases (see Chapter 2 and Forsman et al. 2016).

We observed only one significant relationship between our index of annual productivity in tree voles and annual spotted owl reproductive rates. In the Coast Ranges

demographic study area, annual net increase/decrease in tree vole productivity was negatively associated with the annual net increase/decrease in the number of young produced by female spotted owls in the following year. This effect was contrary to our predictions and probably meaningless. Unfortunately, the recent invasion of the barred owl (*Strix varia*) within the range of the northern spotted owl may make it extremely difficult, if not impossible, to examine predator-prey interactions of spotted owls because of the confounding effects of competition with barred owls (Wiens et al. 2014).

All of the competitive models for the Tyee demographic study area included positive effects of annual or seasonal precipitation. Annual precipitation may benefit the production of tree vole young by increasing the availability of fresh conifer needles and increasing the water content in the needles. Tree voles obtain the majority of their water from consumption of conifer needles (Forsman and Price 2011) and may also obtain water by licking dew or rain from the surface of the needles (Howell 1926, Maser 1966). Thus, more precipitation in the comparatively dry regions of southern Oregon could increase the availability of water for tree voles via their primary food source. The mechanism relating annual variation in precipitation and annual tree vole productivity cannot be determined from our data, but it suggests interesting avenues for further research, especially given that global climate change may result in warmer, wetter winters in the Pacific Northwest (Mote and Salathé 2010).

Because of their solitary nature (Swingle 2005, Forsman et al. 2009), it is unlikely that annual variation in productivity in tree vole populations is driven by density-dependent causes. It is more likely that annual variation is driven by extrinsic factors such as climate regimes, resource abundance, or predation pressure, which would classify multi-annual fluctuation in tree voles as “periodic annual variation” rather than “cycling” (Garsd and Howard 1981). Although predation by spotted owls and other predators such as weasels (*Mustela spp.*) undoubtedly plays some role in regulating tree vole populations (Swingle et al. 2010), we suspect that annual variation in age distribution is largely driven by climate and local weather conditions, most notably precipitation effects, which result in annual rates of tree vole productivity that are inherently unpredictable.

## TABLES AND FIGURES

Figure 2.1. Measurements taken from the buccal aspect of lower M1 molars of red tree voles: anterior length (AL), posterior length (PL), crown height (CH) and crown length (CL). Examples include molars from individuals at ages 38 days (a), 60 days (b), 240 days (c), and 480 days (d). Note the increase in root lengths (R) and decrease in crown height with increasing age.

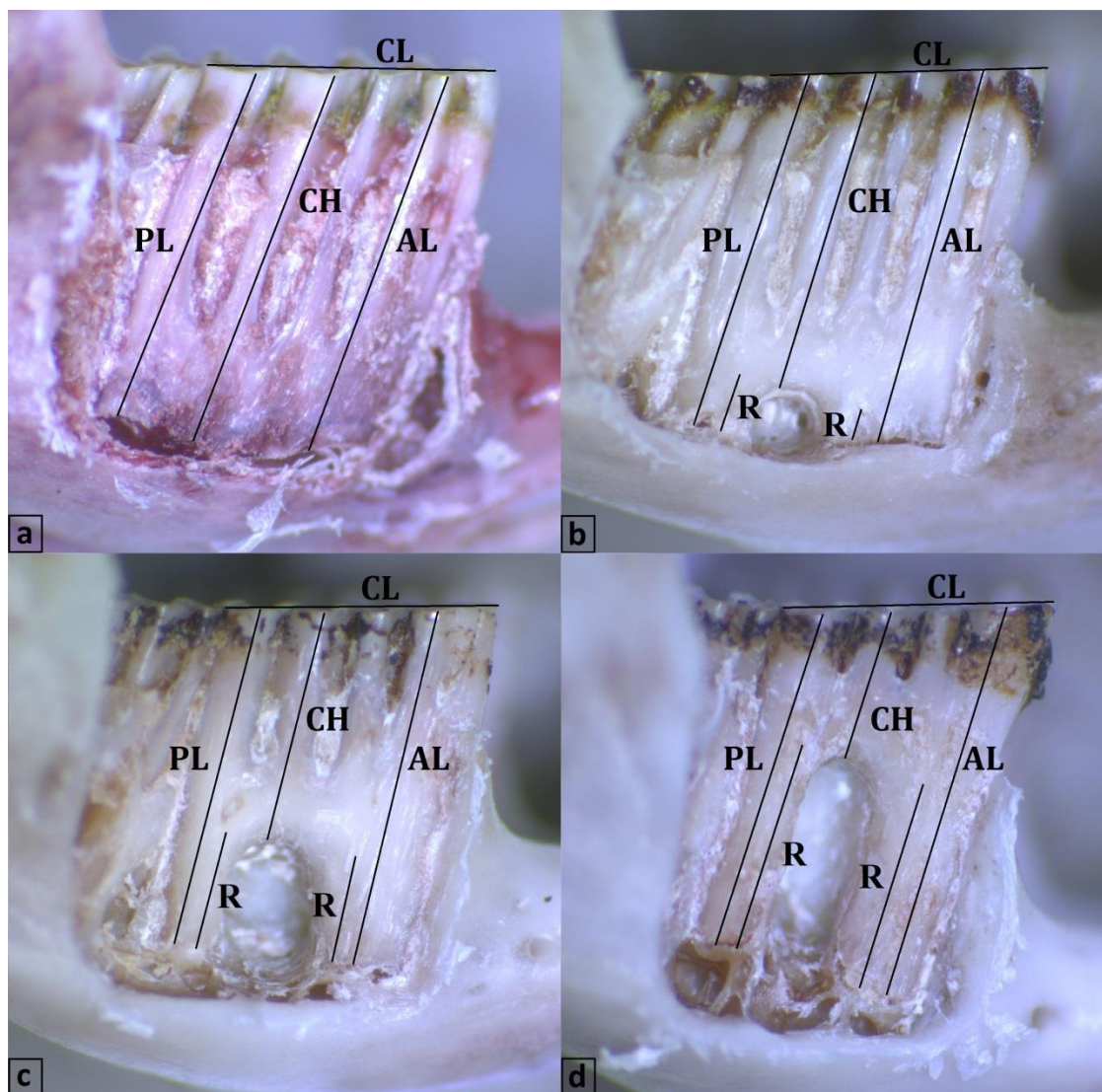


Figure 2.2. Development of the cementum neck of lower M1 molars of red tree voles at age 12 days (a), 19 days (b), 38 days (c), and 60 days (d). The crutch peak and early root development are evident at 60 days.

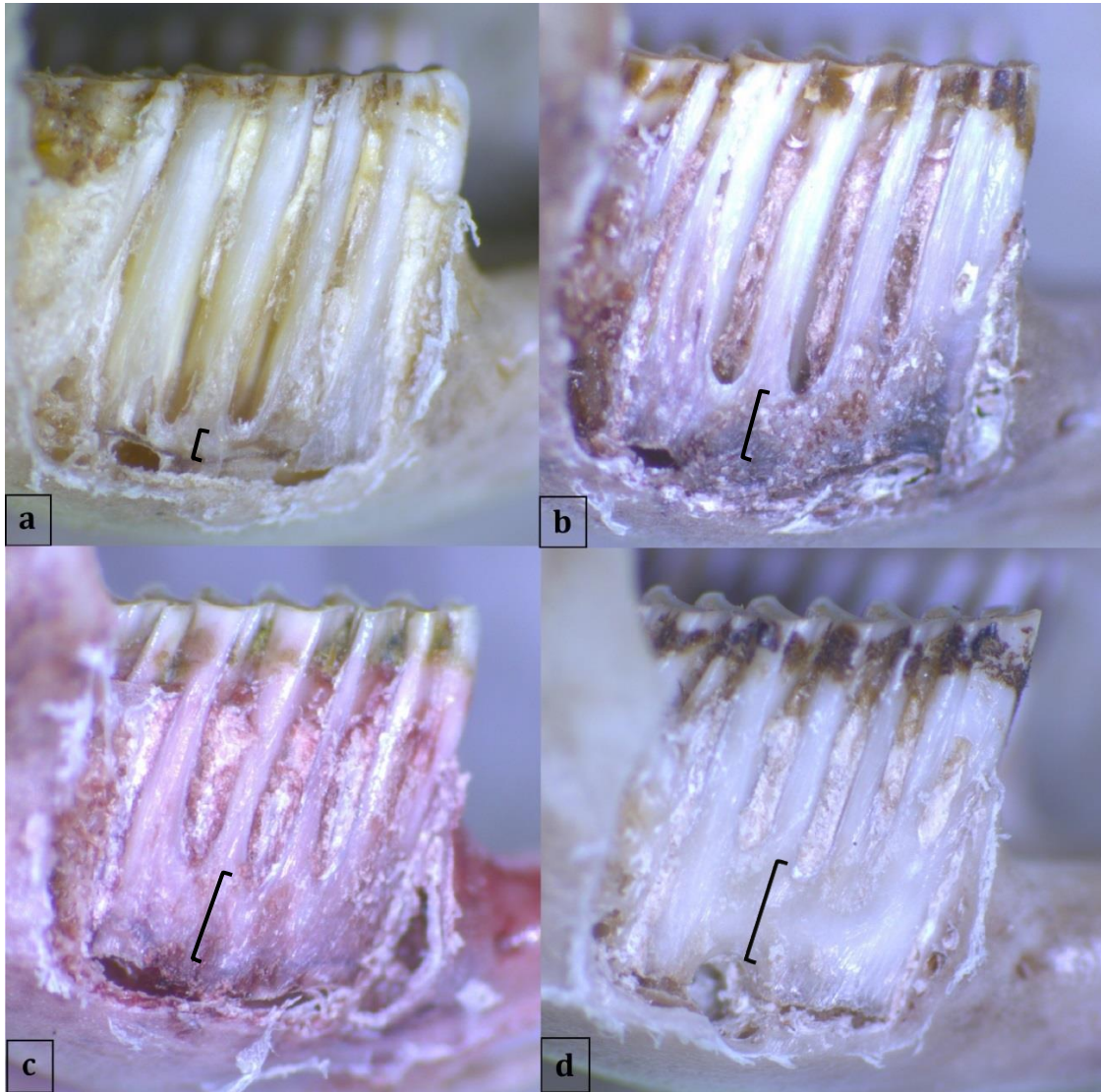


Table 2.1. *A priori* models used in the regression analysis of red tree vole age as a function of measurements of lower M1 molars obtained from known-age specimens.

| Ratio <sup>a</sup>                        |
|---|
| CH / AL                                   |
| CH / PL                                   |
| CH / ((AL + PL) / 2)                      |
| CH / (AL – CH)                            |
| CH / (PL – CH)                            |
| CH / (((AL – CH) + (PL – CH)) / 2)        |
| AL / CL                                   |
| PL / CL                                   |
| CH / CL                                   |
| (AL – CH) / CL                            |
| (PL – CH) / CL                            |
| (CH / AL) / CL                            |
| (CH / PL) / CL                            |
| (CH / ((AL + PL) / 2)) / CL               |
| (CH / (AL – CH)) / CL                     |
| (CH / (PL – CH)) / CL                     |
| (CH / (((AL – CH) + (PL – CH)) / 2)) / CL |

<sup>a</sup> Codes for tooth measurements indicate: anterior length (AL), posterior length (PL), crown height (CH), and crown length (CL).

Table 2.2. *A priori* models used to evaluate the effects of sample source (SAMPLE) and sex (SEX) on the relationship between the best tooth ratio (BTR) and age of red tree voles.

| Model                | Model description   |
|----------------------|---|
| BTR*SAMPLE + BTR*SEX | Best tooth ratio with interaction effects of sample source and sex. |
| BTR*SAMPLE           | Best tooth ratio with interaction effect of sample source.          |
| BTR*SEX              | Best tooth ratio with interaction effect of sex.                    |
| BTR                  | Best tooth ratio with no effects.                                   |

Table 2.3. Number of red tree vole specimens obtained from northern spotted owl pellets in western Oregon, subdivided by spatial unit and year. Bold numbers indicate spatial unit\*year combinations that were used in analyses of annual tree vole productivity ( $\geq 10$  specimens).

| Year | Geographic Subregion |               |             |                    |                  |                |
|------|----------------------|---------------|-------------|--------------------|------------------|----------------|
|      | North Coast          | Central Coast | South Coast | Interior Southwest | Central Cascades | North Cascades |
| 1970 | 0                    | <b>14</b>     | 0           | 0                  | 2                | 0              |
| 1971 | 0                    | 0             | 0           | 0                  | 0                | 0              |
| 1972 | 0                    | <b>14</b>     | 0           | 0                  | 5                | 0              |
| 1973 | 0                    | 3             | 0           | 4                  | 2                | 0              |
| 1974 | 0                    | 2             | <b>15</b>   | 3                  | 2                | 0              |
| 1975 | 0                    | 6             | 0           | 0                  | 7                | 0              |
| 1976 | 0                    | 0             | 5           | 2                  | <b>16</b>        | 0              |
| 1977 | 0                    | 1             | 5           | 0                  | 4                | 0              |
| 1978 | 0                    | 3             | 7           | 1                  | 9                | 0              |
| 1979 | 0                    | 0             | 5           | 0                  | 2                | 0              |
| 1980 | 0                    | 1             | 0           | 0                  | 0                | 0              |
| 1981 | 0                    | 0             | 0           | 0                  | 3                | 0              |
| 1982 | 0                    | 0             | 0           | 0                  | 3                | 0              |
| 1983 | 0                    | <b>14</b>     | <b>13</b>   | 0                  | <b>56</b>        | 0              |
| 1984 | 0                    | 4             | <b>86</b>   | 0                  | <b>18</b>        | 0              |
| 1985 | 0                    | 0             | <b>10</b>   | 0                  | <b>11</b>        | 0              |
| 1986 | 0                    | 0             | <b>39</b>   | 0                  | 5                | 0              |
| 1987 | 0                    | 2             | <b>36</b>   | 0                  | <b>13</b>        | 0              |
| 1988 | 0                    | 0             | <b>25</b>   | 0                  | 8                | 0              |
| 1989 | 0                    | 1             | 0           | 0                  | 2                | 0              |
| 1990 | 0                    | 8             | 3           | 0                  | 2                | 0              |
| 1991 | 0                    | <b>12</b>     | 0           | 0                  | 8                | 0              |
| 1992 | 1                    | <b>27</b>     | <b>21</b>   | 0                  | <b>11</b>        | 0              |
| 1993 | 0                    | 4             | 1           | 0                  | 5                | 0              |
| 1994 | 0                    | <b>28</b>     | 8           | 1                  | 3                | 0              |
| 1995 | 0                    | <b>13</b>     | 5           | 0                  | 6                | 0              |
| 1996 | 1                    | 5             | <b>13</b>   | 0                  | <b>11</b>        | 0              |
| 1997 | 1                    | 7             | 8           | 0                  | 2                | 1              |
| 1998 | 0                    | 7             | 8           | 0                  | 9                | 0              |
| 1999 | 0                    | 6             | 3           | 0                  | 0                | 0              |
| 2000 | 0                    | <b>18</b>     | <b>24</b>   | 0                  | <b>10</b>        | 0              |
| 2001 | 0                    | <b>54</b>     | <b>53</b>   | 0                  | <b>16</b>        | 0              |
| 2002 | 0                    | <b>25</b>     | <b>52</b>   | 0                  | <b>64</b>        | 0              |
| 2003 | 0                    | 8             | <b>38</b>   | 4                  | <b>10</b>        | 0              |
| 2004 | 1                    | <b>30</b>     | <b>49</b>   | 7                  | <b>21</b>        | 0              |
| 2005 | 1                    | 4             | <b>27</b>   | 0                  | <b>31</b>        | 0              |
| 2006 | 3                    | 7             | <b>25</b>   | 2                  | 6                | 0              |
| 2007 | 0                    | <b>56</b>     | <b>54</b>   | 0                  | <b>10</b>        | 0              |
| 2008 | 0                    | <b>79</b>     | <b>84</b>   | 0                  | <b>22</b>        | 0              |
| 2009 | 0                    | <b>22</b>     | <b>32</b>   | 1                  | <b>24</b>        | 0              |

Table 2.3. (Continued)

| Year | Northern Spotted Owl Demographic Study Areas |            |         |                |            |
|------|--|------------|---------|----------------|------------|
|      | Coast Ranges                                 | HJ Andrews | Klamath | South Cascades | Tyee       |
| 1970 | <b>14</b>                                    | 2          | 0       | 0              | 0          |
| 1971 | 0  | 0          | 0       | 0              | 0          |
| 1972 | <b>14</b>                                    | 5          | 0       | 0              | 0          |
| 1973 | 3  | 2          | 4       | 0              | 0          |
| 1974 | <b>17</b>                                    | 2          | 3       | 0              | 0          |
| 1975 | 6  | 7          | 0       | 0              | 0          |
| 1976 | 5  | <b>16</b>  | 2       | 0              | 0          |
| 1977 | 1  | 4          | 0       | 0              | 5          |
| 1978 | 4  | 6          | 1       | 0              | 9          |
| 1979 | 5  | 2          | 0       | 0              | 0          |
| 1980 | 1  | 0          | 0       | 0              | 0          |
| 1981 | 0  | 0          | 0       | 0              | 3          |
| 1982 | 0  | 0          | 0       | 0              | 3          |
| 1983 | 0  | 0          | 0       | 0              | <b>83</b>  |
| 1984 | 0  | 0          | 0       | 0              | <b>108</b> |
| 1985 | 0  | 0          | 0       | 0              | <b>21</b>  |
| 1986 | 0  | 0          | 0       | 0              | <b>44</b>  |
| 1987 | 2  | 1          | 0       | 0              | <b>48</b>  |
| 1988 | 0  | 0          | 0       | 0              | <b>33</b>  |
| 1989 | 1  | 0          | 0       | 0              | 2          |
| 1990 | <b>11</b>                                    | 2          | 0       | 0              | 0          |
| 1991 | <b>12</b>                                    | 8          | 0       | 0              | 0          |
| 1992 | <b>39</b>                                    | 7          | 0       | 0              | <b>13</b>  |
| 1993 | 5  | 5          | 0       | 0              | 0          |
| 1994 | <b>36</b>                                    | 3          | 0       | 1              | 0          |
| 1995 | <b>18</b>                                    | 6          | 0       | 0              | 0          |
| 1996 | <b>18</b>                                    | <b>11</b>  | 0       | 0              | 0          |
| 1997 | <b>14</b>                                    | 2          | 0       | 0              | 1          |
| 1998 | <b>15</b>                                    | 9          | 0       | 0              | 0          |
| 1999 | 9  | 0          | 0       | 0              | 0          |
| 2000 | <b>21</b>                                    | 6          | 0       | 0              | <b>27</b>  |
| 2001 | <b>55</b>                                    | 4          | 0       | 0              | <b>64</b>  |
| 2002 | <b>33</b>                                    | <b>52</b>  | 0       | 0              | <b>56</b>  |
| 2003 | 8  | 7          | 4       | 0              | <b>41</b>  |
| 2004 | <b>29</b>                                    | <b>18</b>  | 2       | 5              | <b>53</b>  |
| 2005 | 7  | <b>11</b>  | 0       | 6              | <b>40</b>  |
| 2006 | 8  | 4          | 0       | 2              | <b>26</b>  |
| 2007 | <b>61</b>                                    | <b>10</b>  | 0       | 0              | <b>49</b>  |
| 2008 | <b>110</b>                                   | <b>20</b>  | 0       | 0              | <b>55</b>  |
| 2009 | <b>23</b>                                    | <b>16</b>  | 0       | 1              | <b>39</b>  |

Figure 2.3. Spatial reference units used in analyses of age structure of red tree voles in spotted owl pellets in western Oregon, including eight geographic subregions (Forsman et al. 2004a) and five northern spotted owl demographic study areas (Lint et al. 1999, Forsman et al. 2011).

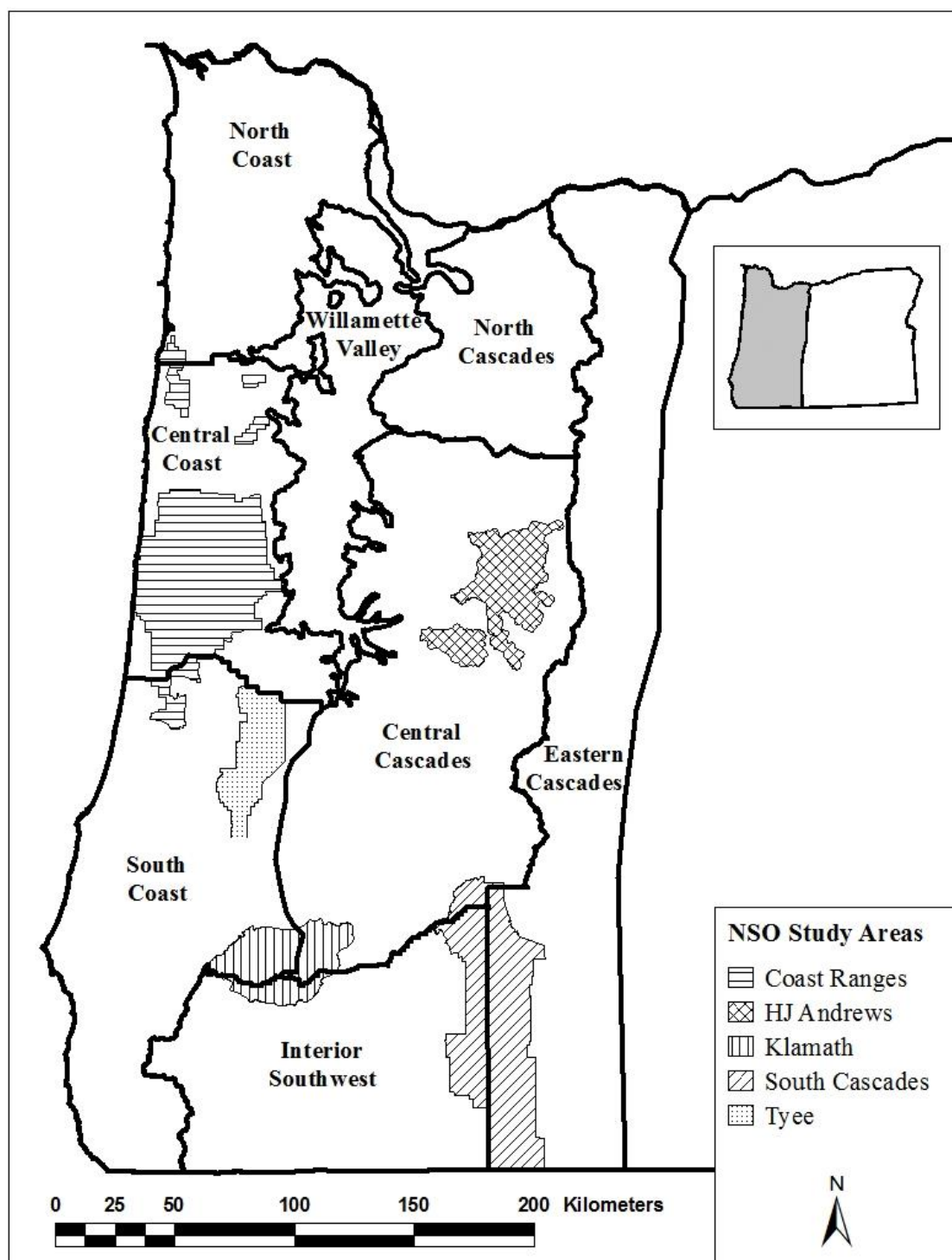


Table 2.4. Regression models used to evaluate the effects of annual red tree vole productivity (Pr75) on annual northern spotted owl productivity (NYF) in the Coast Ranges, HJ Andrews, and Tyee spotted owl demographic study areas in western Oregon, 1990-2009.

| NYF / $\Delta$ NYF <sup>a</sup> | Pr75 / Pr75 <sub>(t-1)</sub> / $\Delta$ Pr75 / $\Delta$ Pr75 <sub>(t-1)</sub> <sup>b</sup> | n <sup>c</sup> |
|---------------------------------|--|----------------|
| Coast Ranges                    | Central Coast  | 11             |
|                                 | South Coast  | 12             |
|                                 | (Central Coast + South Coast)  | 18 (15)        |
|                                 | Coast Ranges   | 15 (10)        |
| HJ Andrews                      | Central Cascades   | 11             |
| Tyee                            | Central Coast  | 11             |
|                                 | South Coast  | 12             |
|                                 | (Central Coast + South Coast)  | 18 (15)        |
|                                 | Tyee   | 11             |

<sup>a</sup> Annual northern spotted owl productivity (NYF) and annual net increase/decrease in spotted owl productivity relative to the previous year ( $\Delta$ NYF).

<sup>b</sup> Annual tree vole productivity (Pr75), annual tree vole productivity with a one-year lag (Pr75<sub>(t-1)</sub>), annual net increase/decrease in tree vole productivity relative to the previous year ( $\Delta$ Pr75), and annual net increase/decrease in tree vole productivity relative to the previous year with a one-year lag ( $\Delta$ Pr75<sub>(t-1)</sub>).

<sup>c</sup> Sample sizes for annual productivity models (sample sizes for annual net increase/decrease models in parentheses).

Table 2.5. Variables used in univariate regression models to evaluate the effects of annual climate and weather variables on annual red tree vole productivity (Pr75) in the Coast Ranges and Tyee spotted owl demographic study areas in western Oregon, 1990-2009.

| Study Area   | Climate or weather variable          |
|--------------|--------------------------------------|
| Coast Ranges | Temperature (early nesting)          |
|              | Temperature (late nesting)           |
|              | Temperature (winter)                 |
|              | Precipitation (early nesting)        |
|              | Precipitation (late nesting)         |
|              | Precipitation (winter)               |
|              | Precipitation (annual)               |
|              | Palmer Drought Severity Index        |
|              | Southern Oscillation / El Niño Index |
|              | Pacific Decadal Oscillation          |
| Tyee         | Temperature (early nesting)          |
|              | Temperature (late nesting)           |
|              | Temperature (winter)                 |
|              | Precipitation (early nesting)        |
|              | Precipitation (late nesting)         |
|              | Precipitation (winter)               |
|              | Precipitation (annual)               |
|              | Palmer Drought Severity Index        |
|              | Southern Oscillation / El Niño Index |
|              | Pacific Decadal Oscillation          |

Table 2.6. Model selection results from the regression analysis of tooth measurement ratios and age of red tree voles. Results also included an *a posteriori* model\* using the quadratic structure of the best tooth ratio.<sup>a</sup>

| Model <sup>b</sup>                          | $\Delta AIC_c$ | $w_i$ | $R^2$ |
|---|----------------|-------|-------|
| $(CH / AL) + (CH / AL)^2 *$                 | 0.000          | 0.999 | 0.912 |
| CH / AL                                     | 18.269         | 0.001 | 0.898 |
| CH / ((AL + PL) / 2)                        | 23.283         | 0.000 | 0.894 |
| CH / CL                                     | 25.086         | 0.000 | 0.893 |
| CH / PL                                     | 42.560         | 0.000 | 0.878 |
| $(CH / ((AL + PL) / 2) / CL$                | 51.300         | 0.000 | 0.870 |
| $(CH / PL) / CL$                            | 55.251         | 0.000 | 0.866 |
| $(CH / AL) / CL$                            | 55.265         | 0.000 | 0.866 |
| $(AL - CH) / CL$                            | 83.934         | 0.000 | 0.835 |
| $(PL - CH) / CL$                            | 92.069         | 0.000 | 0.824 |
| PL / CL                                     | 273.005        | 0.000 | 0.336 |
| CH / (PL - CH)                              | 297.276        | 0.000 | 0.206 |
| CH / (AL - CH)                              | 297.489        | 0.000 | 0.205 |
| $(CH / (PL - CH)) / CL$                     | 297.613        | 0.000 | 0.204 |
| $(CH / (AL - CH)) / CL$                     | 297.781        | 0.000 | 0.203 |
| $CH / (((AL - CH) + (PL - CH)) / 2)$        | 306.156        | 0.000 | 0.152 |
| $(CH / (((AL - CH) + (PL - CH)) / 2)) / CL$ | 306.572        | 0.000 | 0.150 |
| AL / CL                                     | 306.762        | 0.000 | 0.149 |
| Intercept-only model                        | 326.553        | 0.000 | NA    |

<sup>a</sup> Column headings indicate differences in  $AIC_c$  values relative to the best model ( $\Delta AIC_c$ ), Akaike weights ( $w_i$ ), and  $R^2$ . Lowest  $AIC_c = -10.156$ .

<sup>b</sup> Codes for tooth measurements indicate: anterior length (AL), posterior length (PL), crown height (CH), and crown length (CL).

Figure 2.4. Relationship between the best tooth ratio (BTR: crown height / anterior length) and age ( $\ln(\text{age})$ ) of red tree voles. Plotted lines indicate regression equations based on the linear structure of BTR and the quadratic form (BTRQ) as the independent variable, and a locally-weighted smoothing line (LOESS) for comparison.

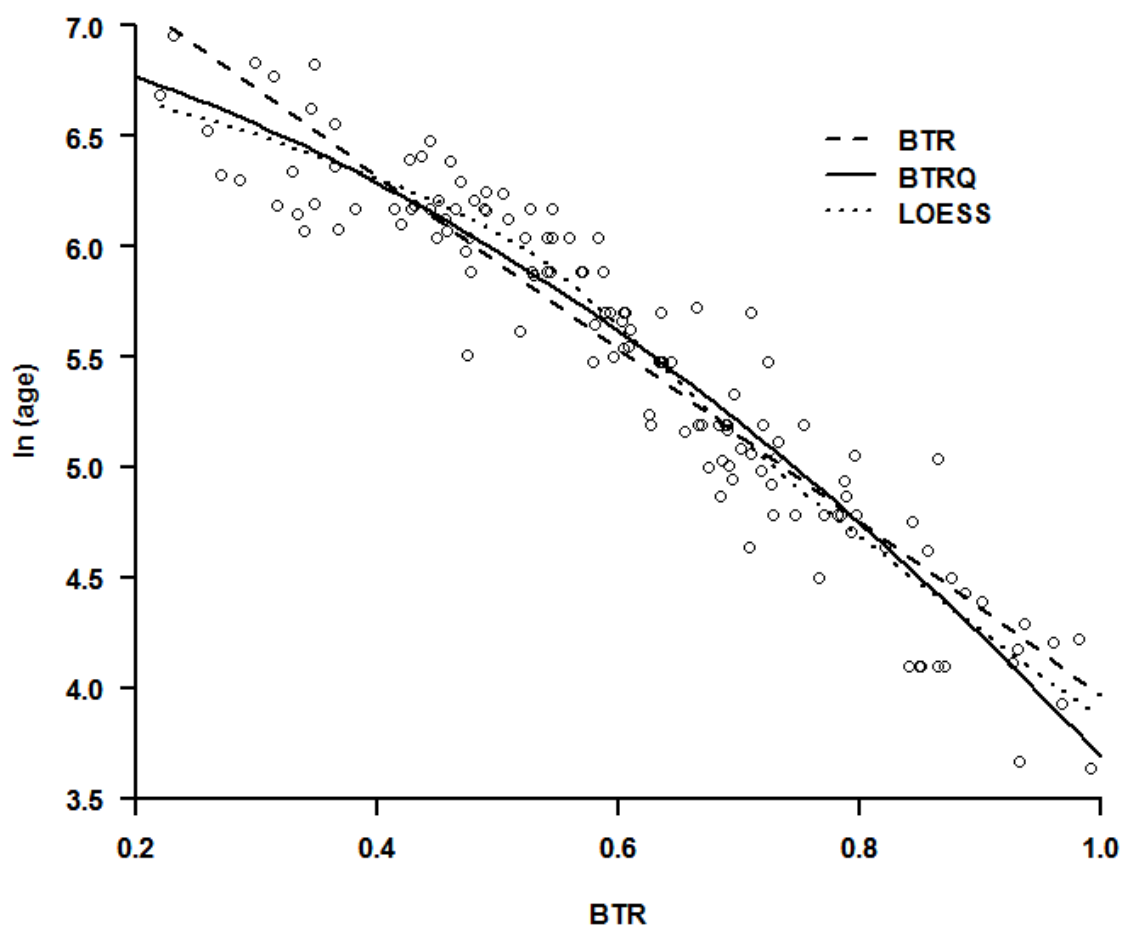


Figure 2.5. Plot of the variation in the 10-fold cross validation analysis of the regression model reflecting the relationship between the quadratic structure of the best tooth ratio (crown height / anterior length) and age ( $\ln(\text{age})$ ) of red tree voles.

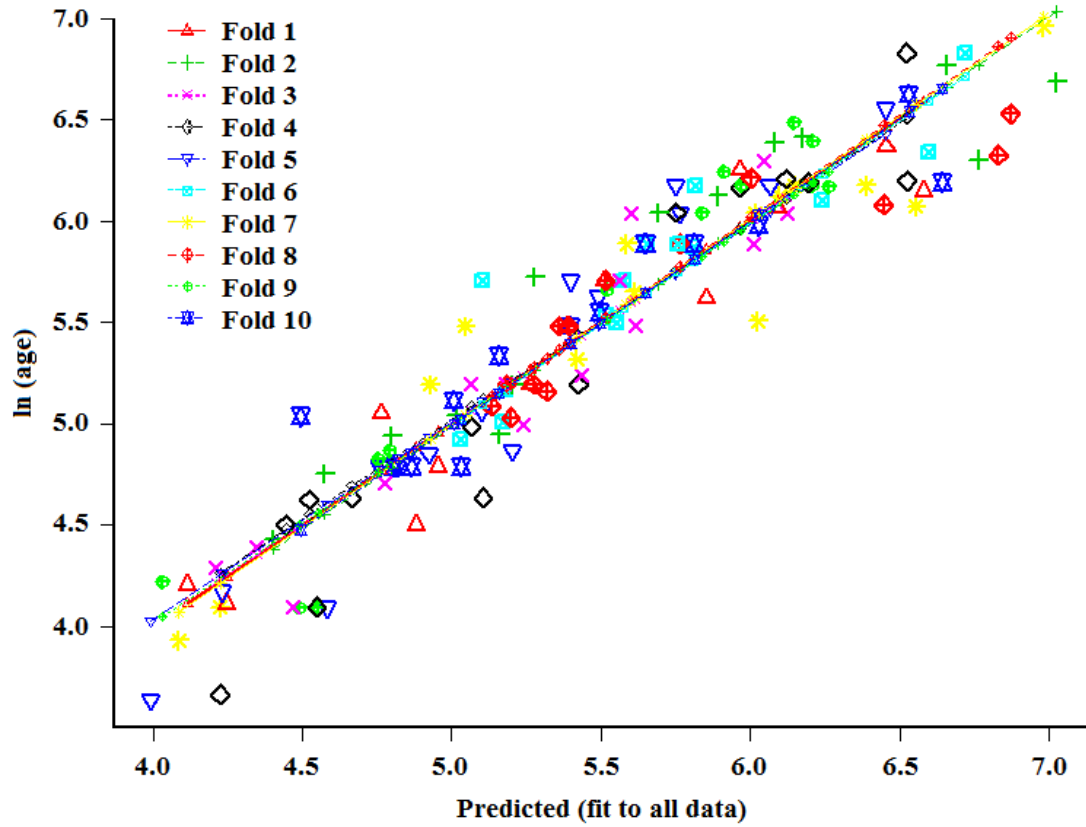


Table 2.7. Model selection results from the analysis of effects of sample source (SAMPLE) and sex (SEX) on the relationship between the quadratic structure of the best tooth ratio (BTRQ: crown height / anterior length) and age of red tree voles.<sup>a</sup>

| Model                  | $\Delta AIC_c$ | $w_i$ | $R^2$ |
|------------------------|----------------|-------|-------|
| BTRQ*SAMPLE            | 0.000          | 0.744 | 0.921 |
| BTRQ*SAMPLE + BTRQ*SEX | 2.153          | 0.254 | 0.918 |
| BTRQ                   | 12.467         | 0.002 | 0.905 |
| BTRQ*SEX               | 18.816         | 0.000 | 0.907 |

<sup>a</sup> Column headings indicate differences in  $AIC_c$  values relative to the best model ( $\Delta AIC_c$ ), Akaike weights ( $w_i$ ), and  $R^2$ . Lowest  $AIC_c = -10.156$ .

Figure 2.6. Tooth measurement ratio data from known-age red tree voles by sample source (museum vs. OSU lab). The solid line indicates regression of the quadratic form of the best tooth ratio (BTRQ: crown height / anterior length) on vole age ( $\ln(\text{age})$ ) for museum samples and the dashed line represents the same regression for OSU lab samples.

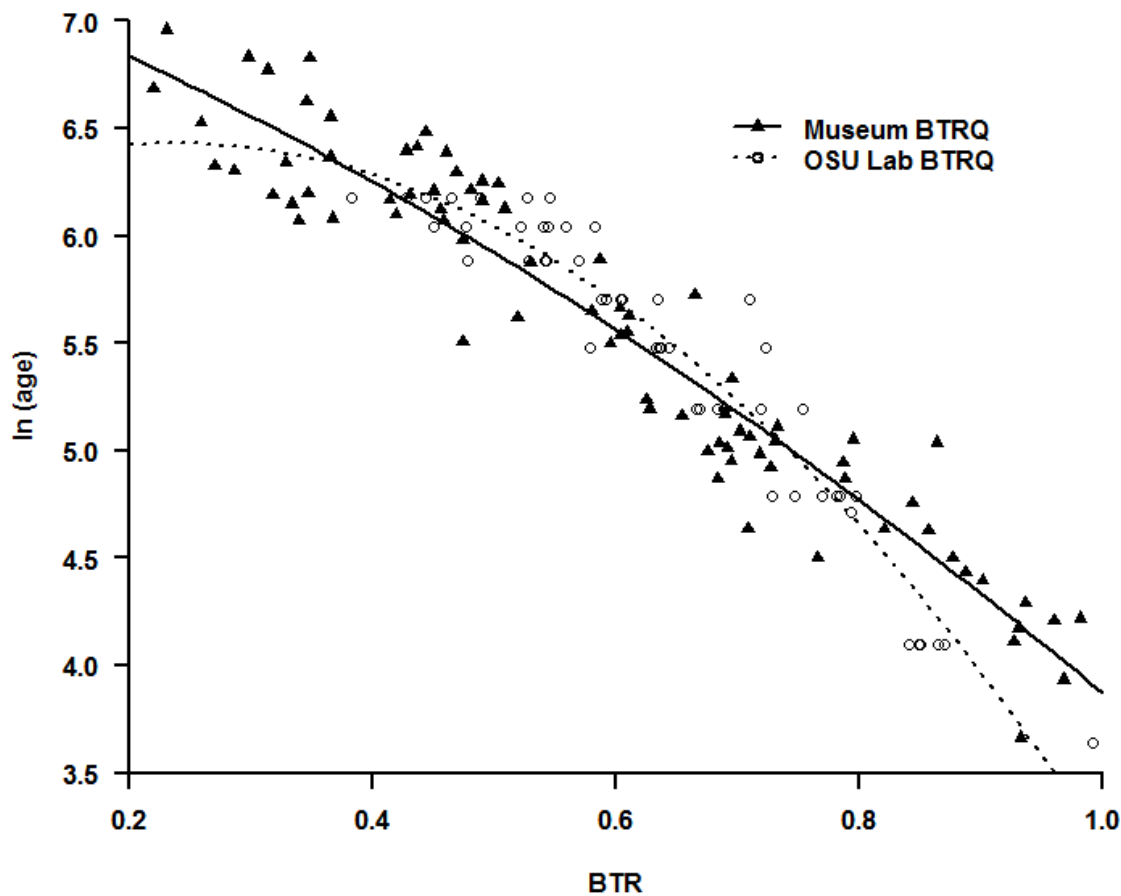


Figure 2.7. Estimated age distribution of 1,717 red tree voles identified in northern spotted owl pellets in western Oregon during 1970-2009, subdivided by 30-day age classes.

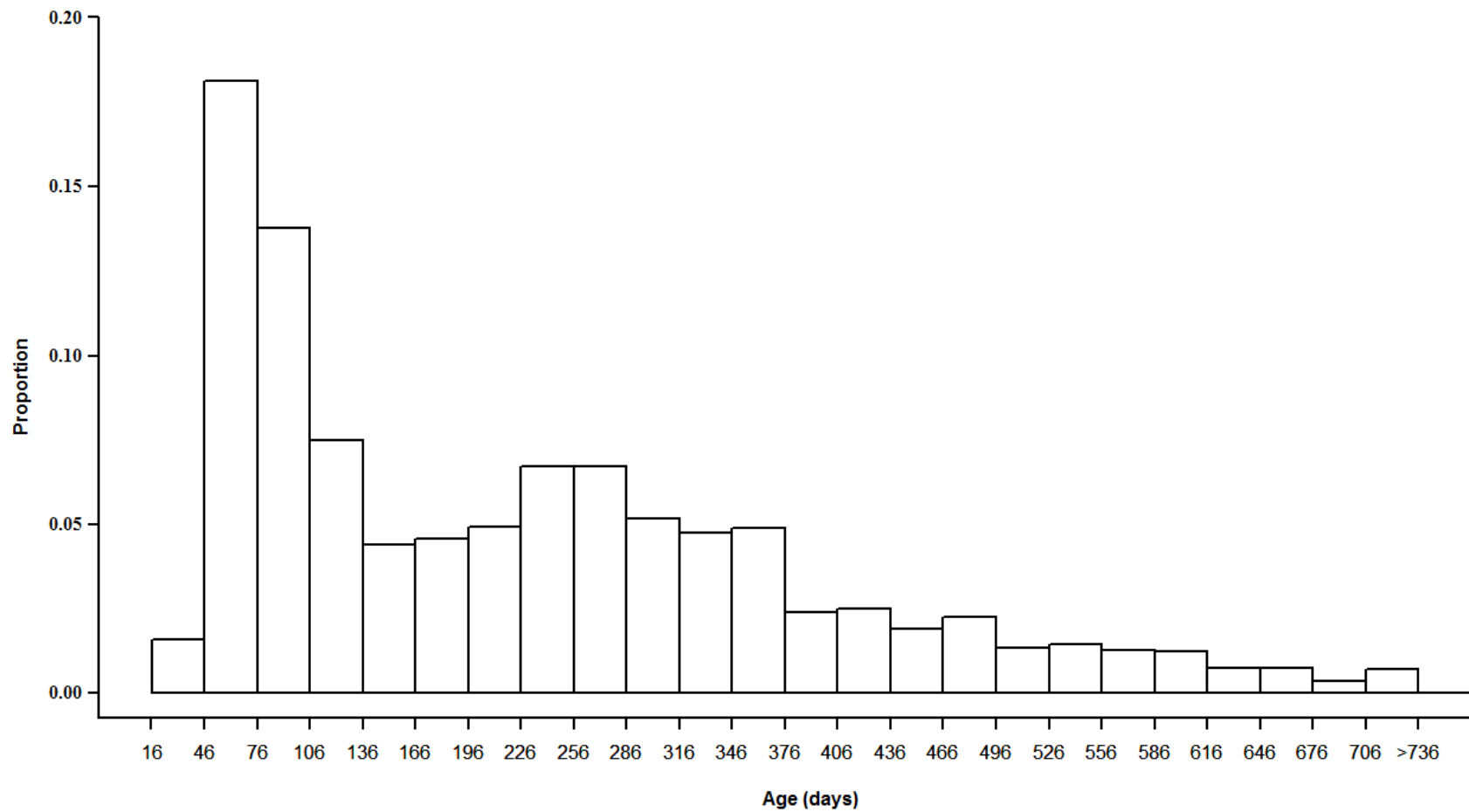


Table 2.8. Estimates of the mean annual proportion ( $\overline{\text{Pr75}}$ ) and mean difference between consecutive years ( $\overline{\Delta\text{Pr75}}$ ) of juvenile red tree voles ( $\leq 75$  days old) in pellets of northern spotted owls, estimated for various spatial units in western Oregon, 1970-2009.

| Measurement and spatial unit   | n  | $\bar{X} \pm SE$  | 95% CI          |
|--------------------------------|----|-------------------|-----------------|
| $\overline{\text{Pr75}}$       |    |                   |                 |
| Central Coast                  | 14 | $0.159 \pm 0.019$ | $0.122 - 0.196$ |
| South Coast                    | 19 | $0.223 \pm 0.024$ | $0.177 - 0.270$ |
| Central Cascades               | 16 | $0.194 \pm 0.029$ | $0.137 - 0.251$ |
| Coast Ranges                   | 18 | $0.185 \pm 0.022$ | $0.142 - 0.228$ |
| Tyee                           | 17 | $0.206 \pm 0.016$ | $0.174 - 0.239$ |
| $\overline{\Delta\text{Pr75}}$ |    |                   |                 |
| South Coast                    | 14 | $0.090 \pm 0.017$ | $0.056 - 0.123$ |
| Coast Ranges                   | 10 | $0.140 \pm 0.026$ | $0.090 - 0.191$ |
| Tyee                           | 14 | $0.077 \pm 0.013$ | $0.052 - 0.101$ |

Figure 2.8. Estimates of the mean annual proportion of juvenile red tree vole remains ( $\leq 75$  days old: Pr75) recovered from pellets of northern spotted owls, estimated for various spatial units in western Oregon, 1970-2009.

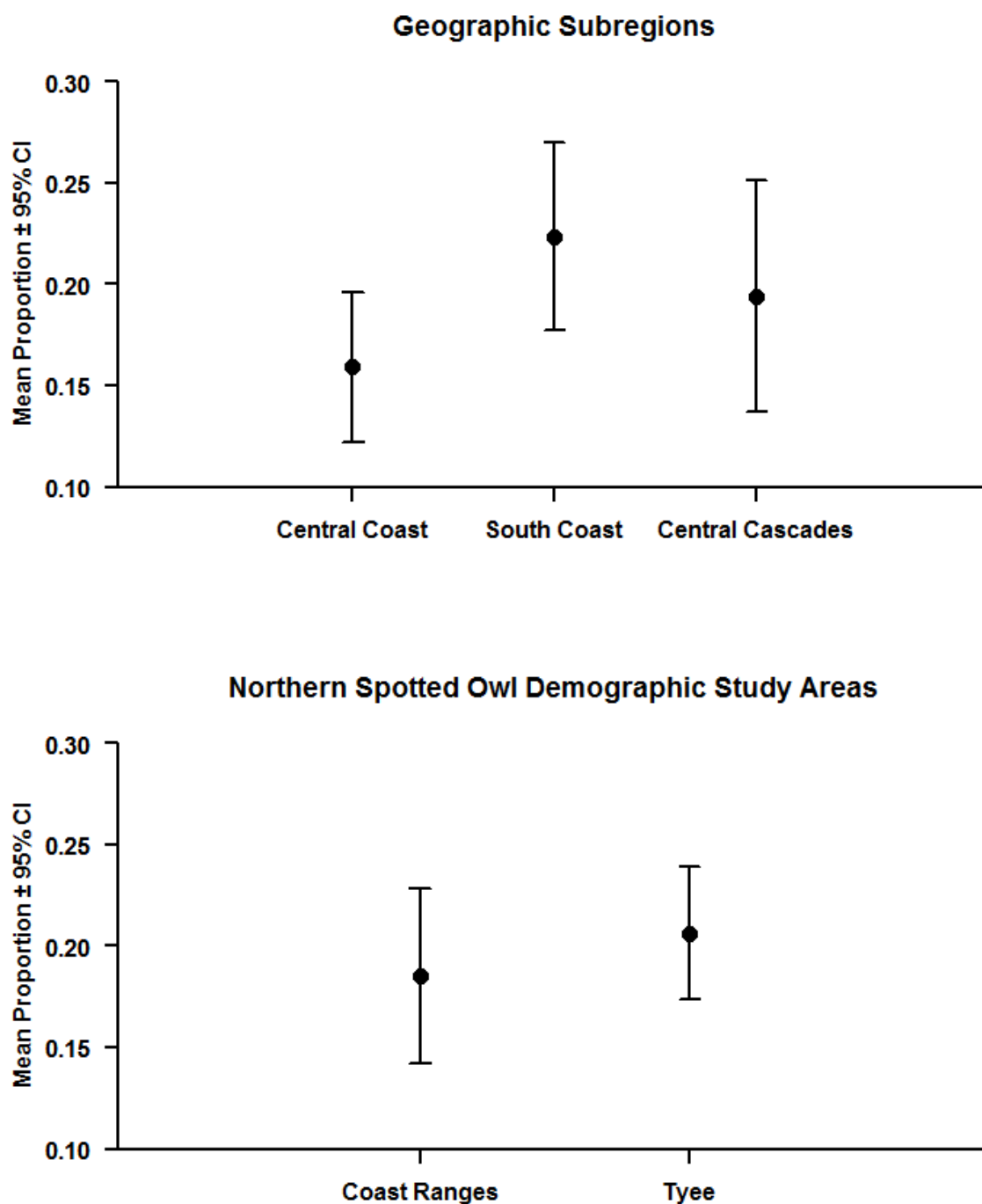


Figure 2.9. The annual proportion of juvenile red tree vole remains ( $\leq 75$  days old: Pr75) recovered from pellets of northern spotted owls in the South Coast geographic subregion in western Oregon, 2000-2009.

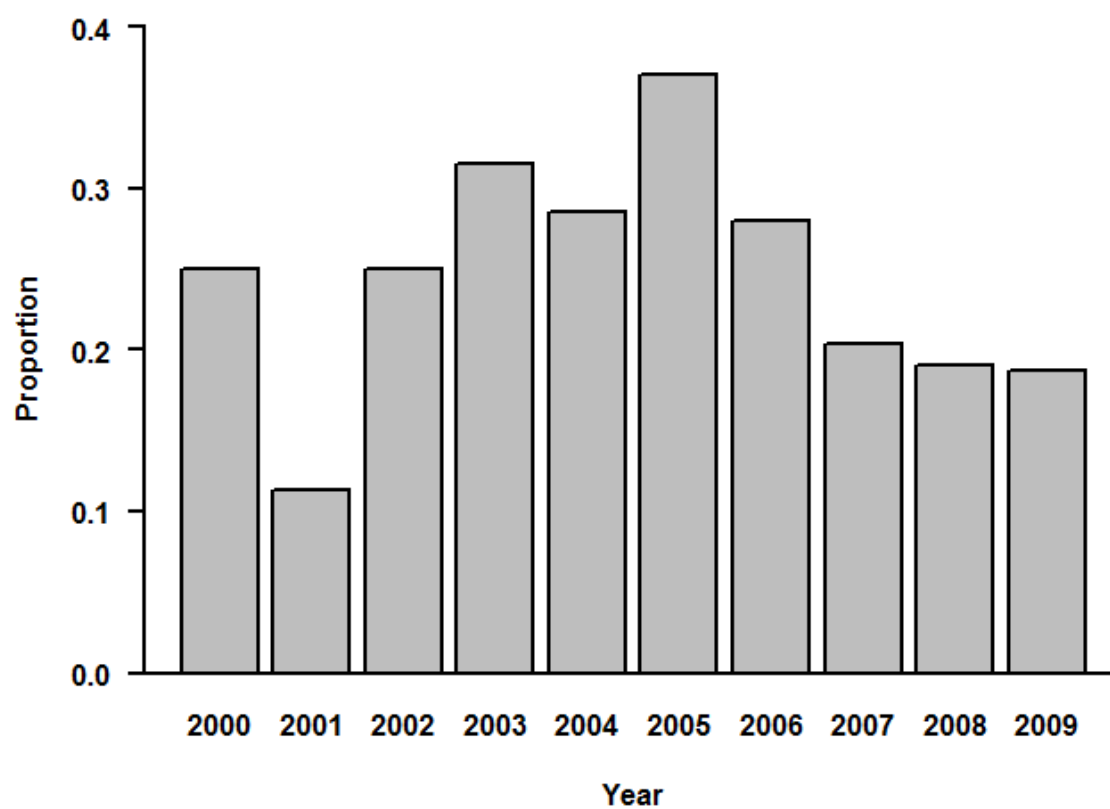


Figure 2.10. Estimates of mean difference between consecutive years in the proportion of juvenile red tree voles ( $\leq 75$  days old) recovered from pellets of northern spotted owls collected in the Coast Ranges and Tyee spotted owl demographic study areas in western Oregon, 1970-2009.

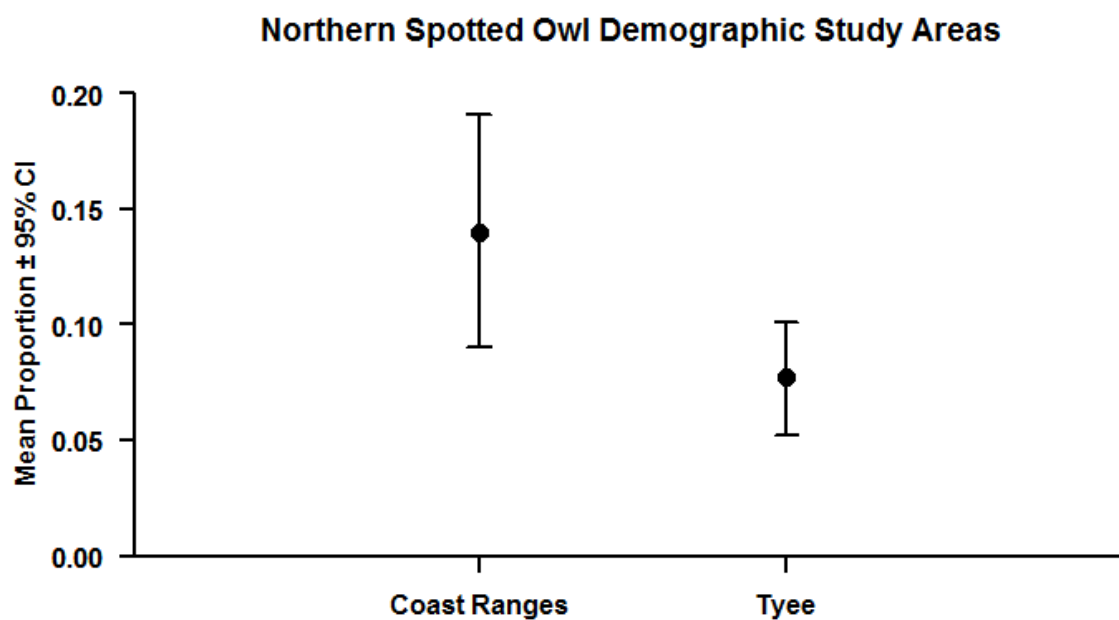


Table 2.9. Sample size ( $n$ ),  $P$ -values ( $P$ ), and  $R^2$  estimates for regression models used to evaluate the effects of annual red tree vole productivity ( $Pr75$ ,  $Pr75_{(t-1)}$ ) on annual productivity of northern spotted owls (NYF) in select study areas in western Oregon, 1990-2009.

| NYF          | $Pr75 / Pr75_{(t-1)}$                   | $n$ | $P$   | $R^2$ |
|--------------|---|-----|-------|-------|
| Coast Ranges | $Coast Ranges_{(t-1)}$                  | 15  | 0.280 | 0.062 |
|              | Coast Ranges                            | 15  | 0.318 | 0.077 |
|              | $(Central Coast + South Coast)_{(t-1)}$ | 18  | 0.338 | 0.073 |
|              | $Central Coast_{(t-1)}$                 | 11  | 0.389 | 0.043 |
|              | South Coast                             | 12  | 0.708 | 0.001 |
|              | $(Central Coast + South Coast)$         | 18  | 0.761 | 0.020 |
|              | Central Coast                           | 11  | 0.959 | 0.000 |
|              | $South Coast_{(t-1)}$                   | 12  | 0.999 | 0.001 |
| HJ Andrews   | $Central Cascades_{(t-1)}$              | 11  | 0.423 | 0.073 |
|              | Central Cascades                        | 11  | 0.953 | 0.000 |
| Tyee         | $(Central Coast + South Coast)_{(t-1)}$ | 18  | 0.260 | 0.073 |
|              | $Central Coast_{(t-1)}$                 | 12  | 0.277 | 0.050 |
|              | Central Coast                           | 11  | 0.397 | 0.005 |
|              | Tyee                                    | 11  | 0.485 | 0.056 |
|              | $Tyee_{(t-1)}$                          | 11  | 0.793 | 0.008 |
|              | South Coast                             | 12  | 0.838 | 0.003 |
|              | $(Central Coast + South Coast)$         | 18  | 0.858 | 0.017 |
|              | $South Coast_{(t-1)}$                   | 12  | 0.861 | 0.000 |

Table 2.10. Sample size ( $n$ ),  $P$ -values ( $P$ ), and  $R^2$  estimates for regression models used to evaluate the effects of annual net increase/decrease in red tree vole productivity relative to the previous year ( $\Delta\text{Pr75}$ ,  $\Delta\text{Pr75}_{(t-1)}$ ) on annual net increase/decrease in productivity of northern spotted owls relative to the previous year ( $\Delta\text{NYF}$ ) in select study areas in western Oregon, 1990-2009.

| $\Delta\text{NYF}$ | $\Delta\text{Pr75} / \Delta\text{Pr75}_{(t-1)}$ | $n$ | $P$   | $R^2$ |
|--------------------|---|-----|-------|-------|
| Coast Ranges       | Coast Ranges <sub>(t-1)</sub>                   | 10  | 0.089 | 0.340 |
|                    | (Central Coast + South Coast) <sub>(t-1)</sub>  | 15  | 0.199 | 0.115 |
|                    | Coast Ranges                                    | 10  | 0.214 | 0.167 |
|                    | (Central Coast + South Coast)                   | 15  | 0.782 | 0.005 |
| Tyee               | (Central Coast + South Coast)                   | 15  | 0.782 | 0.005 |
|                    | (Central Coast + South Coast) <sub>(t-1)</sub>  | 15  | 0.782 | 0.005 |

Table 2.11. Model selection results from the analysis of effects of regional climate and weather variables on annual productivity of red tree voles (Pr75) in the Coast Ranges northern spotted owl demographic study area in western Oregon, 1990-2009.<sup>a</sup>

| Climate or weather variable          | $\Delta AIC_c$ | $w_i$ | $R^2$ | $\beta \pm SE$     | $\beta$ 95% CI |
|--------------------------------------|----------------|-------|-------|--------------------|----------------|
| Intercept-only model                 | 0.000          | 0.038 | NA    | NA                 | NA             |
| Palmer Drought Severity Index        | 0.957          | 0.024 | 0.138 | $0.371 \pm 0.258$  | -0.133 - 0.876 |
| Pacific Decadal Oscillation          | 1.655          | 0.017 | 0.097 | $0.311 \pm 0.264$  | -0.206 - 0.828 |
| Temperature (early nesting)          | 1.859          | 0.015 | 0.084 | $0.291 \pm 0.265$  | -0.230 - 0.811 |
| Precipitation (late nesting)         | 2.984          | 0.009 | 0.013 | $-0.114 \pm 0.276$ | -0.426 - 0.654 |
| Southern Oscillation / El Niño Index | 2.984          | 0.009 | 0.013 | $0.115 \pm 0.276$  | -0.655 - 0.426 |
| Temperature (winter)                 | 3.065          | 0.008 | 0.008 | $0.088 \pm 0.276$  | -0.454 - 0.629 |
| Temperature (late nesting)           | 3.129          | 0.008 | 0.003 | $-0.059 \pm 0.277$ | -0.602 - 0.484 |
| Precipitation (annual)               | 3.136          | 0.008 | 0.003 | $0.055 \pm 0.277$  | -0.488 - 0.598 |
| Precipitation (early nesting)        | 3.150          | 0.008 | 0.002 | $0.046 \pm 0.277$  | -0.497 - 0.589 |
| Precipitation (winter)               | 3.176          | 0.008 | 0.000 | $-0.019 \pm 0.277$ | -0.563 - 0.524 |

<sup>a</sup> Column headings indicate differences in  $AIC_c$  values relative to the best model ( $\Delta AIC_c$ ), Akaike weights ( $w_i$ ),  $R^2$ , standardized beta coefficients ( $\beta$ ), and beta coefficient 95% confidence intervals. Lowest  $AIC_c = -29.072$ .

Table 2.12. Model selection results from the analysis of effects of regional climate and weather variables on annual productivity of red tree voles (Pr75) in the Tyee northern spotted owl demographic study area in western Oregon, 1990-2009.<sup>a</sup>

| Climate or weather variable          | $\Delta AIC_c$ | $w_i$ | $R^2$ | $\beta \pm SE$     | $\beta$ 95% CI |
|--------------------------------------|----------------|-------|-------|--------------------|----------------|
| Precipitation (annual)               | 0.000          | 0.023 | 0.539 | $0.638 \pm 0.272$  | 0.104 - 1.172  |
| Precipitation (early nesting)        | 1.173          | 0.013 | 0.481 | $0.602 \pm 0.282$  | 0.049 - 1.155  |
| Precipitation (late nesting)         | 1.904          | 0.009 | 0.442 | $0.451 \pm 0.316$  | -0.167 - 1.070 |
| Pacific Decadal Oscillation          | 2.417          | 0.007 | 0.413 | $0.642 \pm 0.271$  | 0.111 - 1.173  |
| Southern Oscillation / El Niño Index | 2.961          | 0.005 | 0.380 | $-0.616 \pm 0.278$ | -1.162 - 0.071 |
| Intercept-only model                 | 3.454          | 0.004 | NA    | NA                 | NA             |
| Temperature (early nesting)          | 4.199          | 0.003 | 0.298 | $0.602 \pm 0.282$  | 0.049 - 1.155  |
| Temperature (late nesting)           | 4.737          | 0.002 | 0.259 | $-0.491 \pm 0.308$ | -1.095 - 0.112 |
| Temperature (winter)                 | 6.479          | 0.001 | 0.118 | $0.431 \pm 0.319$  | -0.194 - 1.056 |
| Palmer Drought Severity Index        | 7.739          | 0.000 | 0.000 | $0.016 \pm 0.354$  | -0.677 - 0.709 |
| Precipitation (winter)               | 7.739          | 0.000 | 0.000 | $0.059 \pm 0.353$  | -0.633 - 0.750 |

<sup>a</sup> Column headings indicate differences in  $AIC_c$  values relative to the best model ( $\Delta AIC_c$ ), Akaike weights ( $w_i$ ),  $R^2$ , standardized beta coefficients ( $\beta$ ), and beta coefficient 95% confidence intervals. Lowest  $AIC_c = -21.134$ .

## CHAPTER 3

### ESTIMATES OF DETECTION RATES AND DENSITY OF RED TREE VOLES AND THEIR NESTS IN THE OREGON COAST RANGE USING DISTANCE SAMPLING

Chad A. Marks-Fife, Eric Forsman, and Katie M. Dugger

## ABSTRACT

We used line-transect distance sampling surveys and tree climbing surveys to estimate detection probabilities and density of red tree voles (*Arborimus longicaudus*) and their nest trees with consideration to forest age, abiotic survey conditions, observer bias, and various covariates describing individual nests and trees. Surveyors tended to detect nests disproportionately in relation to nest volume and nest support structure, and  $\geq 15\%$  of active nests were built on support structures that made them completely undetectable from the ground. We estimated that  $< 10\%$  of tree vole nest trees were detected in mature and old forest based on the survey protocol used by federal agencies.

We also found that density of tree vole nest trees increased with increasing forest age, whereas detection probability of nest trees at distance zero from the transect decreased with forest age. In forest areas occupied by tree voles we estimated that the minimum density of adult voles was 1.91/ha, and that density of adult home ranges was 4.2/ha. Nest trees tended to be larger than the stand average, with greater quantity of live crown and more connecting pathways with adjacent trees. Full-tree climbing surveys were necessary to determine the activity status of trees, and alternative ground-based methods such as scanning nests for conifer cuttings and searching for resin ducts around the base of the tree did not significantly increase nest tree detection rates.

## INTRODUCTION

One of the greatest challenges associated with management and conservation of red tree voles (*Arborimus longicaudus*) is a lack of rigorous methods for estimating their density and distribution. The arboreal lifestyle and specialized diet of tree voles make them difficult to detect or capture (Swingle et al. 2004), which precludes the use of capture-recapture models to estimate density or abundance (e.g., White et al. 1982). The only systematic attempt to estimate density of tree voles at the stand-level was conducted by Maser (1966), who inspected every arboreal nest detected from the ground within a 12.4 ha stand of forest. Maser provided a rough estimate of minimum tree vole density (0.97 adults/ha) but had no way to estimate the number of voles or vole nests that were not detected using his survey method. Because of the near impossibility of capturing large numbers of tree voles by climbing trees in old forests, methods to estimate tree vole density will likely rely on indirect sampling methods such as the detection of secondary cues (e.g., nests, auditory monitoring, etc.) that act as indicators of tree vole presence. Indirect indices of population size are often useful when cues produced by an animal are more available to sampling than the animals themselves (Buckland et al. 2001). By comparing cue density with estimates of the expected number of animals per cue, it is sometimes possible to estimate population density (Buckland et al. 2001).

Federal land managers in western Oregon are required to conduct pre-disturbance surveys for tree voles before they can perform management actions that are likely to have a significant negative impact on tree voles (Huff et al. 2012). If surveyors locate trees containing “active” tree vole nests during pre-disturbance surveys, managers are required to protect a 100 m buffer of unharvested forest around each nest tree for a period of  $\geq 10$  years following documentation of occupancy (Huff et al. 2012). The efficacy of this approach to tree vole conservation is poorly understood, at least partly because detection probability of occupied tree vole nests based on ground-based surveys is not well documented.

Federal tree vole surveys typically include some combination of visual surveys of individual trees (Individual Tree Examination) and Modified Line Transect surveys in which observers walk a transect line through the forest while visually scanning the

canopy for potential tree vole nests (Huff et al. 2012). Trees with potential nests are generally climbed to determine the species and activity status of each nest. The survey protocol includes recommendations of minimum survey effort (90 m of transect per acre) and strip width per observer (Huff et al. 2012). However, current protocols do not incorporate estimates of tree vole nest detection rates (from the ground or during tree climbing), so data collected from these surveys cannot be used to extrapolate information regarding tree vole nest distribution on the landscape beyond minimum density.

Tree vole nests visually detected from ground-based surveys tend to be biased toward large nests, and management actions based on protection of large nests alone could result in destruction of occupied nests not detectable from the ground (Swingle 2005). In addition, the Modified Line Transect survey method is vulnerable to variability in detection rates across differing habitat conditions because detectability of tree vole nests varies relative to visibility from the ground. Visibility of arboreal nests can vary in relation to a variety of forest structural features associated with forest successional stages including, but not limited to, average tree height, total tree density, depth of the forest canopy, abundance of cavities in trees, and vegetative composition of the understory. It is likely that tree vole nests are under-detected or missed entirely in forests where visibility of nests from the ground is low (Carey et al. 1991, Swingle 2005). A study in Oregon suggested that approximately 78% of active tree vole nests were either difficult to detect (24%) or completely undetectable (55%) from the ground, regardless of forest age (Swingle 2005). It is important to remember, however, that tree vole management in project areas is based on documentation of nest trees (trees containing  $\geq 1$  tree vole nest), not individual nests. Trees containing multiple active nests are managed the same as trees with only a single active nest. Additionally, adult tree voles use multiple nest trees within their home ranges, and nest trees are infrequently occupied by more than one tree vole at a time, regardless of how many nests are present in the tree. At best, the federal ground-based survey protocols provide stand-specific estimates of minimum nest trees density, but without estimates of nest tree detection rates from ground surveys and the number of nest trees associated with a single tree vole home range, these data cannot be used to accurately estimate density or abundance of tree voles on the landscape.

The primary objectives of this study were to estimate detection probabilities and density of active red tree vole nest trees in forest stands of differing age from ground-based line-transect surveys using distance sampling (Buckland et al. 2001). These estimates of nest tree detection probability can be used in a management context to assess the proportion of nest trees that are being detected during Modified Line Transect surveys as outlined in the federal survey protocol (Huff et al. 2012), as well as evaluate optimal survey design and layout. In addition, we attempted to describe tree vole nest tree selection based on characteristics of a randomly-selected sample of trees associated with the distance sampling surveys. This information will help increase our understanding of red tree vole habitat preferences and other aspects of the species' life history.

## STUDY AREA

The study was conducted in forests managed by the USDA Forest Service (USFS) and USDI Bureau of Land Management (BLM) in the Oregon Coast Range between the Yaquina River on the north (latitude 44° 36' 50" N) and the Oregon-California border (latitude 41° 59' 54" N) on the south (Figure 3.1). Current data from federal surveys suggest that conifer forests within this region have relatively high densities of red tree voles in comparison to other portions of the species range (USDA and USDI 2011). Vegetation in the study area was generally dominated by Douglas-fir (*Pseudotsuga menziesii*) with variable amounts of western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja plicata*), Pacific yew (*Taxus brevifolia*), bigleaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*). In the southern third of the study area coast redwood (*Sequoia sempervirens*), grand fir (*Abies grandis*), canyon live oak (*Quercus chrysolepis*), and tanoak (*Lithocarpus densiflorus*) were commonly associated with Douglas-fir. Forest age was highly variable, ranging from small seedlings on recent clear-cuts or burns to old-growth forests that were > 350 years old. Forests in much of the study area had been clear-cut and replanted, resulting in even-aged stands of young trees that were typically < 80 years old. Remnant stands of mature and old-growth forest mostly occurred on federal lands, and were typically characterized by high

variation in tree size, tree age, canopy connectivity, and vertical complexity. Topography within the study area was characterized by mountainous terrain, deeply incised by numerous streams and rivers. Elevation ranged from sea level to 1,250 m.

## METHODS

### Sample Delineation and Stratification

We hypothesized that detection probability and density of red tree vole nest trees were influenced by forest structure, which can be indexed by stand age, so we initially stratified the study area into three forest age classes: “young” (25-79 years old), “mature” (80-200 years old), and “old” (> 200 years old). Forest stands < 25 years old were considered poor habitat for tree voles (Thompson and Diller 2002, Swingle 2005, Biswell and Forsman *unpubl. data*) and were not included in the study. Although the federal tree vole survey protocol identifies suitable habitat as conifer forest  $\geq 80$  years old (Huff et al. 2012), tree voles have been documented in relatively high numbers in some forests that were < 80 years old (Thompson and Diller 2002, Swingle 2005, Biswell and Forsman *unpubl. data*). Because the relative suitability of young forest as tree vole habitat is not well understood, we chose to include this age class in our estimates of nest tree detection probability and density.

Two hundred years is considered a general milestone of early onset “old-growth” structural conditions in forests of Douglas-fir and western hemlock (Spies and Franklin 1988, Huff et al. 2012, Davis et al. 2016). The mature forest age class (80-200 years) represents the period of transition between even-aged young forest and old-growth conditions. We delineated forest age classes using a model in ArcMap 10.0 (Environmental Systems Resource Institute, Redlands, CA) that regressed Douglas-fir height on age by comparing stand height indexes from western Oregon (Means and Helm 1985, Means and Sabin 1989) and canopy heights from LiDAR data (2008-2012) provided by the Oregon Department of Forestry. We then used resampling techniques based on majority cell values (from 1-30 m) in ArcMap to convert the stand and canopy data into homogenous stand-level age classes (Fig. 3.2).

Because our primary objectives were to estimate detection probability and density of nest trees in areas where tree voles were present (i.e., “occupied” forest), we took steps to increase the probability that our sampling occurred in occupied stands so that our encounter rate of nest trees was high enough to accurately estimate nest tree detection functions. In the interest of sampling large, continuous stands of homogenous forest and minimizing dispersal effects from adjacent stands of differing age, we excluded stands of all ages that were  $< 10$  ha in size. We also cross-referenced the study area with a layer of historic red tree vole observations, and excluded young and mature stands that occurred both  $> 2$  km from historic tree vole observations and  $> 2$  km from stands of old forest. All stands of old forest  $\geq 10$  ha were retained.

### **Distance Sampling**

Sample stands were surveyed during April-October 2014 using distance sampling techniques described by Buckland et al. (2001, 2004). Distance sampling includes a group of methods used to estimate the density or abundance of sample objects while accounting for detection rates  $< 1.0$ , estimated from spatial distribution measurements. We used line-transect distance sampling where an observer walked along a predetermined transect and recorded sample objects (i.e., potential tree vole nest trees) that were visible on either side of the line, as well as the perpendicular distance from the survey line to each sample object. It was not possible to confirm the species and activity status of nests based on the ground-based survey alone, so after potential nests were detected from the transect line, we climbed every tree in which we detected a potential nest to determine the species and activity status of nest structures detected from the transect.

Under the federal survey protocol for red tree voles, arboreal nests detected during surveys are classified into one of three categories based on the presence or absence of diagnostic features such as conifer cuttings, de-barked twigs (small twigs from which the bark has been removed), resin ducts, and fecal pellets (Huff et al. 2012). The three occupancy categories are: “confirmed tree vole nest”, “confirmed non-tree vole nest”, and “unconfirmed species nest” (Huff et al. 2012: 13). “Confirmed tree vole nests”

are further classified based on the activity status of the nest as “active”, “inactive”, or “status undetermined” (Huff et al. 2012: 14). “Active” nests are those that are either known to be occupied at the time of examination (“animal observed”) or that are “likely occupied or occupied within the moderately recent past” (Table 3.1; Huff et al. 2012: 15). “Inactive” tree vole nests are unoccupied and contain old, desiccated tree vole sign that does not indicate recent occupancy (Huff et al. 2012: 15).

In this study we estimated detection probability and density of active tree vole nest trees (trees containing  $\geq 1$  active tree vole nest). Since trees often contain multiple nests, the detection probability of an active nest tree was equal to the combined detection probabilities of its individual active nests. An active nest tree was only considered to be “detected” from ground-based surveys if  $\geq 1$  of the potential nests detected from the ground was confirmed as “active” during climbing. Active nests that were discovered during climbing, but not detected from the ground, were coded as “undetected”, and potential nest trees that contained only “undetected” active tree vole nests were also coded as “undetected”. Therefore, active nest tree detection probability (from the ground) was contingent upon, but not analogous to, detection probability (from the ground) of individual active nests. Hereafter, all references to “nest trees” should be taken to mean “active tree vole nest trees” unless otherwise specified. Activity status of individual tree vole nests will be specified on a per-nest basis.

There are two sources of bias that can influence detection of tree vole nests or nest trees from ground-based surveys or during climbing. The first is perception bias (or “observer bias”), meaning variation in detection rates due to observer differences (Marsh and Sinclair 1989, Buckland et al. 2004). Observers have unequal probabilities of detecting nests because of differences in personal experience, physical characteristics (e.g., height, eyesight, etc.), or changing survey conditions (e.g., weather). As a result, some nests will remain undetected or misclassified by one observer that might have been correctly classified by another observer or by the original observer under different conditions. To evaluate the effect of perception bias on estimates of nest tree detection, we divided the survey effort equally between two observers and included “observer” as a covariate in our detection probability models. Each observer was responsible for

surveying half of the transect in each stand. Each observer also climbed half the potential nest trees to collect data on potential nest structures detected from the transect. All climbing was performed by the two primary observers, with the exception of seven trees in one stand that were sampled by a volunteer climber. We also double-sampled (i.e., double-climbed) a subset of trees along each transect to test for perception bias among climbers.

The second source of bias in line-transect distance sampling is availability bias, which occurs when a nest is unavailable to detection by any observer (Marsh and Sinclair 1989, Buckland et al. 2004). In this case, some arboreal nests could be completely undetectable from the ground due to height, location in the tree, or other factors. However, the location and availability of tree vole nests (and nest trees) do not change over the course of the survey period, so availability bias was “static” (Buckland et al. 2004). The most effective method to compensate for static availability bias is to incorporate covariates related to detection probability. Stratifying the study area by forest age (i.e., young, mature, old) was a useful coarse-scale method for quantifying differences in nest availability and nest tree detection rates associated with line-transect distance sampling. We hypothesized that nest availability to detection would be lowest in older forests because nest visibility would be inversely related to factors like average tree height and stand vertical complexity (Swingle 2005). In addition to forest age, we investigated the effects of other covariates related to forest structure and visibility at the stand, nest tree, and individual nest levels (Tables 3.2-3.6).

There are three primary assumptions of line-transect distance sampling:

1. Objects are detected at their initial location.
2. Measurements are exact.
3. Objects at distance zero from the transect line are detected with certainty:  
 $g(0) = 1$ .

Assumptions #1 and #2 were immediately satisfied in our study. Nests and nest trees did not move from their initial locations during the course of the survey so we were able to measure distances with certainty. However, assumption #3 was not initially satisfied because we could not assume that 100% of nest trees at distance zero from the transect line would be detected or correctly classified due to variable availability of nests to detection from the ground. Typical examples of distance sampling generally occur in a 2-dimensional plane, where horizontal distance from the line is the only distance measurement to consider. In our study, nest availability to detection was affected by height above the ground, regardless of horizontal distance from the line. Fortunately, a variety of recent studies have used distance sampling to survey wildlife species that exhibit imperfect detection at distance zero ( $g(0) < 1$ , notated as “ $p(0)$ ”). Research into the distribution of marine and fossorial wildlife has often had to account for bias in sampling availability at distance zero in a 3-dimensional sampling plane (Marsh and Sinclair 1989, Laake et al. 1997, Swann et al. 2002, Grant and Doherty 2007, Couturier et al. 2013). Unmodeled heterogeneity in detection availability can be mitigated by incorporating estimates of nest tree detection probability along the zero-distance line ( $p(0) = x$ ; Buckland et al. 2004).

### **Selection of Sample Stands**

We used the ArcMap model to generate a random sample of 10 stands in each of the three forest age classes (young, mature, old). After these stands were surveyed we continued sampling in additional randomly-selected mature stands to increase sample size in the age class in which federal tree vole surveys are most commonly performed. Stands selected for sampling priority were surveyed unless they exhibited one or more of the following characteristics, in which case a nearby stand of comparable age was sampled instead:

1. The stand was of a different age or composition than was indicated by the ArcMap model. This usually occurred if the stand had been thinned since the year the LiDAR data were recorded (2008-2012). No stands were sampled that had undergone tree removal treatments in the previous 10 years.
2. The stand did not include at least some Douglas-fir. Douglas-fir was not the dominant tree species in every stand sampled, but we did not perform surveys in stands where Douglas-fir was rare or absent.
3. Safety or access problems. Extreme slope or distance from a drivable road occasionally made it difficult or dangerous to access a selected stand while carrying the sizable amount of climbing gear necessary for the study. We regularly surveyed stands with  $\leq 85\%$  slopes and individually assessed safety concerns at steeper sites.

In addition to stratifying the study area by forest age class, we developed a method to post-stratify survey sites based on forest structural characteristics. In ArcMap, we delineated spatial polygons encompassing all the line-transect surveyed at each site with 50 m buffers. For each sample polygon, we used LiDAR to estimate the individual tree heights that comprised the dominant canopy (1 m cone resolution), then calculated a series of polygon-specific canopy height covariates on a continuous scale including the mean, quadratic mean, median, mode, and tallest tree heights at the 90<sup>th</sup>, 97.5<sup>th</sup>, and 99<sup>th</sup> percentiles (Table 3.2; Fig. 3.3). We also calculated total dominant-canopy tree density in each sample polygon and compared mean values among forest age classes using student's t-tests (Table 3.2). The significance level for t-tests was set at  $P < 0.10$  to account for small sample sizes and potential lower power to detect differences. Quadratic mean tree height was calculated using the following equation:

$$\sqrt{\frac{\sum (Height)_i^2}{n}}$$

### **Line-Transect Surveys**

In each of the sample stands we surveyed 400 m of line transect in four 100 m segments that were  $\geq 50$  m apart. The starting point of the first transect segment was determined by generating a random distance value (50-100 m) and walking the selected distance into the stand along a randomly-selected bearing. Once a starting point was established for the first transect segment, the transect direction was randomly selected from a spectrum of bearings that avoided crossing the stand boundaries. In large stands it was often possible to select the bearing from a wide spectrum ( $\leq 270^\circ$ ). In small or narrow stands, the stand boundaries sometimes limited the spectrum to as little as  $30^\circ$ . After the first transect was installed the starting point of the second transect was determined by walking a randomly-selected distance (50-100 m) and bearing to the starting point of the next segment. The bearings of each successive transect segment were randomly selected from a spectrum of directions that would avoid intersecting stand boundaries or passing within 50 m of previous segments.

The two observers alternated between 100 m transect segments so that neither surveyed consecutive segments. While walking to the start point of a new segment, observers directed their gaze downward so as not to accidentally observe nest structures before the survey began. We geo-referenced the start point of each transect segment with Universal Transverse Mercator (UTM) coordinates using the North America Datum of 1983 (NAD83). At the start point of each segment, we recorded the median diameter at breast height (DBH) of trees in a 10 m radius as well as abiotic survey conditions including the observer, date, time, elevation, transect bearing, transect gradient, slope aspect, slope gradient, wind strength, and weather conditions (Table 3.3). Diameter at breast height was measured using a standard DBH tape and wind and weather conditions were estimated visually (Table 3.3). Aspects and gradients were recorded using a magnetic compass and clinometer. All starting point data were recorded directly on a Dell Axim X51v Personal Digital Assistant (PDA) loaded with ArcPad and linked to a Holux M-1000 Wireless GPS receiver. Mean values of elevation and slope gradient were compared among forest age classes using student's t-tests.

Each 100 m transect segment was surveyed by an observer and 1-2 assistants (the off-duty observer acted as an assistant) who aided in data collection and tree-marking. At the start point of a transect segment, the observer held the end of a 100 m measuring tape stationary while an assistant extended the tape along the randomly-selected bearing. When the tape was fully extended, both parties laid the tape on the ground and the survey began. The observer walked along the transect ( $\leq 1$  m on either side of the tape) while scanning the canopy with binoculars for potential nests, taking as much time as necessary. Assistants refrained from talking or looking into the canopy during this time so as not to communicate any verbal or non-verbal cues to the observer. When a potential nest was detected, assistants flagged, labeled, and geo-referenced the tree with UTM coordinates so that it could be located later for climbing. For each potential nest tree, we recorded the location along the transect line where the nest was first observed, horizontal distance to the tree bole, compass bearing, gradient to the tree base, and presence/absence of an observable broken top (Table 3.4). We also recorded characteristics of the potential nest structures, including gradient of visual detection (vertical angle of the nest from the observation point on the ground) and presence/absence of visible conifer cuttings or resin ducts on the nest. All ground-based observations of nest structures were recorded from the transect line (e.g., observers did not leave the line to improve their view). Distances and gradients were recorded using a laser rangefinder (Impulse LR, Laser Technology, Inc., Centennial, Colorado). Descriptions of potential nest structures from the transect (e.g., nest height in the tree, aspect in relation to the bole, etc.) were included in the notes so that the detected structure could be correctly identified during climbing. Only conifer trees of the species Douglas fir, western hemlock, Sitka spruce, coast redwood, and grand fir were sampled. Tree vole nests have been reported in rare cases in other tree species (Swingle 2005), but not in sufficient frequency to warrant survey effort in this study. All detection data were recorded on the Dell Axim PDA.

To estimate detection probabilities of nest trees at distance zero from the transect line ( $p(0)$ ), we flagged, geo-referenced (UTM coordinates), and later climbed all trees for which any portion of the trunk at breast height was  $\leq 1$  m from the transect line (1 m half-strip width; Buckland et al. 2004). The sample of trees climbed along the zero distance

line (“p(0) trees”) could also include potential nest trees that were detected during line-transect surveys, and thus be included in both samples. Estimates of nest tree p(0) were generated for each forest age class by comparing our ground-based detection data at distance zero with estimates of the “true” nest tree population (from climbing) at distance zero.

### **Inspection of Nests and Nest Trees**

Sample stands typically required 2-5 days of survey effort, with line-transect surveys performed on the first day and the remaining days reserved for climbing. All trees were inspected within four days of their initial detection (potential nest trees) or identification (p(0) trees), reducing the risk that nests changed availability or activity status in the time between the line-transect survey and climbing survey. At each tree we collected data on the structural characteristics of the tree, the site surrounding the base of the tree, and all nests located while climbing the tree. Data collected on each tree from the ground included the climber, date, elevation, slope aspect, slope gradient, tree species, DBH, tree height, height to the first live limb, height to the continuous live crown, number of adjacent connecting trees, number of connecting pathways to other trees, tree crown density, canopy closure, and presence/absence of any tree vole sign on the ground (e.g., fallen resin ducts; Table 3.5). Connectivity between sample trees and adjacent trees was quantified by counting the number of trees with limbs that were in contact with the sample tree. Relative abundance of interconnected limbs was estimated on a geometric scale ( $2^n$ ) with range = 0-512 (Swingle 2005). Aspects and gradients were recorded using a magnetic compass and clinometer. Diameter at breast height was measured with a DBH tape and all heights (e.g. trees tops, limbs) were measured with a laser rangefinder.

We attempted to document all nests in each tree that was climbed, regardless of whether the nests were detected from the ground. Trees were climbed as high as was considered safe, usually within 5 m of the top, so that the entire tree was searched for nests. The only potential nest trees not climbed were a few trees that were deemed unsafe or were so small that they could be inspected from the ground or from adjacent trees without any chance of nests going undetected. Climbers maintained contact with ground

support using hand-held radios throughout the climb and ascended trees using a combination of spur climbing, 3-point climbing, and single rope technique (SRT). When spur climbing, climbers used spurs to ascend and then used ropes to rappel down on a Petzl Rig®. Adjacent trees were sometimes inspected concurrently by climbing one tree and doing pendulum swings on the rope to inspect both trees during descent. For each tree inspected, we recorded the inspection method, presence/absence of a broken top, presence/absence of a broken top with a cavity that could potentially contain a tree vole nest, and presence/absence of a broken top with  $\geq 1$  secondary leader (Table 3.5).

Data collected at every nest included the nest height in the tree, aspect from the bole, diameter of the trunk at nest height, horizontal distance from the bole, vertical distances to the first live limbs above and below the nest, quantity and condition of conifer cuttings, resin ducts, fecal pellets, and debarked twigs, nest dimensions (length, width, depth), nest support structure, and whether the nest was theoretically visible from the ground (Table 3.6). Nest heights were recorded by a ground observer using a laser rangefinder. We recorded nest measurements and nest aspect relative to the bole using a metric tape and magnetic compass.

Each nest detected during climbing was assigned a species code referring to the most recent occupant, as determined from an examination of the nest's physical characteristics and the presence/absence of diagnostic nest materials (Table 3.1). Tree vole nests were identified based on the presence of conifer cuttings, resin ducts, fecal pellets, and de-barked twigs (Howell 1926, Benson and Borell 1931, Clifton 1960, Maser 1966, Gillesberg and Carey 1991, Forsman et al. 2009). Nests in which tree voles were the most recent occupants were assigned an activity status referring to how recently the nest had been occupied and a condition status describing the structural condition of the nest (Table 3.1). Quantity and freshness of conifer cuttings and resin ducts were the most common clues regarding a nest's activity status, though other signs were considered. Tree vole nests that had been occupied within 2-3 weeks of examination were labeled "very recent," while nests that had been occupied any time within the current breeding season (spring-summer) were labeled "moderately recent." In both cases, we attempted to determine if the nest was currently occupied by gently probing the nest with a stiff piece

of wire to flush any adult tree vole occupant out of the nest (Swingle et al. 2004). This procedure was considered effective in the vast majority of cases and was relatively non-invasive, since tree voles have commonly been shown to return to their nests after being flushed out by researchers (Swingle 2005). All “moderately recent”, “very recent”, or “currently occupied” nests were classified as “active,” and any tree containing  $\geq 1$  active nest was considered an active nest tree. Tree and nest data were recorded on paper data forms rather than on the Dell Axim PDA, since the PDA was inconvenient for recording lengthy comments and difficult to carry in the tree during climbing.

The federal tree vole survey protocol does not require climbers to conduct full-tree nest searches. In many cases climbers ascend the tree with the singular objective of investigating a potential nest structure that was detected from the ground. In contrast, our full-tree nest searches were designed to determine each tree’s “true” activity status and document how often nest trees could be misclassified if only nest structures detected from the ground were examined. Nests of species other than tree voles were documented in the process, but these other nests were not included in our analyses.

A randomly-selected subset of potential nest trees and p(0) trees were double-sampled to assess climber perception bias. This sample was limited to trees with DBH > 45 cm because the primary concern was that perception bias would be particularly likely in large trees with complex crown structures (Dunk and Hawley 2009). Trees in this sample were climbed by two consecutive observers who alternated as primary and secondary climbers, neither of whom was present when the other was climbing. Double-sampled trees were selected in advance of sampling so that the secondary climber could plan to be out of the immediate vicinity during the primary climber’s ascent. This prevented the secondary climber from being biased by the survey actions of the primary climber. The first climber always installed a top rope in the tree, so the second climber could use SRT climbing methods on the pre-installed rope, regardless of the ascent method used by the first climber. It was imperative that the primary climber minimized his physical impact/footprint in the tree so as not to influence the observations of the secondary climber, so primary climbers took care to leave all nest structures and potential nest structures as undisturbed as possible.

### Attributes of Nests and Nest Trees

We used student's t-tests to compare attributes of nest trees that could help explain variation in detection probabilities or nest tree selection. For these analyses we used the p(0) trees. This constituted a randomly-selected sample because the availability of nests to detection during line-transect surveys did not affect their inclusion in the sample (i.e., no bias toward trees with nests that were more available to detection from the ground). Nest tree attributes that we examined were mean DBH, tree height, depth of the live crown (vertical distance from the first live limb to the tree top), number of connecting branch pathways, and number of connecting trees in trees with active nests vs. trees in which no tree vole nests (active or inactive) were documented. We hypothesized that trees with active nests would be larger (i.e., DBH, tree height, depth of live crown) and exhibit greater connectivity with adjacent trees because voles would select trees that provided greater availability of nesting sites and food, and that facilitated horizontal movement within the forest canopy (Swingle 2005).

For comparisons of nest volume, we limited the analysis to external nests because there was no way to calculate the volume of nests inside tree cavities. Mean nest volumes (length x width x depth = dm<sup>3</sup>) were calculated for three categories: active nests from the randomly-selected sample of trees (p(0) trees), active nests detected from the ground during line-transect surveys, and occupied nests that contained  $\geq 1$  adult tree vole at the time of examination. We compared mean volume of nests in the two latter groups with mean volume of nests in the randomly-selected sample of trees using student's t-tests. Shared observations between groups were rare and had little impact on estimates of mean volume, so the few shared observations were excluded to maintain independence among samples. We only included active or occupied nests in analyses of nest volume since volume was affected by age, and inactive nests could have decreased in volume since the time of their most recent occupation. Analyses of horizontal and vertical nest location in trees included all intact nests (nest condition "intact"; Table 3.1) since location in the tree was not affected by nest age. Horizontal nest position was represented as a two-factor categorical covariate that indicated whether a nest occurred  $\leq 1$  m or  $> 1$  m horizontally from the tree bole. Vertical nest position was represented as a four-factor categorical

covariate, indicating where the nest occurred in relation to the live crown (i.e., upper third, middle third, lower third, or below the first live limb).

We used one-way analysis of variance (ANOVA) with factorial design to compare the percent of intact nests observed with respect to horizontal distance from the tree bole, vertical position in the tree, and among eight nest support structures in each forest age class (Table 3.6). In this analysis nests were also subdivided based on detection method, including nests located in the randomly-selected sample of  $p(0)$  trees during climbing and nests either “detected” or “undetected” from the ground during line-transect surveys [potential nest trees and  $p(0)$  trees]. The few observations shared between categories were excluded to maintain independence among samples.

### **Climber Perception Bias from Double-Sampling**

We examined climber perception bias in identification of nest trees using the double-sampling data collected when trees were independently climbed by two observers. The probability of a climber correctly classifying a nest tree was estimated using two sets of criteria. Under the first set of criteria, a tree’s activity status was determined from the climber’s examination of the potential nest structure(s) detected during the line-transect survey, so other nest structures in the tree that were not detected during the line-transect survey were not considered. In this scenario, the activity status of a nest tree was dependent entirely on a climber’s ability to correctly identify/interpret materials in nests detected from the ground, not on the climber’s ability to detect new nests during climbing. The data were analyzed as a closed population capture-recapture model with two sampling occasions since neither the activity status or the quantity of nest trees changed between sampling occasions (Huggins 1989). The two sampling occasions denoted the two observers, with active nests identified by observer 1 coded as “1” in the first sampling occasion, active nests identified by observer 2 coded as “1” in the second sampling occasion, and active nests identified by both observers coded as “11”. We used the model denoting the probability of initial detection, or in this case correct classification of active nests by observer 1 ( $p$ ) during the first sampling occasion, set equal to the probability of correct classification by observer 2 ( $c$ ) during the second sampling

occasion [ $p(.) = c(.)$ ] to estimate the detection rate of active tree vole nest trees across both observers. Model estimates were generated using Program R (R Development Core Team 2012).

Under the second set of criteria, a tree's activity status was determined from a climber's examination of all nests in the tree, regardless of whether the nests were detected from the ground. In this case, climbers performed full-tree nest searches and documented every nest they found. Correct classification of a nest tree was dependent not only on a climber's ability to interpret nest materials, but also on the climber's ability to detect nests previously undetected from the ground. Two climbers in this scenario might both designate a tree as "active" based on the detection of two different active nests. The data were analyzed as a closed population capture-recapture model with two sampling occasions (Huggins 1989). For the first sampling occasion, trees in which  $\geq 1$  active nest was detected by observer 1 during climbing were coded as "1". For the second sampling occasion, trees in which  $\geq 1$  active nest was detected by observer 2 during climbing were coded as "1", and trees where  $\geq 1$  active nest was detected by both observers were coded "11". We used the model denoting the probability of initial detection, or in this case correct classification of active nest trees by observer 1 ( $p$ ) during the first sampling occasion, set equal to the probability of correct classification of the nest tree by observer 2 ( $c$ ) during the second sampling occasion [ $p(.) = c(.)$ ] to estimate the detection rate of active tree vole nest trees across both observers.

### **Detection Probability of Nest Trees at Distance Zero**

We estimated detection probabilities of tree vole nest trees at distance zero from the transect line [ $p(0)$ ] using data from the sample of  $p(0)$  trees. The objective was to estimate the proportion of  $p(0)$  trees containing  $\geq 1$  active tree vole nest for which  $\geq 1$  active tree vole nest was detected from the ground during line-transect surveys. The data were subdivided by forest age class and analyzed as a closed population capture-recapture model with two sampling occasions (Huggins 1989). The first sampling occasion denoted  $p(0)$  trees in which  $\geq 1$  active nest was discovered during climbing surveys (the "true" sample of nest trees). The second sampling occasion denoted  $p(0)$

trees in which  $\geq 1$  active nest was detected from the ground during line-transect surveys. The *a priori* model set included two models evaluating estimates of  $p(0) < 1$  stratified and unstratified by forest age class, and a third model testing the null hypothesis that there was no difference in detection probabilities between line-transect surveys and climbing surveys at distance zero [ $g(0) = 1$ ; Table 3.7]. We used an information-theoretic approach to evaluate model likelihood using Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002). Models with  $\Delta AIC_c < 2$  were considered competitive with the top model and Akaike weights were included for comparison. Model estimates were generated using Program R.

### **Modeling Detection Probability and Density of Nest Trees**

Based on estimates of encounter rates of tree vole nests from previous USFS surveys (Biswell and forsman *unpubl. data*), we estimated that 400 m of line-transect distance sampling was more than twice the survey effort needed to visually detect  $\geq 1$  active nest in occupied stands of young forest, the age class believed to be the least suitable for tree voles. Climbing the sample of  $p(0)$  trees was an additional source of survey effort. Therefore, after completion of line-transect surveys and climbing surveys of  $p(0)$  trees, forest stands with no detections of active tree vole nests from any method were considered unoccupied for the purposes of our study and excluded from further analyses. Our objective was to estimate detection probabilities of nest trees at the stand level in occupied stands, and thus, incorporating survey data from unoccupied stands would negatively bias mean detection rates and density estimates across the study area. The fact that we excluded stands that did not have evidence of tree vole occupancy from our analysis is an important point to remember in all subsequent analyses. Our estimates of density only apply to stands with evidence of occupancy by tree voles and do not represent average conditions on the landscape.

We used the Multiple-Covariate Distance Sampling (MCDS) routine in Program Distance 6.2 to estimate nest tree detection probability ( $P_d$ ), nest tree density ( $D$ ), effective strip width (ESW), coefficients of variation (CV), and chi-square statistics ( $X^2$ ). Effective strip width was the perpendicular distance at which the number of nest trees

detected at greater distances was equal to the number of nest trees not detected at lesser distances. We also used the MCDS routine to evaluate hypothesized relationships between nest tree detection probabilities and a variety of environmental and stand-level covariates (Thomas et al. 2010). Abundance parameters in Program Distance are estimated by modeling a detection function,  $g(x)$ , which specifies the conditional probability that a survey object (i.e., nest tree) is detected, given its perpendicular distance from the transect line (Ramsey et al. 1987, Beavers and Ramsey 1998, Anderson et al. 2001). Nest tree distance data were entered into Program Distance as radial horizontal distances and angles in relation to the transect bearing, since data were collected in this format during line-transect surveys, and converted to perpendicular distance data.

Program Distance allows for a variety of key functions and expansion terms for modeling the detection function (Thomas et al. 2010). We tested half-normal (cosine and hermite polynomial expansion terms) and hazard-rate (cosine and simple polynomial expansion terms) models with our nest tree detection data from line-transect surveys (Table 3.8). We hypothesized that the half-normal cosine model would provide the best fit, based on visual inspection of the data (Fig. 3.4). When performing this analysis, we truncated the data at 49 m to exclude two outliers because extreme values added little to density estimation and could have strong negative effects on model fit (Buckland et al. 2001). Based on an examination of the remaining perpendicular distance data at multiple scales across forest age classes (Fig. 3.5), we binned the data with upper distance limits of 9 m, 22 m, 33 m, and 49 m. These bin parameters fit the data best out of several combinations that were considered. Model likelihood was evaluated using  $AIC_c$ .

Nest trees were only included in the analysis if  $\geq 1$  active nest was detected during line-transect surveys and verified during climbing surveys. Incidental nest trees (nest trees where the potential nest structure detected from the ground was not an active tree vole nest, but  $\geq 1$  active nest was discovered in the tree during climbing surveys) were not included in the analysis since the active nest structure was not detected from the ground. Although tree vole nest trees are known to be unevenly-distributed and often occur in clusters that denote home ranges (Swingle 2005), we hypothesized that low

detection probability would prevent us from detecting more than one nest tree per cluster during distance sampling. Therefore, we did not analyze nest trees as clustered groups or incorporate estimates of mean cluster size at the detection level.

We used an information-theoretic approach to evaluate 18 *a priori* models that included effects of various covariates on nest tree  $P_a$  (Table 3.9). Models with  $\Delta AIC_c < 2$  were considered competitive with the top model. We used coefficients of variation and chi-square estimates to evaluate model fit based on comparison of the observed and expected frequencies of observations (Thomas et al. 2010). The effects of canopy structure (i.e., age, height, density) on nest tree  $P_a$  in each sample polygon were tested using nine *a priori* models representing various stratifications from LiDAR data (Table 3.9). The effects of abiotic survey conditions recorded at the start point of each 100 m transect segment were tested using nine *a priori* models that included covariates such as observer, transect topography, weather, and transect orientation in relation to slope aspect. Transect orientation in relation to slope aspect was represented in two models as both a two-factor categorical variable (perpendicular/parallel) and a three-factor categorical variable (perpendicular/parallel-uphill/parallel-downhill), for which we hypothesized that transect segments laid parallel to the slope would result in increased  $P_a$  (Table 3.9). To determine whether nest tree  $P_a$  would be better explained using multiple covariates, we included some *a posteriori* multi-factor additive models in cases where single-factor models were highly competitive. An intercept-only model was also included to test the null hypothesis that neither canopy structure nor abiotic survey conditions had any effect on nest tree  $P_a$ .

Program Distance allows for the incorporation of detection multipliers at the global level but not at stratified levels (Thomas et al. 2010). Our estimates of climber perception bias from double-sampling were incorporated in this analysis as global multipliers. Estimates of  $p(0)$  stratified by forest age were incorporated post-analysis by adjusting nest tree  $P_a$  estimates from the top competitive models. Adjusted estimates of  $P_a$  at given perpendicular distances were calculated in 1-m increments from 1-49 m, then reported as mean detection probability ( $\bar{P}_a$ ) in increments of 5 m (0-5 m, 0-10 m, 0-15 m, etc.). We also calculated  $\bar{P}_a$  for stratified estimates of effective strip width.

Estimates of nest tree density per ha were calculated from the top two competitive models in the detection probability model set. Since Program Distance does not allow for stratified  $p(0)$  detection multipliers, we used a technique whereby the total quantity of transect in each forest age class was multiplied by the corresponding  $p(0)$  estimate. This provided reliable stratified estimates of nest tree density on the landscape.

### **Tree Vole Density Estimates**

We used two methods to estimate density of adult tree voles per ha. First, we used data collected during nest probing to create a two-factor categorical covariate indicating when an adult tree vole was observed in a nest tree. We then post-stratified our distance sampling models to estimate the density of nest trees that contained an adult tree vole occupant at the time of the climbing survey (i.e., “occupied” nest trees). This provided estimates of the minimum density of adult tree voles per ha.

In the second method, we used our estimates of nest tree density to estimate the density of individual adult tree vole home ranges as a proxy measure for density of adult tree voles. Because tree vole nest trees are unevenly distributed in the forest and occur in clusters which often consist of multiple nest trees used by individual adults, we divided our estimates of nest tree density by estimates of mean nest tree cluster size per adult tree vole home range (nest trees/range) from Swingle (2005) to estimate density of adult tree vole home ranges per ha. Mean estimates of nest tree cluster size per home range from Swingle (2005) were stratified by sex, with males averaging  $3.0 \pm 0.4$  nest trees per home range and females averaging  $2.1 \pm 0.3$  nest trees per home range. We adjusted estimates of standard error to reflect unknown tree vole sex ratios in wild populations.

## **RESULTS**

### **Stand Characteristics**

We surveyed 36 forest stands during April – October 2014, including 10 young, 16 mature, and 10 old stands. Sample stands occurred in an elevation range of 182-651 m and spanned the entire latitudinal range of the study area ( $44^{\circ} 36' 50''$  N -  $41^{\circ} 59' 54''$  N),

with locations in Lincoln, Benton, Lane, Douglas, Coos, and Curry counties (Fig. 3.6). Slope gradients in sampled stands ranged from 1-156%. No active tree vole nests were detected from line-transect or climbing surveys in five of the 10 young stands sampled, so the five stands with no detections were excluded from further analyses. Mean estimates of stand attributes in the 31 occupied stands are listed in Table 3.10.

### **Nest Tree Characteristics**

We collected data from a total of 865 trees in the 31 occupied stands, including 191 potential nest trees detected from the transect line and 674 p(0) trees. Of the p(0) trees, 54 (8%) were visually surveyed from the ground in lieu of climbing, primarily because they were so small that they did not warrant climbing (mean DBH =  $18.5 \pm 0.9$  cm). A total of 113 active nest trees were identified from climbing surveys in potential nest trees and p(0) trees (Table 3.11). Of these, 51 (45%) were detected from ground-based line-transect surveys and subsequently used in our analysis of nest tree detection probability and density. We also identified 132 trees that contained inactive tree vole nests but no active nests, 54 (41%) of which were detected from line-transect surveys. In young, mature, and old forest stands, the percentages of active nest trees containing only a single active tree vole nest were 100%, 95%, and 61%, respectively (Table 3.12). The majority of trees sampled were Douglas-fir (80.5%) and western hemlock (16.5%), though we also sampled Sitka spruce, coast redwood, and grand fir (Table 3.13). Active nests were documented in all species sampled except coast redwood. Resin ducts were found on the ground below 12 trees, of which four contained active nests (3.5% of active nest trees), four contained only inactive nests (3% of inactive nest trees), and four contained nests that had been recently predated. Resin ducts found on the ground were old and brown in all but one case in which green ducts were found under a recently predated nest.

Mean values of DBH, tree height, and depth of the live crown in the randomly-selected sample of p(0) trees were greater for active nest trees than for trees containing no tree vole nests in mature and old forest (all  $P$ -values  $< 0.01$ ), but not in young forest (Table 3.14). Our hypothesis that nest trees had greater connectivity than non-nest trees

was not supported in young or old forest (all  $P$ -values  $> 0.10$ ), but received some support in mature forest, where nest trees had more connecting trees ( $P = 0.02$ ) and more connecting pathways between trees ( $P = 0.09$ ).

There were 67 potential nest trees in which we found active tree vole nests during full-tree climbing surveys, 16 (23.9%) of which would have been misclassified as “inactive” or “non-nest” trees based solely on examination of structures detected from the line-transect. Of the 16 potential false negative detections, six were in old forest, 10 were in mature forest, and none occurred in young forest.

### **Nest Characteristics**

We inspected 526 arboreal nest structures, including 157 active tree vole nests, 276 inactive tree vole nests, and 93 nests most recently occupied by other species and containing no tree vole sign (Table 3.11). Of the 93 nests belonging to other species, 27 (29%) were occupied or recently occupied. Northern flying squirrels (*Glaucomys sabrinus*) were observed at two nests and four recently-hatched western wood pewees (*Contopus sordidulus*) were observed in one nest. Individual clouded salamanders (*Aneides ferreus*) were found in two tree vole nest trees (Douglas-fir), although only one was found in a tree vole nest. A third clouded salamander was observed inside the broken top cavity of a coast redwood in which there was no tree vole sign.

The majority (96%) of tree vole nests were located in Douglas-fir trees (Table 3.13). Resin ducts from western hemlock were found in two vole nests, though both nests were located in Douglas-fir trees. Approximately two thirds (66%) of active nests in p(0) trees had some fresh to moderately fresh conifer cuttings incorporated into the nest; the average number of cuttings was  $6.1 \pm 0.7$  (range = 0-60). Cuttings were not always piled on top of the nest. In many cases, cuttings were pulled partially or entirely into an entrance and were not visible from the ground. Only 6% of active nests detected from transects had green cuttings that were observed from the transect line.

Mean volume of active nests detected from ground transects was greater than mean volume of active nests detected by climbing in p(0) trees in all three forest age classes (all  $P$ -values  $< 0.05$ ; Table 3.15). The mean horizontal distance of intact tree vole

nests from the tree bole in p(0) trees was  $0.2 \pm 0.1$  m (range = 0-3.2 m) in young stands,  $1.4 \pm 0.1$  m (range = 0-6.6 m) in mature stands, and  $0.9 \pm 0.1$  m (range = 0-4.5 m) in old stands. Intact nests in p(0) trees occurred more frequently  $\leq 1$  m horizontally from the tree bole than  $> 1$  m from the bole across forest age classes ( $P = 0.07$ ; Table 3.16). However, the distribution of nests in the two horizontal positions ( $\leq 1$  m and  $> 1$  m) did not differ among forest age classes, nor did observers tend to detect intact tree vole nests from the ground disproportionately in either horizontal position relative to nest distribution (Table 3.16).

Intact tree vole nests in p(0) trees were unevenly distributed among the four vertical quadrants of the live crown across forest age classes, occurring most frequently in the middle third of the crown (39-66%;  $P = 0.04$ ). Vertical distribution of nests did not differ among forest age classes ( $P = 0.12$ ; Table 3.16), although we suspect this would be different with a larger sample size (particularly in young forest). Observers on the transect line tended to detect a higher proportion of intact tree vole nests in the lower two vertical quadrants than the upper two quadrants relative to average nest distribution in p(0) trees ( $P = 0.08$ ; Table 3.16). Active nests were detected from the transect at an average height of  $23.6 \pm 6.7$  m (range = 7.3-53 m;  $n = 53$ ) and an average height above the first live limb of  $6.9 \pm 2.2$  m (range = -3.9-37 m). Mean volume of active nests in the lower third of the live crown was approximately 70% greater than mean volume of active nests in the middle and upper thirds ( $P = 0.04$ ), which could partially explain their disproportionate detection rates from the ground.

The distribution of nest support structures in p(0) trees was highly variable across forest age classes ( $P = 0.02$ ; Table 3.17). Observers on line-transect surveys tended to detect nest support structures disproportionately relative to their occurrence, with the highest proportion of detected nests in forked trunks and the lowest proportion in broken tops/cavities and dwarf mistletoe growths ( $P = 0.046$ ; Table 3.17). Tree vole nests in broken top cavities were common, yet were among the most difficult nests to detect from line-transect surveys and were documented by climbers as “unavailable” to detection from the ground in 11 of 12 (92%) occurrences. Of 85 trees in this study with broken tops documented during climbing, only 26 (31%) of those broken tops were detected from the

ground during line-transect surveys. Similarly, we documented 52 tree vole nests (active and inactive) in mature and old forest that occurred entirely underneath living moss mats on limbs where they were unavailable to detection from the ground. We estimated that between nests located in broken tops, cavities, and under moss mats,  $\geq 15\%$  of all active nests were completely unavailable to detection from the ground, regardless of nest size, distance from the transect line, or survey conditions.

Single adult tree voles were flushed from 10 nests during the study; four in young forest, four in mature forest, and two in old forest. All 10 occupied nests were in trees classified as potential nest trees from line-transect surveys. However, only 6 of the 10 occupied nests were actually detected from the transect. The other four were found while climbing to examine other nests that were detected from transects, so they were not considered detected from the ground. No voles were flushed during probing of 64 active nests in p(0) trees (Table 3.18). Of 53 active nests detected from the ground during line-transect surveys, we estimated that 11.3% were occupied by an adult tree vole at the time of examination (11.8% of active nest trees; Table 3.18). The mean volume of nests that were occupied at the time of examination was greater than mean volume of active nests in p(0) trees ( $P = 0.012$ ; Table 3.15). Seventy percent of occupied nests occurred in the lower third of the live crown, with the remaining 30% in the middle third of the live crown. Ninety percent of occupied nests were located  $\leq 1$  m of the tree bole. On average, occupied nests had  $12.7 \pm 4.3$  (range = 5-50) fresh to moderately fresh green conifer cuttings on the nest, compared to  $6.1 \pm 0.7$  (range = 0-60) cuttings for active nests in the randomly-selected sample of trees.

### **Climber Perception Bias from Double-Sampling**

We double-sampled 105 trees with mean DBH =  $94.4 \pm 3.8$  cm (range = 46-193 cm), including 27 trees in which climbers detected  $\geq 1$  active tree vole nests. Climbers assigned the same activity status to 45 of 45 active nests detected from the ground, so we estimated that the single climber (or single survey) detection probability for individual nests was 1 (i.e., 100%). Climbers assigned the same activity status to 104 of 105 trees and to 26 of 27 trees in which  $\geq 1$  active nest was located. In the one case where only one

of the two climbers correctly classified an active nest tree, the tree in question was large (DBH = 102 cm) with a broken top cavity where the single active nest was located. One of the climbers decided not to ascend all the way to the broken top for safety reasons and thus, did not observe the nest. Based on the nearly identical survey results between climbers we concluded that climber perception bias was negligible and that there was no need to include a multiplier for climber perception bias in the analysis of nest tree detection probability in Program Distance.

### **Detection Probability of Nest Trees at Distance Zero**

We sampled 698  $p(0)$  trees, 85 of which contained  $\geq 1$  active tree vole nest detected during climbing surveys. We found strong evidence for differences in nest detectability between line-transect surveys and climbing surveys of  $p(0)$  trees and for forest age-related differences in detection rates from line-transect surveys (Table 3.19). Nest tree detection probabilities on the zero-distance line were inversely related with forest age as predicted (Table 3.20). The unstratified estimate of nest tree detection probability on the zero-distance line across all forest age classes was  $0.082 \pm 0.030$  (Table 3.20).

### **Detection Probability of Nest Trees**

The key function that best fit our data was the half-normal function, with the cosine and hermite polynomial series expansion term models receiving identical support (Table 3.21). Neither of the hazard-rate key function models were competitive ( $\Delta AIC_c > 2$ ). Since the pairing of the half-normal key function and cosine series expansion term is considered to be standard, while pairing with the hermite polynomial is more theoretical and most often used with untruncated data sets (Buckland et al. 2001), we chose to proceed using the half-normal cosine model.

The MCDS model in program Distance that best described detection probability ( $P_d$ ) of active nest trees was the intercept-only model, which included no covariates related to the structural composition of the dominant canopy or abiotic survey conditions (Table 3.22). There were four competitive models in the model set (Table 3.22). The

competitive models suggested that nest tree  $P_a$  in relation to strip width varied among forest age classes (Fig. 3.7), and decreased relative to increased tree density per ha, stand elevation, and slope gradient. None of the multi-factor additive models were competitive. All competitive models had  $X^2$  values between 0.716-0.949, indicating that there was no substantial deviation between expected and observed values, and in fact, the top 15 models ( $\Delta AIC_c \leq 2.16$ ) fell within this  $X^2$  range, possibly indicating that many of these covariates would exhibit more strength in a data set with larger sample size. The model that included wind speed [p(Wind)] had too few observations per category and failed to converge.

We calculated nest tree  $P_a$  from the intercept-only model [p(.)] and from the second best model [p(AGE)] to evaluate potential differences in  $P_a$  among forest age classes. Because detection functions from the initial models represented perfect detection at distance zero from the transect line, we adjusted each function by its corresponding estimate of imperfect detection probability at distance zero (Table 3.20, Fig. 3.7). The series expansion adjustment term for the intercept-only model was  $20.74 \pm 2.84$  (CV = 12.04%), from which we estimated mean detection probability ( $\bar{P}_a$ ; post-adjustment for p(0)) of  $0.054 \pm 0.02$  within the half-strip width of 49 m (Table 3.23). Mean detection probabilities ( $\bar{P}_a$ ) within the half-strip width of 49 m for young, mature, and old forest [adjusted by stratified p(0) estimates] were  $0.165 \pm 0.081$  (CV = 21.58%),  $0.029 \pm 0.016$  (CV = 16.55%), and  $0.020 \pm 0.020$  (CV = 31.72%), respectively (Table 3.23). Nest tree detection probabilities from line-transect distance sampling were inversely correlated with forest age as predicted (Fig. 3.7). Forest age-stratified and unstratified estimates of  $\bar{P}_a$  within given half-strip widths were calculated in 5-m increments (0-5 m, 0-10 m, 0-15 m, etc.) from 0-49 m, along with estimates of effective strip width (Table 3.23).

### **Nest Tree Density Estimates**

Estimates of nest tree density in occupied stands were lowest in young forest and higher in mature and old forest (Table 3.24). The average estimate of nest tree density for all forest age classes combined (no-effects model) was  $8.46 \pm 1.59$  per ha (Table 3.24). The average proportion of trees in the dominant canopy that contained  $\geq 1$  active tree

vole nest (nest trees) was 0.10 across all forest age classes and 0.03, 0.13, and 0.16 in young, mature, and old forest, respectively. We estimated that, at a half-strip width of 49 m, the minimum amount of transect necessary to detect a single active tree vole nest (without climbing p(0) trees) was 112 m, 295 m, and 444 m in stands of young, mature, and old forest, respectively.

### **Tree Vole Density Estimates**

We estimated that the overall minimum density of “occupied” tree vole nest trees in the occupied stands that we surveyed was  $1.91 \pm 0.97$  per ha. The number of voles detected during climbing surveys was too small to calculate separate estimates for different age classes.

Based on our estimates of nest tree density and estimates of mean home range size from Swingle 2005, we estimated that the density of tree vole home ranges per ha was  $2.6 \pm 1.5$  in young forest,  $5.5 \pm 2.9$  in mature forest, and  $5.6 \pm 3.9$  in old forest, with an overall mean of  $4.2 \pm 2.0$  across all forest age classes combined. These estimates apply only to stands that were occupied by tree voles, as we restricted our analyses to occupied stands.

## **DISCUSSION**

### **Detection Probability of Nest Trees**

The use of distance sampling techniques in our study allowed us to estimate nest tree density while incorporating estimates of nest tree detection probability from ground-based surveys. Tree climbing was fundamental to this effort because it allowed us to confirm activity status of nests and adjust for imperfect detection rates. Detection rates of nest trees were generally low, supporting concerns that survey protocols that do not account for imperfect detection result in underestimates of tree vole density and may, at least occasionally, result in false negatives of vole occupancy. While the best model in our analysis did not include any of the covariates hypothesized to affect detection

probability, the four competitive models suggested some support for other factors that may influence detection rates, including forest age.

Estimates of dominant-canopy tree density varied with forest age, and stands of old forest in our sample exhibited lower mean elevation compared to stands of young and mature forest (Table 3.10). The observed effects of tree density and elevation on nest tree detection were probably not independent of the forest age class covariate, and it is possible that forest age could be used as a general proxy covariate for many of the stand characteristics that affect nest tree detection probability. There were no observable age effects in the distribution of slope gradients at survey locations, so the suggested inverse relationship between slope gradient and nest tree detection probability should be considered independent of forest age. We found no support for the hypothesis that transect orientation in relation to the slope aspect (i.e., perpendicular/parallel) had any effect on detection probability. However, low encounter rates of nest trees led to low sample sizes throughout our study. All of the top 15 covariate models in the model set received some support and should not be entirely discounted (Table 3.22). Some of these models might be more strongly supported with larger sample sizes.

There were other potential factors associated with tree vole nest characteristics that could influence nest tree detection probability. Certain characteristics of individual nests resulted in differences in detectability from the ground. Active nests detected from the ground during line-transect surveys tended to be at least twice the average volume of active nests documented from climbing  $p(0)$  trees. Observers also tended to detect nests relative to specific nest support structures, with the highest number of active nests detected in forked trunks. A significant proportion of tree vole nests occurred in broken tops and cavities, but these nests were under-represented in our study because they were only rarely detected from the ground and problematic to examine even by climbing the tree. We probably underestimated the average volume of nests, particularly in the upper third of the live crown, because we could not measure nests that were inside cavities or the dead tops of old, large trees.

We found little evidence of an observer effect on detection probability of tree vole nests or nest trees. However, both observers in this study were well-trained, with many

hours of experience in nest identification and tree climbing. It is likely that surveys by less experienced observers could result in lower nest tree detection rates or higher variation among observers. In addition, surveys performed at different times of the year could produce results that differ from ours. For example, it is likely that detection probabilities of tree vole nests could be higher in winter after deciduous trees in the forest understory lose their leaves.

### **Detection Probability of Nest Trees at Distance Zero**

Age-stratified estimates of nest tree detection probability at distance zero from the transect line ( $p(0)$ ) exhibited relatively large standard errors and overlapping 95% confidence intervals (Table 3.20), suggesting that  $p(0)$  was highly variable among forest age classes. The difference in  $p(0)$  between young and mature forest was noticeably larger than between mature and old forest, possibly indicating that the most abrupt rate of decrease in  $p(0)$  occurs at about 80 years of age.

In general, we were surprised by how low our estimates of  $p(0)$  were in this study (Table 3.20). The initial models calculated in Program Distance provided stratified estimates of nest tree  $\bar{P}_a$  in relation to survey strip width. However, after adjustment for  $p(0)$ , the significance of strip width as a variable was decreased nearly to the point of triviality. For example, pre-adjustment estimates of  $\bar{P}_a$  from line-transect surveys in mature forest with half-strip widths of 10 m and 30 m would be 93% and 60% mean detection, respectively, a difference of 33%. After adjustment for  $p(0)$ , those estimates become 7% and 4%, a difference of only 3% (Table 3.23; Fig. 3.7). If future studies aim to improve upon our estimates of nest tree  $\bar{P}_a$  from distance sampling, the most effective approach would be to dedicate further effort toward improving our understanding of the relationship between forest age and specific  $p(0)$ , since detection at distance zero appears to have a much larger influence on overall detection probability than strip width.

### **Density Estimates**

Our estimate of minimum density of occupied nest trees ( $1.91 \pm 0.97$  per ha) across all forest age classes was twice as high as the minimum adult tree vole density

estimate (0.97 per ha) from Maser (1966), who inspected every arboreal nest detected from the ground within a 12.4 ha stand of young forest in the Oregon Coast Range. Our estimates of density of active nest trees were more than eight times higher than estimates produced by Biswell and Forsman ( $0.23 \pm 0.07$  per ha; *unpubl. data*) who also conducted surveys in the Oregon Coast Range. In both cases, at least some of the differences can probably be attributed to differences in age stratification or structure of the forests that were sampled. For example, Maser (1966) sampled young forest only, and Biswell and Forsman sampled three forest age classes with means of 40 years, 51 years, and 188 years. Sixteen (52%) of our 31 sample stands occurred in mature forest (80-200 years), and 10 (32%) occurred in old forest (> 200 years), meaning that our study was, in large part, performed in older forest than either of the earlier studies. In addition, Biswell and Forsman sampled a large number of study sites (78%) where no tree voles were found and where the stands had been thinned in the recent past. Thus, Biswell and Forsman attempted to estimate mean nest tree density at the landscape level across all potentially suitable tree vole habitat regardless of the occupancy status of specific stands. In contrast, we sampled randomly-selected stands from a subset of suitable habitat across the landscape where tree voles were believed to be present based on previous information, and then we excluded stands where we could not confirm occupancy by tree voles. Thus, our estimates of nest tree density are applicable to occupied stands but are almost certainly not applicable at the landscape level to all potentially suitable tree vole habitat. More importantly, neither previous survey effort (Maser 1966; Biswell and Forsman *unpubl. data*) made adjustments for imperfect detection of tree vole nests from the ground. The assumption of perfect detection at distance zero ( $g(0) = 1$ ) in both studies likely resulted in positively biased detection rates, which would result in underestimates of density.

Our estimate of the density of individual adult tree vole home ranges was higher than our estimate of the minimum density of occupied nest trees, and was probably closer to “true” density of adult tree voles in occupied stands. Even so, our estimates exhibited high variability and there were sources of bias to consider. First, the number of nest trees per tree vole home range differs between sexes (Swingle 2005), and we lacked estimates

of tree vole sex ratios in wild populations (but see Forsman et al. 2016). Second, the estimates of nest trees per home range that we used were calculated using different (though not radically) forest age-stratification criteria (Swingle 2005). It is likely that the number of nest trees per home range varies by forest age, but we lacked age-stratified estimates and calculated our estimates of adult home range density from an unstratified estimate.

### **Management Recommendations**

The objectives of this study were to estimate detection probabilities and density of red tree vole nest trees from line-transect surveys with the intent of improving the quality of data collected during Modified Line Transect surveys performed by land managers. Based on our study, the minimum transect length necessary to establish stand occupancy by tree voles was 112 m in young stands, 295 m in mature stands, and 444 m in old stands. The current federal survey standard of 90 m of transect per acre (222 m/ha; Huff et al. 2012) is equivalent to approximately 22.5 m half-strip width, resulting in a mean nest tree detection probability ( $\bar{P}_a$ ) of  $0.054 \pm 0.03$  in stands of mature forest (where tree vole surveys are most commonly performed) or  $0.074 \pm 0.027$  using the unstratified model. However, performing surveys using our estimate of effective strip width in mature forest (19.7 m, equivalent to 103 m of transect per acre) would only increase  $\bar{P}_a$  to  $0.057 \pm 0.032$ , a 0.3% difference. It is important to understand that detection rates of tree vole nest trees from ground-based line-transect surveys will be low, regardless of the survey strip width (Table 3.23).

If increased climbing effort is not possible, land managers could continue to perform tree vole surveys as outlined in the federal protocol (Huff et al. 2012), and in stands where tree vole occupancy is verified, the estimated density of nest trees relative to forest age from our study could be applied (Table 3.24). However, given that nest trees are often distributed in clusters (Howell 1926; Maser 1998), the appropriate course of action might be to manage for our estimates of density of tree vole home ranges, using estimates of mean home range size from Swingle and Forsman (2009). We also suggest conducting supplementary climbing searches in large trees within a 100 m radius of

confirmed nest trees, as outlined in the federal protocol (Huff et al. 2012). Our results indicated that tree voles used nest trees of greater-than-average DBH, height, and depth of live crown, so large trees should generally be targeted in cases where trees are selected for climbing surveys without a nest detection from the ground.

Alternatively, it might be more accurate to estimate nest tree density using stand-specific survey data while correcting for negative detection bias using our estimates of mean detection probability ( $\bar{P}_a$ ). These correction factors could be applied relative to forest age and survey strip (half) width (Table 3.23). In accordance with our survey methods, the pre-correction density of nest trees would include only those trees in which  $\geq 1$  active tree vole nest was detected during the ground-based portion of the line-transect survey.

In mature and old forests, we found that climbers who conducted full-tree nest searches correctly identified  $\geq 31\%$  more nest trees than climbers who only climbed as high as the particular nest structures detected from the ground. Thus, encouraging mandatory full-tree nest searches is an additional, relatively efficient way to increase nest tree detection, thereby decreasing the negative bias inherent in current federal survey protocols. Resin ducts removed by tree voles were found on the ground below only 3.5% of active tree vole nest trees in our study, so ground searches for fallen resin ducts are an unreliable method of surveying for nest trees. Similarly, only 6% of active nests detected from the ground during line-transect surveys had conifer cuttings that were visible from the transect line. This estimate would probably increase if observers were allowed to leave the transect and observe nests from multiple angles, but attempting to observe cuttings on a nest from the ground is an unreliable indicator of either the species occupying the nest or the activity status of the nest.

## TABLES AND FIGURES

Figure 3.1. Sampling area in the ArcMap model used for the study of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

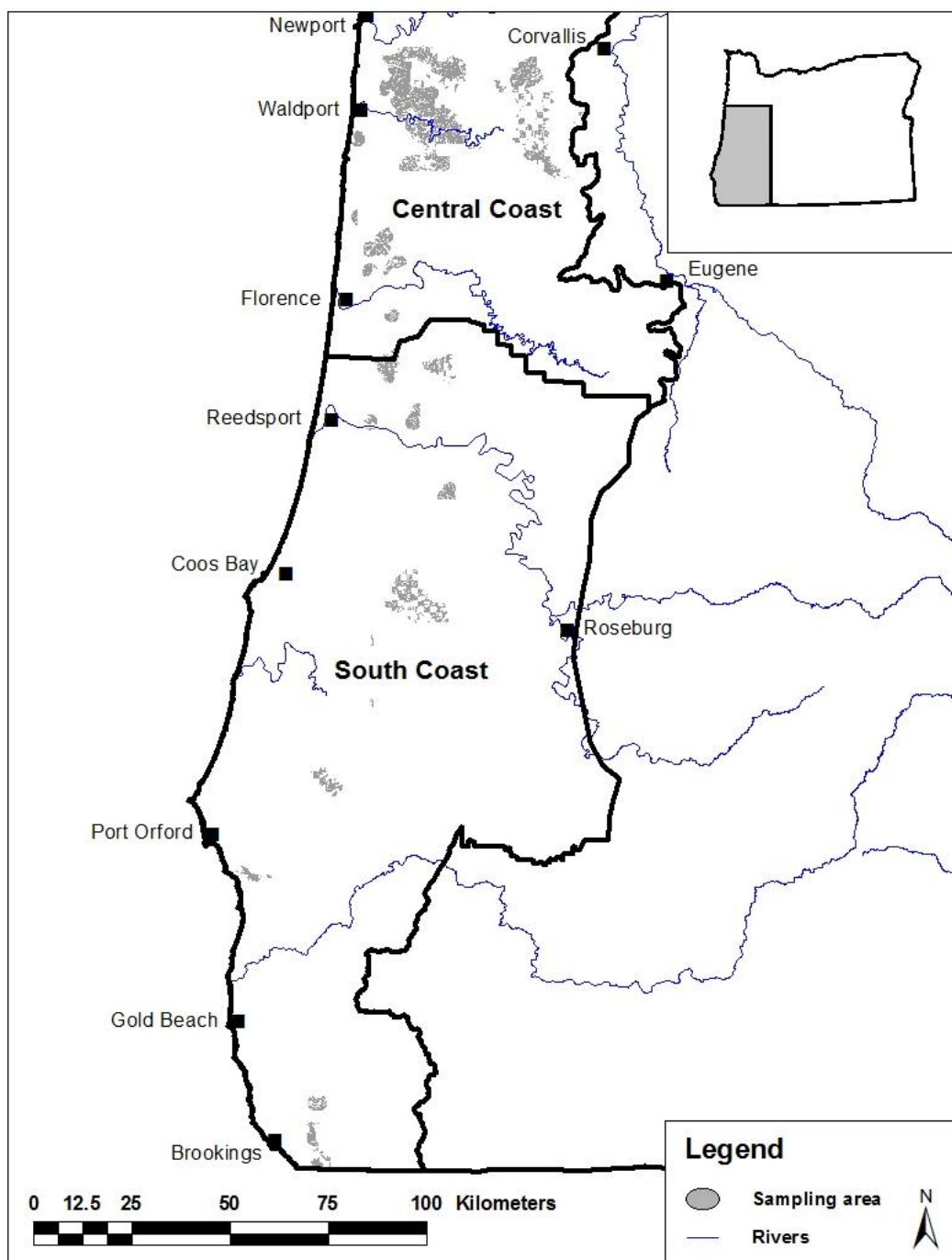


Figure 3.2. Example of LiDAR tree height data (left) used to develop stand-level age classes (right) for the study of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

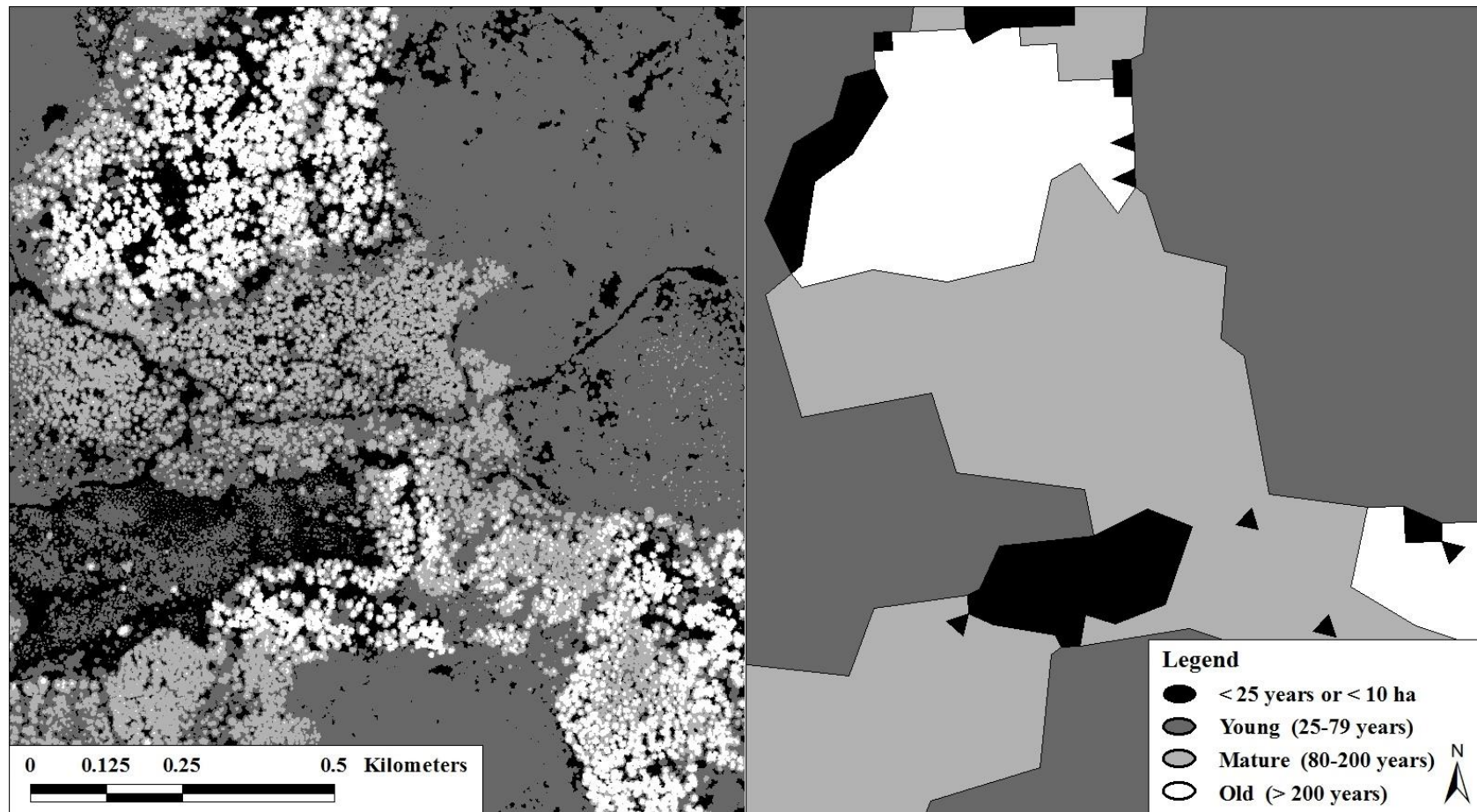


Table 3.1. Categorical codes used to classify species occupant, activity status, and condition of nests during the study of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Code                  | Description   |
|-----------------------|---|
| <u>Nest species</u>   |   |
| ARLO                  | Red tree vole.  |
| BIRD                  | Bird (possible in some cases to determine exact species).                               |
| SQRL                  | Squirrel (possible in some cases to determine exact species).                           |
| NESP                  | Dusky-footed ( <i>Neotoma fuscipes</i> ) or bushy-tailed ( <i>N. cinerea</i> ) woodrat. |
| <u>Nest activity</u>  |   |
| Animal observed       | Tree vole observed in the nest.   |
| Very recent           | Fresh green conifer cuttings and/or fresh green resin ducts.                            |
| Moderately recent     | Desiccated green conifer cuttings and/or desiccated green resin ducts.                  |
| Moderately old        | Brown or tan resin ducts or old intact feces.   |
| Very old              | Decayed resin ducts, feces, and/or de-barked twigs.                                     |
| <u>Nest condition</u> |   |
| I                     | Intact.   |
| OF                    | Old and flattened.  |
| OC                    | Old and collapsed.  |
| RP                    | Recently predated (i.e., recently active but currently uninhabited).                    |
| OP                    | Old and predated.   |

Table 3.2. Dominant-canopy variables from LiDAR (2008-2012) used as covariates in models of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Variable  | Description  |
|-----------|--|
| Mean      | Mean tree height.  |
| QMH       | Quadratic mean tree height. $\sqrt{\frac{\sum (Height)_i^2}{n}}$ |
| Median    | Median tree height.  |
| Mode      | Modal tree height.   |
| Perc.90   | Tallest tree height at the 90 <sup>th</sup> percentile.          |
| Perc.97.5 | Tallest tree height at the 97.5 <sup>th</sup> percentile.        |
| Perc.99   | Tallest tree height at the 99 <sup>th</sup> percentile.          |
| Density   | Trees per ha.  |

Table 3.3. Variables recorded at the starting point of each 100 m transect segment during the study of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Variable          | Description   |
|-------------------|---|
| UTM coordinates   | Universal Transverse Mercator coordinates (NAD83).  |
| Observer          | Observer name.                                      |
| Date              | Calendar date (mm/dd/yyyy).                         |
| Time              | Time of day (24 hour).                              |
| Elevation         | Elevation (m).                                      |
| Transect bearing  | Compass bearing of transect layout (°).             |
| Transect gradient | Gradient of transect bearing (%).                   |
| Slope aspect      | Compass bearing of slope downhill (°).              |
| Slope gradient    | Gradient of slope (%).                              |
| Median DBH        | Median DBH (cm) of trees within 10 m radius.        |
| Wind              | Categorical.  |
| Low               | < 5 mph.  |
| Medium            | 5-25 mph.   |
| High              | > 25 mph.   |
| Weather           | Categorical.  |
| Clear             | Clear sky with no clouds visible.                   |
| Scattered         | Scattered clouds, but predominantly clear.          |
| Overcast          | Mostly overcast (> 50% cloud cover).                |
| Rain              | Rain falling perceptibly through the forest canopy. |
| Fog               | Fog decreases maximum detection distance by > 50%.  |

Table 3.4. Data collected from the point of initial detection along the transect line for each potential nest and potential nest tree detected during the study of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Variable                   | Description  |
|----------------------------|--|
| <u>Potential nest</u>      |  |
| Gradient                   | Vertical gradient of nest relative to observer (%).      |
| Cuttings present           | Conifer cuttings detected from ground? (yes/no)          |
| Resin ducts present        | Resin ducts detected from ground? (yes/no)               |
| <u>Potential nest tree</u> |  |
| UTM coordinates            | Universal Transverse Mercator coordinates (NAD83).       |
| Location on transect       | Observation point location along the transect line (m).  |
| Distance                   | Horizontal distance to tree bole (m).                    |
| Bearing                    | Compass bearing of tree (°).                             |
| Base gradient              | Vertical gradient of tree base relative to observer (%). |
| Broken top                 | Broken top detected from ground? (yes/no)                |

Table 3.5. Data collected at all trees climbed during the study of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Variable             | Description  |
|----------------------|--|
| Climber              | Climber name.  |
| Elevation            | Elevation at the base of the tree (m).                                   |
| Slope aspect         | Compass bearing of slope downhill (°).                                   |
| Slope gradient       | Gradient of slope (%).   |
| Tree species         | Tree species.  |
| Tree DBH             | Tree DBH (cm; continuous and categorical).                               |
| Small                | ≤ 45 cm.   |
| Medium               | 46-90 cm.  |
| Large                | > 90 cm.   |
| Tree height          | Tree height (m).   |
| HFL                  | Height to first live limb (m).   |
| HCLC                 | Height to bottom of continuous live crown (m).                           |
| Connecting trees     | Number of trees connected by branch pathways.                            |
| Connecting pathways  | Number of connecting branch pathways<br>(2 <sup>n</sup> [range = 0-512]) |
| Crown density        | Categorical (1-5) where 1 = low and 5 = high.                            |
| Canopy closure       | Canopy closure surrounding tree (%).                                     |
| Ground sign          | Presence/absence of tree vole sign at base of tree.                      |
| Tree sampling method | Categorical.   |
| Climbed: Spurs       | Tree ascended using spur technique.                                      |
| Climbed: Other       | Tree ascended using technique other than spurs.                          |
| Visual: Adjacent     | Tree surveyed visually from an adjacent tree.                            |
| Visual: Ground       | Tree surveyed visually from the ground but not climbed.                  |
| Broken top           | Presence/absence of broken top (categorical).                            |
| BT                   | Broken top without obvious cavity.                                       |
| BT CAV               | Broken top with cavity.  |
| BT 2L                | Broken top with secondary leader(s).                                     |

Table 3.6. Data collected for all nests documented during the study of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Variable                  | Description   |
|---------------------------|---|
| Nest height               | Nest height in tree (m).  |
| Nest aspect               | Aspect of nest from tree bole (degrees).                        |
| DNH                       | Diameter of tree at nest height (cm).                           |
| Distance from bole        | Nest distance from the bole (m).                                |
| FLLA                      | Vertical distance from nest to first live limb above (m).       |
| FLLB                      | Vertical distance from nest to first live limb below (m).       |
| Cuttings                  | Presence/absence of conifer cuttings on nest, plus description. |
| Resin ducts               | Presence/absence of resin ducts in nest, plus description.      |
| Fecal pellets             | Presence/absence of fecal pellets in nest, plus description.    |
| De-barked twigs           | Presence/absence of de-barked twigs in nest, plus description.  |
| Ground detectability      | Visible/not visible from the ground.                            |
| Nest dimensions           | Length, width, and depth (cm).                                  |
| Support structure         | Type of nest support structure (categorical).                   |
| Branch whorl              |   |
| Broken top                |   |
| Cavity                    |   |
| Dwarf mistletoe deformity |   |
| Forked branch cluster     |   |
| Forked trunk              |   |
| Palmate branch cluster    |   |
| Single limb               |   |

Figure 3.3. Distribution of tree heights as a proportion of the total number of trees in the stand from LiDAR (2008-2012) in representative stands of young, mature, and old Douglas-fir forest in the Oregon Coast Range, 2014.

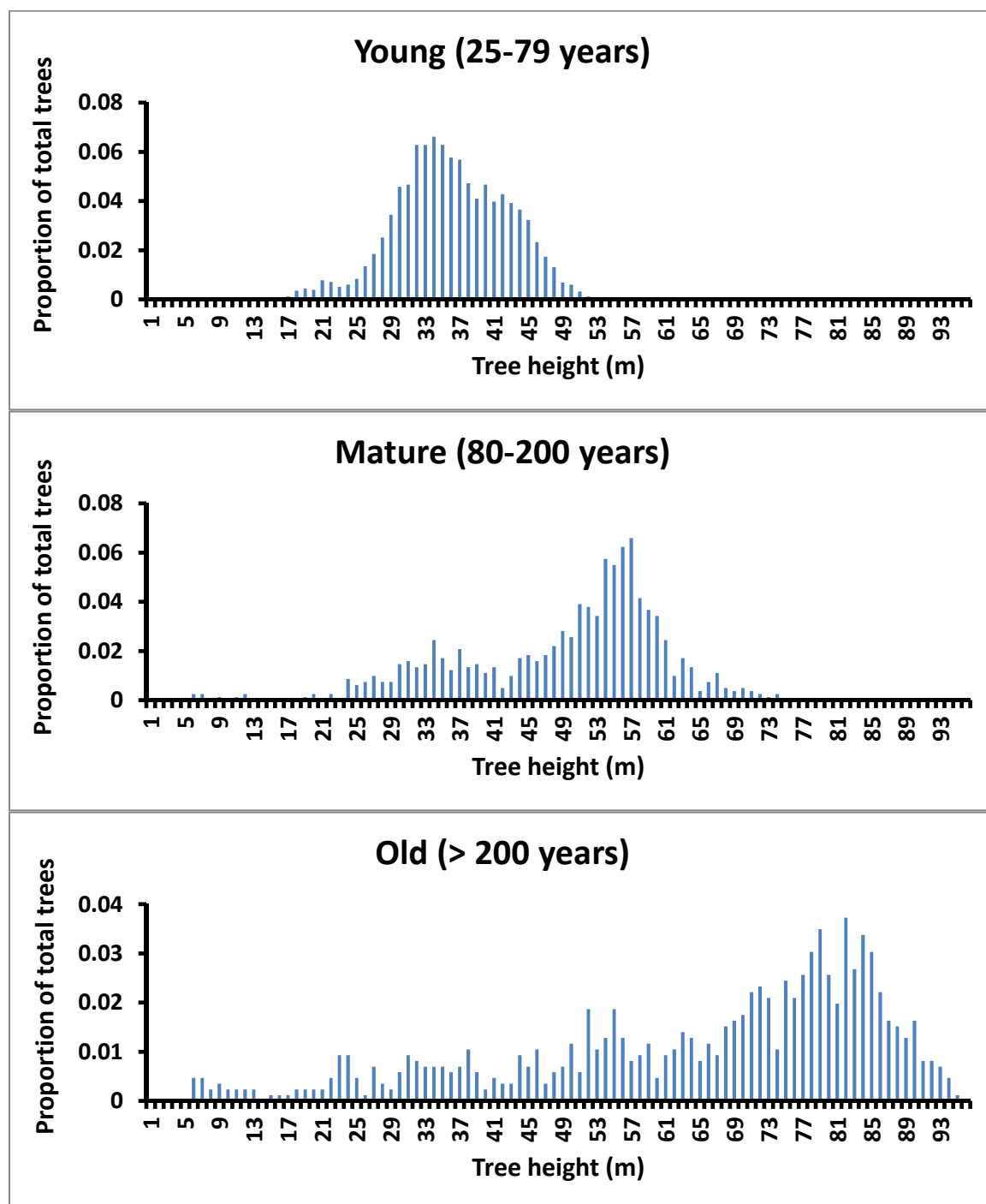


Table 3.7. *A priori* models used to test predicted effects of tree survey type (ground vs. climbing) and forest age class on detection probability of active red tree vole nest trees at distance zero from the transect line ( $p(0)$ ) in the Oregon Coast Range, April-October 2014.

| Model               | Description   |
|---------------------|---|
| $p(.)=c(.)$         | Detection probability is constant across survey methods and forest age.                                       |
| $p(.)c(.)$          | Detection probability differs between survey methods and is constant across forest age within survey methods. |
| $p(.)c(\text{age})$ | Detection probability differs between survey methods and differs by forest age in line-transect surveys.      |

Table 3.8. *A priori* models used to test the effects of key functions and expansion terms for modeling the detection function of active red tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Model      | Description  |
|------------|--|
| p(HN.cos)  | Half-normal key function with cosine expansion term.             |
| p(HN.her)  | Half-normal key function with hermite polynomial expansion term. |
| p(HzR.cos) | Hazard-rate key function with cosine expansion term.             |
| p(HzR.sim) | Hazard-rate key function with simple polynomial expansion term.  |

Figure 3.4. Perpendicular detection distances of active red tree vole nest trees, overlaid with a half-normal distribution curve, from line-transect distance sampling in the Oregon Coast Range, April-October 2014.

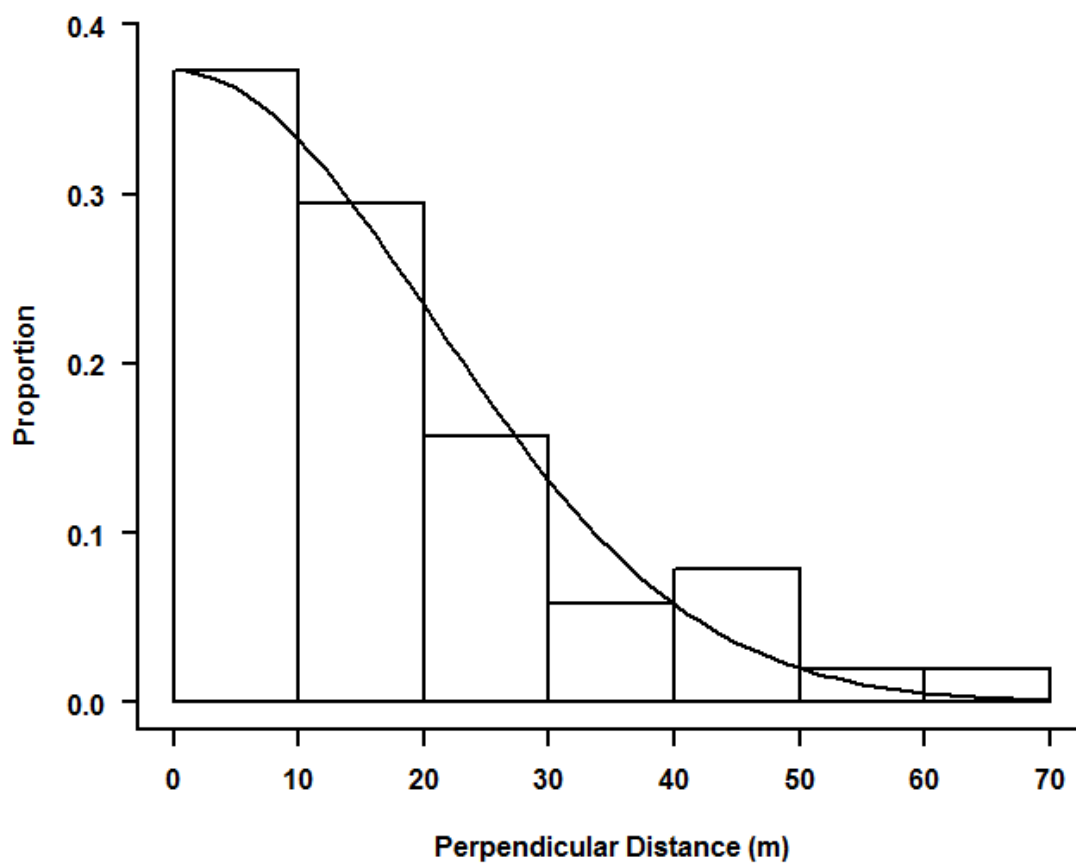


Figure 3.5. Perpendicular detection distances of active red tree vole nest trees, binned every 3 m and truncated at 49 m, from line-transect distance sampling in the Oregon Coast Range, April-October 2014. This is one example of several histograms used to determine the global bin limits (9 m, 22 m, 33 m, and 49 m) used in the analysis of nest tree detection probability.

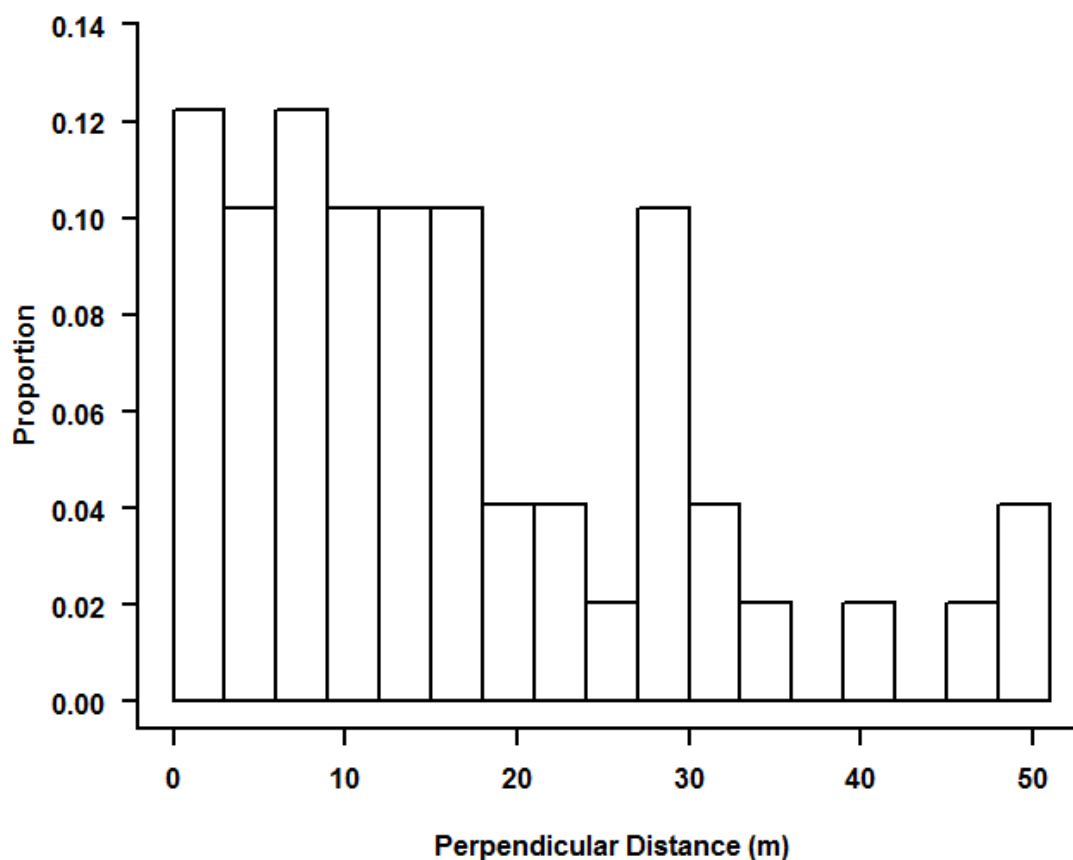


Table 3.9. *A priori* models used to evaluate predicted effects of canopy structure and abiotic survey conditions on detection probability of active red tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Model                   | Predicted effect | Description   |
|-------------------------|------------------|---|
| <u>Canopy structure</u> |                  |   |
| p(AGE)                  | $\beta < 0$      | Categorical (linear).                                     |
| Young                   |                  | 25-79 years old.  |
| Mature                  |                  | 80-200 years old.   |
| Old                     |                  | > 200 years old.  |
| p(MH)                   | $\beta < 0$      | Mean tree height.   |
| p(QMH)                  | $\beta < 0$      | Quadratic mean tree height.                               |
| p(MedH)                 | $\beta < 0$      | Median tree height.                                       |
| p(ModH)                 | $\beta < 0$      | Mode tree height.   |
| p(P90H)                 | $\beta < 0$      | Tallest tree height at the 90 <sup>th</sup> percentile.   |
| p(P97.5H)               | $\beta < 0$      | Tallest tree height at the 97.5 <sup>th</sup> percentile. |
| p(P99H)                 | $\beta < 0$      | Tallest tree height at the 99 <sup>th</sup> percentile.   |
| p(DEN)                  | $\beta > 0$      | Density: trees per ha.                                    |

Table 3.9. (Continued)

| Model                     | Predicted effect | Description   |
|---------------------------|------------------|---|
| <u>Abiotic conditions</u> |                  |   |
| p(Obs)                    | $\beta \neq 0$   | Denotes observer (categorical).                                 |
| p(Elev)                   | $\beta < 0$      | Elevation: binned every 30 m.                                   |
| p(SlpGrad)                | $\beta > 0$      | Slope gradient: binned every 20%.                               |
| p(TrnGrad)                | $\beta > 0$      | Transect gradient: binned every 20%.                            |
| p(TrnSlpAsp) <sup>a</sup> | $\beta \neq 0$   | Transect orientation in relation to slope aspect (categorical). |
| Perpendicular             |                  | Bearing: (46°-134°, 226°-314°) where slope aspect = 0°.         |
| Parallel                  |                  | Bearing: (135°-225°, 315°-45°) where slope aspect = 0°.         |
| Downhill                  |                  | Bearing: (315°-45°) where slope aspect = 0°.                    |
| Uphill                    |                  | Bearing: (135°-225°) where slope aspect = 0°.                   |
| p(Season)                 | $\beta \neq 0$   | Categorical.  |
| Spring                    |                  | 1 Apr 2014 – 20 Jun 2014.                                       |
| Summer                    |                  | 21 Jun 2014 – 22 Sep 2014.                                      |
| Fall                      |                  | 23 Sep 2014 – 15 Oct 2014.                                      |
| p(Wind)                   | $\beta < 0$      | Categorical (linear).   |
| Low                       |                  | < 5 mph.  |
| Medium                    |                  | 5-25 mph.   |
| High                      |                  | > 25 mph.   |
| p(Weather)                | $\beta \neq 0$   | Categorical.  |
| Clear                     |                  | Clear sky with no clouds visible.                               |
| Scattered                 |                  | Scattered clouds visible, but still predominantly clear.        |
| Overcast                  |                  | Mostly overcast (> 50% cloud cover).                            |
| Rain                      |                  | Rain falling perceptibly through the forest                     |
| Fog                       |                  | Fog decreases maximum detection distance by > 50%.              |

<sup>a</sup> Transect orientation in relation to slope aspect (p(TrnSlpAsp)) was represented in two models as either a two-factor categorical variable (p(TrnSlpAsp.2): perpendicular/parallel) or a three-factor categorical variable (p(TrnSlpAsp.3): perpendicular/parallel-uphill/parallel-downhill).

Figure 3.6. Locations of 31 occupied stands surveyed in the analysis of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

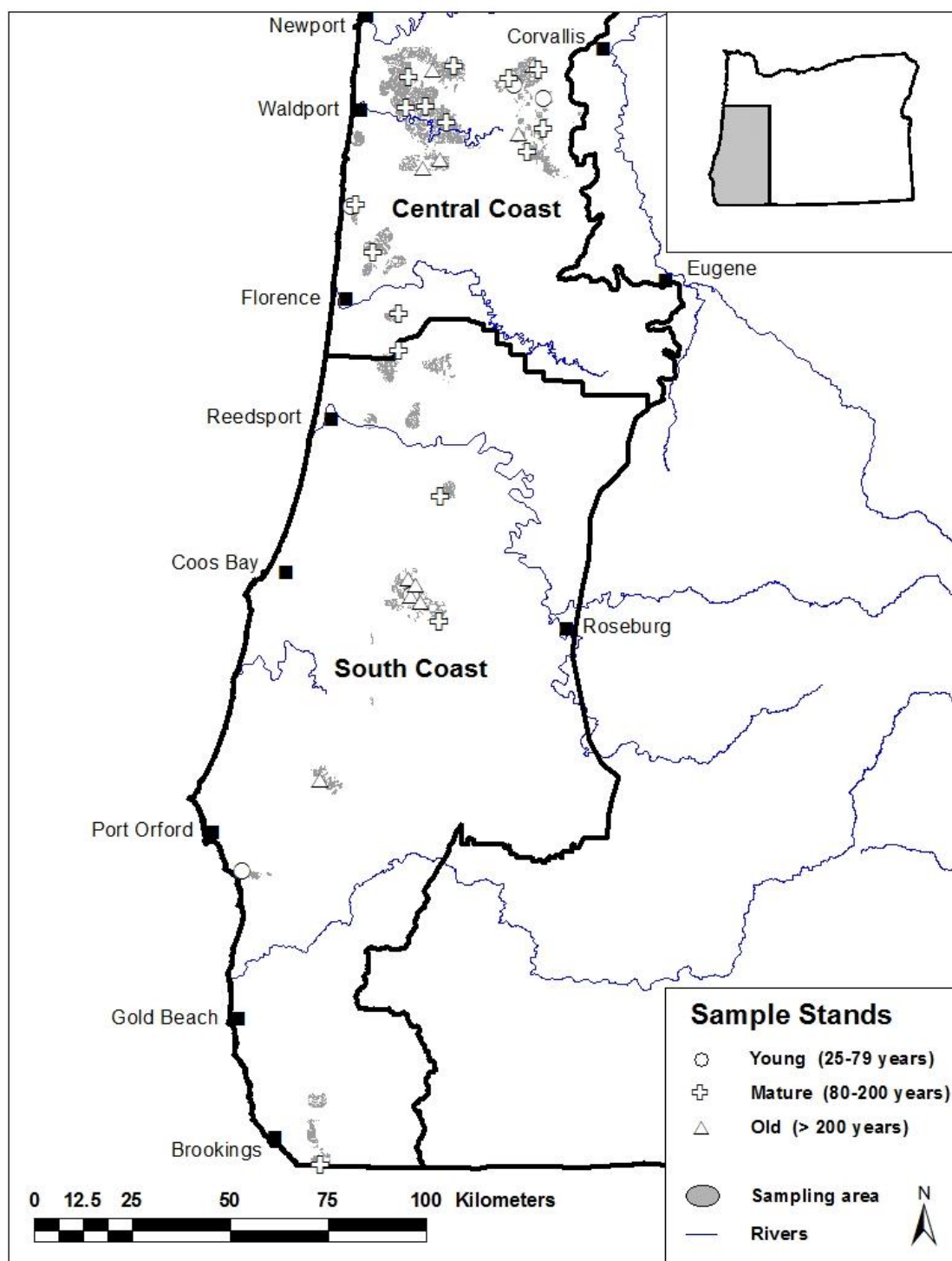


Table 3.10. Mean estimates ( $\bar{x} \pm SE$ ) of tree height, density of trees in the dominant canopy, elevation, and slope gradient in forest stands with active tree vole nests during the study of detection probability and density of red tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Characteristic                  | Forest age class <sup>a</sup>             |   |   |
|---------------------------------|---|---|---|
|                                 | Young                                     | Mature                                    | Old                                       |
| Tree height (m) <sup>b</sup>    | 30.8 $\pm$ 0.1<br>(5.1 – 65.7)<br>14,246  | 51.5 $\pm$ 0.1<br>(5.0 – 81.9)<br>21,564  | 60.0 $\pm$ 0.2<br>(5.0 – 96.6)<br>8,682   |
| Density (trees/ha) <sup>c</sup> | 191.1 $\pm$ 23.6<br>(115.7 – 243.8)<br>5  | 90.9 $\pm$ 2.2<br>(72.9 – 104.0)<br>16    | 70.1 $\pm$ 1.7<br>(64.1 – 79.8)<br>10     |
| Elevation (m) <sup>d</sup>      | 442.6 $\pm$ 21.7<br>(287.7 – 604.4)<br>20 | 417.3 $\pm$ 15.2<br>(192.0 – 650.7)<br>64 | 364.2 $\pm$ 17.1<br>(182.0 – 516.3)<br>40 |
| Slope gradient (%) <sup>e</sup> | 39.7 $\pm$ 3.6<br>(8.9 – 66.7)<br>20      | 36.4 $\pm$ 2.6<br>(2.2 – 84.4)<br>64      | 38.3 $\pm$ 2.9<br>(8.9 – 84.4)<br>40      |

<sup>a</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years). Numbers below means indicate range (in parentheses) and sample size.

<sup>b</sup> Mean tree height was positively correlated with forest age class (all  $P$ -values < 0.01)

<sup>c</sup> Density was negatively correlated with forest age class (all  $P$ -values < 0.01)

<sup>d</sup> Stands of old forest occurred at lower elevation than stands of young or mature forest (all  $P$ -values < 0.05)

<sup>e</sup> Mean slope gradient did not vary among forest age classes (all  $P$ -values > 0.10).

Table 3.11. Total transect length and number of red tree vole nests and nest located in occupied stands during the study of detection probability and density of tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Forest age class <sup>a</sup> | Transect (m) | Nests  |          | Nest trees |          |
|-------------------------------|--------------|--------|----------|------------|----------|
|                               |              | Active | Inactive | Active     | Inactive |
| Young                         | 2,000        | 26     | 24       | 24         | 18       |
| Mature                        | 6,400        | 72     | 145      | 51         | 69       |
| Old                           | 4,000        | 59     | 107      | 38         | 45       |
| All                           | 12,400       | 157    | 276      | 113        | 132      |

<sup>a</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

Table 3.12. Percentage of active red tree vole nest trees containing 1, 2, or  $\geq 3$  (range = 1-5) active nests in the randomly-selected sample of trees examined during the study of detection probability and density of tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Active tree vole | Forest age class <sup>a</sup> |                    |                 |
|------------------|-------------------------------|--------------------|-----------------|
|                  | Young<br>(n = 5)              | Mature<br>(n = 20) | Old<br>(n = 23) |
| 1                | 100                           | 95                 | 61              |
| 2                | 0                             | 5                  | 22              |
| $\geq 3$         | 0                             | 0                  | 17              |

<sup>a</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

Table 3.13. Percentage of red tree vole nests and nest trees by tree species, located in occupied stands during the study of detection probability and density of tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Tree species    | Trees (n) | Nests               |                       | Nest trees          |                       |
|-----------------|-----------|---------------------|-----------------------|---------------------|-----------------------|
|                 |           | Active<br>(n = 158) | Inactive<br>(n = 276) | Active<br>(n = 113) | Inactive<br>(n = 132) |
| Douglas-fir     | 690       | 98.2                | 95.3                  | 97.3                | 93.2                  |
| Western hemlock | 158       | 0.6                 | 4.0                   | 0.9                 | 6.0                   |
| Sitka spruce    | 8         | 0.6                 | 0.7                   | 0.9                 | 0.8                   |
| Coast redwood   | 8         | 0.0                 | 0.0                   | 0.0                 | 0.0                   |
| Grand fir       | 1         | 0.6                 | 0.0                   | 0.9                 | 0.0                   |

Table 3.14. Characteristics ( $\bar{x} \pm SE$ )<sup>a</sup> of active red tree vole nest trees and trees containing no tree vole nests (non-active) in the randomly-selected sample of trees surveyed in occupied stands during the study of detection probability and density of tree vole nest trees in the Oregon Coast Range, April-October 2014.

| Characteristic                    | Forest age class <sup>b</sup> |                              |                              |                              |                               |                              |
|-----------------------------------|-------------------------------|------------------------------|------------------------------|------------------------------|-------------------------------|------------------------------|
|                                   | Young                         |                              | Mature                       |                              | Old                           |                              |
|                                   | Active<br>(n = 5)             | Non-active<br>(n = 200)      | Active<br>(n = 20)           | Non-active<br>(n = 359)      | Active<br>(n = 24)            | Non-active<br>(n = 138)      |
| Diameter at breast height (cm)    | 43.2 $\pm$ 3.7<br>(35-53)     | 37.1 $\pm$ 1.0<br>(11-105)   | 99.3 $\pm$ 8.0<br>(48-186)   | 62.0 $\pm$ 1.8<br>(10-186)   | 139.4 $\pm$ 6.4<br>(75-196)   | 101.6 $\pm$ 3.8<br>(13-206)  |
| Tree height (m)                   | 27.1 $\pm$ 3.0<br>(19.6-36.5) | 26.5 $\pm$ 0.5<br>(9.6-48.6) | 51.7 $\pm$ 2.3<br>(31.3-77)  | 36.5 $\pm$ 0.9<br>(5.2-76.8) | 67.6 $\pm$ 2.3<br>(41.1-86.3) | 50.5 $\pm$ 1.7<br>(6.5-92)   |
| Live crown depth (m) <sup>c</sup> | 9.3 $\pm$ 1.4<br>(6.7-14.2)   | 11.3 $\pm$ 0.4<br>(0.7-35.1) | 30.5 $\pm$ 2.3<br>(8.6-53.6) | 21.0 $\pm$ 0.6<br>(0.5-48.1) | 37.1 $\pm$ 2.0<br>(13.5-52.2) | 30.2 $\pm$ 1.1<br>(2.7-59.5) |
| Connecting pathways <sup>d</sup>  | 19.2 $\pm$ 3.2<br>(16-32)     | 23.8 $\pm$ 1.4<br>(0-128)    | 14.8 $\pm$ 2.2<br>(4-32)     | 10.6 $\pm$ 0.5<br>(0-64)     | 13.5 $\pm$ 2.2<br>(0-32)      | 11.7 $\pm$ 0.9<br>(0-32)     |
| Connecting trees <sup>e</sup>     | 4.2 $\pm$ 0.4<br>(3-5)        | 3.7 $\pm$ 0.1<br>(0-7)       | 3.0 $\pm$ 0.2<br>(2-5)       | 2.5 $\pm$ 0.1<br>(0-6)       | 2.3 $\pm$ 0.3<br>(0-4)        | 2.4 $\pm$ 0.1<br>(0-6)       |

<sup>a</sup> Numbers below means indicate range.

<sup>b</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

<sup>c</sup> Live crown depth was the vertical distance (m) from the first live limb to the tree top.

<sup>d</sup> Connecting pathways: number of interconnecting branch pathways between the nest tree and adjacent trees.

<sup>e</sup> Connecting trees: number of adjacent trees in direct contact with the nest tree by  $\geq 1$  branch pathway.

Table 3.15. Mean volume ( $\text{dm}^3 \pm SE$ )<sup>a</sup> of active and occupied red tree vole nests detected during the study of detection probability and density of tree vole nest trees in the Oregon Coast Range, April-October 2014. Nests were subdivided into three groups, including active nests located by climbing a randomly-selected sample of trees (Random), active nests visually detected from line-transect surveys (Detected), and nests that were occupied by  $\geq 1$  adult tree vole at the time of examination (Occupied).

| Forest age class <sup>b</sup> | Random                            | Detected                            | Occupied                           |
|-------------------------------|-----------------------------------|-------------------------------------|------------------------------------|
| Young                         | $5.9 \pm 2.0$<br>(0.2-10.8)<br>5  | $38.2 \pm 8.6$<br>(3.1-142.5)<br>18 | $26.0 \pm 10.8$<br>(3.1-49.8)<br>4 |
| Mature                        | $5.6 \pm 1.4$<br>(0.7-20.5)<br>17 | $13.2 \pm 3.2$<br>(1.7-81.1)<br>23  | $13.9 \pm 6.3$<br>(3.2-28.2)<br>4  |
| Old                           | $5.4 \pm 0.9$<br>(1.4-18.2)<br>32 | $17.2 \pm 3.2$<br>(1.6-30.6)<br>8   | $26.3 \pm 0.7$<br>(25.6-26.9)<br>2 |
| All                           | $5.5 \pm 0.7$<br>(0.2-20.5)<br>54 | $23.0 \pm 4.1$<br>(1.6-142.5)<br>49 | $21.2 \pm 5.0$<br>(3.1-49.8)<br>10 |

<sup>a</sup> Numbers below means indicate range (in parentheses) and sample size.

<sup>b</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

Table 3.16. Percentage of intact red tree vole nests located in different quadrants of the tree canopy, subdivided by forest age class and method of detection during the study of detection probability and density of tree vole nest trees in the Oregon Coast Range, April-October 2014. Methods of detection included nests located by climbing a randomly-selected sample of trees (Random), nests visually detected from line-transect surveys (Detected), and nests not detected from line-transect surveys that were subsequently found by climbing (Undetected).

| Nest position                 | Forest age class <sup>a</sup> |                      |                       |                    |                      |                        |                    |                      |                        |
|-------------------------------|-------------------------------|----------------------|-----------------------|--------------------|----------------------|------------------------|--------------------|----------------------|------------------------|
|                               | Young                         |                      |                       | Mature             |                      |                        | Old                |                      |                        |
|                               | Random<br>(n = 6)             | Detected<br>(n = 22) | Undetected<br>(n = 9) | Random<br>(n = 46) | Detected<br>(n = 27) | Undetected<br>(n = 88) | Random<br>(n = 55) | Detected<br>(n = 11) | Undetected<br>(n = 79) |
| <u>Horizontal<sup>b</sup></u> |                               |                      |                       |                    |                      |                        |                    |                      |                        |
| 0-1 m from bole               | 100                           | 91                   | 100                   | 70                 | 59                   | 50                     | 64                 | 91                   | 62                     |
| > 1 m from bole               | 0                             | 9                    | 0                     | 30                 | 41                   | 50                     | 36                 | 9                    | 38                     |
| <u>Vertical<sup>c</sup></u>   |                               |                      |                       |                    |                      |                        |                    |                      |                        |
| Below 1st live limb           | 17                            | 9                    | 11                    | 2                  | 4                    | 1                      | 2                  | 9                    | 3                      |
| Lower third                   | 17                            | 50                   | 33                    | 26                 | 63                   | 23                     | 31                 | 64                   | 32                     |
| Middle third                  | 66                            | 32                   | 56                    | 39                 | 26                   | 47                     | 40                 | 27                   | 35                     |
| Upper third                   | 0                             | 9                    | 0                     | 33                 | 7                    | 29                     | 27                 | 0                    | 30                     |

<sup>a</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

<sup>b</sup> Horizontal: horizontal distance from nest to tree bole.

<sup>c</sup> Vertical: vertical quadrant in the live crown.

Table 3.17. Percentage of intact red tree vole nests located on different types of support structures, subdivided by forest age class and method of detection during the study of detection probability and density of tree vole nest trees in the Oregon Coast Range, April-October 2014. Methods of detection included nests located by climbing a randomly-selected sample of trees (Random), nests visually detected from line-transect surveys (Detected), and nests not detected from line-transect surveys that were subsequently found by climbing (Undetected).

| Nest position          | Forest age class <sup>a</sup> |                      |                       |                    |                      |                        |                    |                      |                        |
|------------------------|-------------------------------|----------------------|-----------------------|--------------------|----------------------|------------------------|--------------------|----------------------|------------------------|
|                        | Young                         |                      |                       | Mature             |                      |                        | Old                |                      |                        |
|                        | Random<br>(n = 6)             | Detected<br>(n = 22) | Undetected<br>(n = 9) | Random<br>(n = 46) | Detected<br>(n = 27) | Undetected<br>(n = 88) | Random<br>(n = 55) | Detected<br>(n = 11) | Undetected<br>(n = 79) |
| Branch whorl           | 66                            | 27                   | 45                    | 7                  | 11                   | 3                      | 2                  | 18                   | 4                      |
| Broken top             | 0                             | 14                   | 0                     | 13                 | 0                    | 4                      | 4                  | 0                    | 1                      |
| Cavity                 | 0                             | 0                    | 0                     | 0                  | 0                    | 0                      | 2                  | 0                    | 1                      |
| Dwarf mistletoe growth | 0                             | 0                    | 0                     | 0                  | 0                    | 0                      | 0                  | 0                    | 0                      |
| Forked branch cluster  | 17                            | 14                   | 33                    | 13                 | 30                   | 18                     | 20                 | 9                    | 19                     |
| Forked trunk           | 17                            | 23                   | 0                     | 0                  | 0                    | 0                      | 0                  | 64                   | 1                      |
| Palmate branch cluster | 0                             | 18                   | 11                    | 13                 | 44                   | 10                     | 9                  | 0                    | 10                     |
| Single limb            | 0                             | 4                    | 11                    | 54                 | 15                   | 65                     | 63                 | 9                    | 64                     |

<sup>a</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

Table 3.18. Percentage of active red tree vole nests and nest trees occupied by  $\geq 1$  adult vole at the time of examination during the study of detection probability and density of tree vole nest trees in the Oregon Coast Range, April-October 2014. Data are subdivided based on nests located by climbing a randomly-selected sample of trees (Random) versus nests visually detected from line-transect surveys (Detected). Sample sizes in parentheses indicate number of nests or nest trees inspected in each category.

| Forest age class <sup>a</sup> | Nests  |           | Nest trees |           |
|-------------------------------|--------|-----------|------------|-----------|
|                               | Random | Detected  | Random     | Detected  |
| Young                         | 0 (5)  | 15.8 (19) | 0 (5)      | 15.8 (19) |
| Mature                        | 0 (21) | 8.3 (24)  | 0 (20)     | 8.7 (23)  |
| Old                           | 0 (38) | 10.0 (10) | 0 (24)     | 11.1 (9)  |
| All                           | 0 (64) | 11.3 (53) | 0 (49)     | 11.8 (51) |

<sup>a</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

Table 3.19. Model selection results from the analysis of effects of survey type (ground vs. climbing) and forest age class on detection probability of active red tree vole nest trees at distance zero from the transect line ( $p(0)$ ) in the Oregon Coast Range, April-October 2014.<sup>a</sup>

| Model      | K | $\Delta AIC_c$ | $w_i$ |
|------------|---|----------------|-------|
| p(.)c(age) | 4 | 0.00           | 0.61  |
| p(.)c(.)   | 2 | 0.87           | 0.39  |
| p(.)=c(.)  | 1 | 106.96         | 0.00  |

<sup>a</sup> Column headings indicate number of model parameters (K), difference in Akaike's information criterion corrected for small sample sizes relative to the best model ( $\Delta AIC_c$ ), and Akaike weight ( $w_i$ ). Lowest  $AIC_c = 51.56$

Table 3.20. Detection probabilities of active red tree vole nest trees at distance zero from the transect line ( $p(0)$ ) in different forest age classes in the Oregon Coast Range, April-October 2014.

| Forest age class <sup>a</sup> | Nest trees (n) | $p(0) \pm SE$     | 95% CI      |
|-------------------------------|----------------|-------------------|-------------|
| Young                         | 11             | $0.273 \pm 0.134$ | 0.090-0.586 |
| Mature                        | 41             | $0.073 \pm 0.041$ | 0.024-0.204 |
| Old                           | 33             | $0.030 \pm 0.030$ | 0.004-0.186 |
| All                           | 85             | $0.082 \pm 0.030$ | 0.040-0.163 |

<sup>a</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

Table 3.21. Model selection results from the analysis of key functions and expansion terms used in the detection function of active red tree vole nest trees from line-transect surveys in the Oregon Coast Range, April-October 2014.<sup>a</sup>

| Model      | K | $\Delta AIC_c$ | $w_i$ |
|------------|---|----------------|-------|
| p(HN.cos)  | 1 | 0.00           | 0.39  |
| p(HN.her)  | 1 | 0.00           | 0.39  |
| p(HzR.cos) | 2 | 2.43           | 0.11  |
| p(HzR.sim) | 2 | 2.43           | 0.11  |

<sup>a</sup> Column headings indicate number of model parameters (K), difference in Akaike's information criterion corrected for small sample sizes relative to the best model ( $\Delta AIC_c$ ), and Akaike weight ( $w_i$ ). Lowest  $AIC_c = 127.47$ .

Table 3.22. Model selection results from the analysis of effects of dominant canopy structural composition and abiotic survey conditions on detection probability of active tree vole nest trees from line-transect surveys in the Oregon Coast Range, April-October 2014.<sup>a</sup>

| Model                   | K   | $\Delta AIC_c$ | $w_i$ |
|-------------------------|-----|----------------|-------|
| p(Intercept-only)       | 1   | 0.00           | 0.13  |
| p(AGE)                  | 3   | 1.07           | 0.07  |
| p(Elev)                 | 2   | 1.09           | 0.07  |
| p(SlpGrad)              | 2   | 1.44           | 0.06  |
| p(DEN)                  | 2   | 1.90           | 0.05  |
| p(P99H)                 | 2   | 2.02           | 0.05  |
| p(P90H)                 | 2   | 2.04           | 0.05  |
| p(P97.5H)               | 2   | 2.05           | 0.05  |
| p(MH)                   | 2   | 2.08           | 0.04  |
| p(QMH)                  | 2   | 2.09           | 0.04  |
| p(ModH)                 | 2   | 2.11           | 0.04  |
| p(TrnSlpAsp.2)          | 2   | 2.12           | 0.04  |
| p(SlpGrad)              | 2   | 2.14           | 0.04  |
| p(Obs)                  | 2   | 2.16           | 0.04  |
| p(MedH)                 | 2   | 2.16           | 0.04  |
| p(DEN + SlpGrad)        | 3   | 2.81           | 0.03  |
| p(AGE + SlpGrad)        | 4   | 2.82           | 0.03  |
| p(AGE + Elev)           | 4   | 3.01           | 0.03  |
| p(DEN + Elev)           | 3   | 3.32           | 0.02  |
| p(TrnSlpAsp.3)          | 3   | 3.72           | 0.02  |
| p(Season)               | 3   | 4.26           | 0.01  |
| p(AGE + Elev + SlpGrad) | 5   | 4.30           | 0.01  |
| p(DEN + Elev + SlpGrad) | 4   | 4.48           | 0.01  |
| p(Wind)                 | N/A | N/A            | N/A   |

<sup>a</sup> Column headings indicate number of model parameters (K), difference in Akaike's information criterion corrected for small sample sizes relative to the best model ( $\Delta AIC_c$ ), and Akaike weight ( $w_i$ ). Lowest  $AIC_c = 127.56$ .

Figure 3.7. Detection probability ( $P_a$ ) of active red tree vole nest trees at specific perpendicular distances from the transect line in different forest age classes in the Oregon Coast Range, April-October 2014. Top and bottom figures illustrate estimates pre- and post-adjustment for imperfect detection at distance zero from the transect line ( $p(0)$ ).

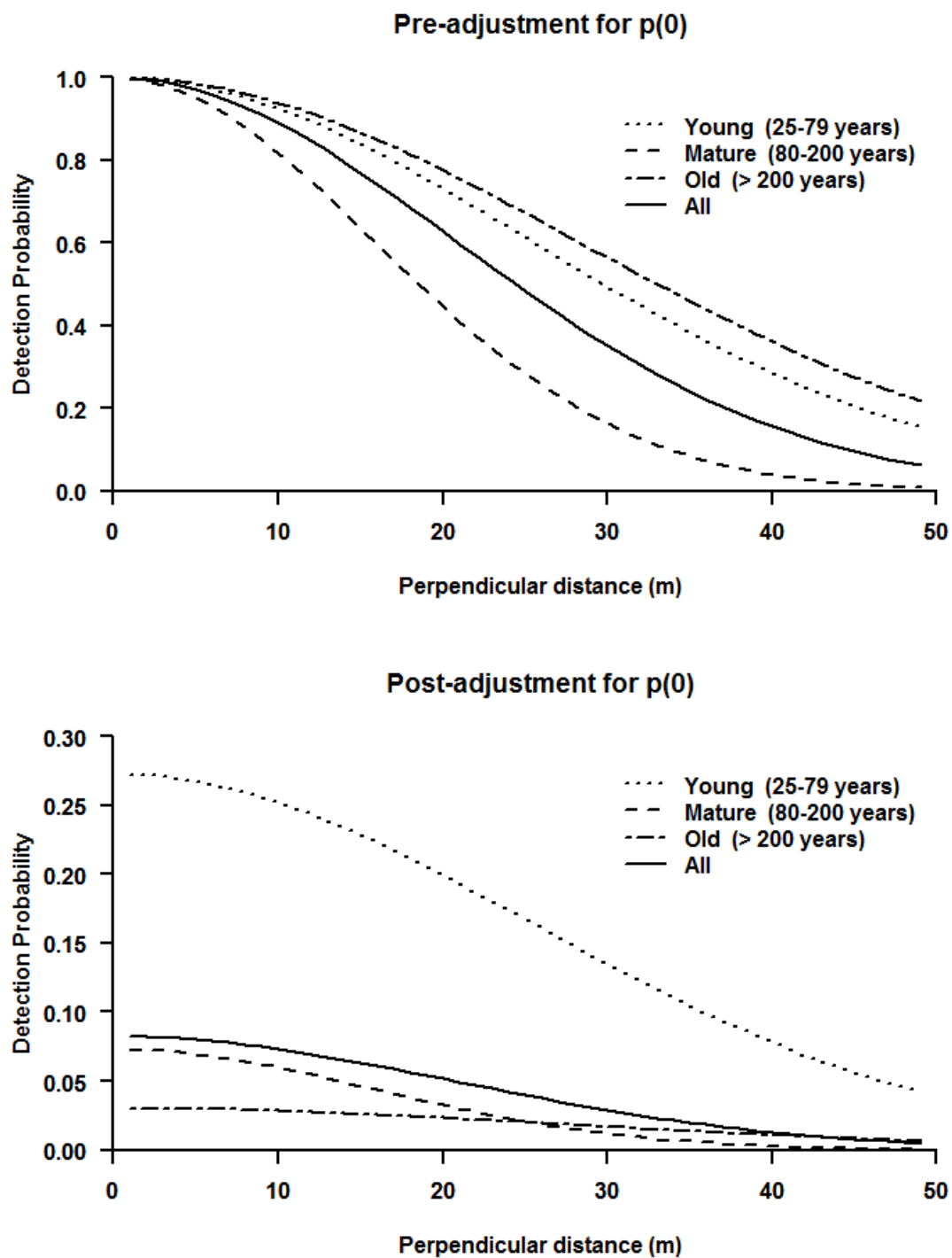


Table 3.23. Mean detection probabilities ( $\bar{P}_a \pm SE$ ) of active red tree vole nest trees from line-transect surveys in the Oregon Coast Range, April-October 2014. Data were subdivided based on (half) strip widths and effective strip width (ESW). Estimates were adjusted for imperfect detection at distance zero from the transect line ( $p(0)$ ) and reported for the best model, which included no age effects on detection rates, and the second best model, which included effects of forest age class<sup>a</sup>.

|                        | Mean detection probability ( $\bar{P}_a$ ) |                   |                   |                   |
|------------------------|--|-------------------|-------------------|-------------------|
|                        | Young                                      | Mature            | Old               | All               |
| <u>Strip width (m)</u> |  |                   |                   |                   |
| 5                      | 0.271 $\pm$ 0.133                          | 0.072 $\pm$ 0.040 | 0.030 $\pm$ 0.030 | 0.082 $\pm$ 0.030 |
| 10                     | 0.265 $\pm$ 0.130                          | 0.068 $\pm$ 0.038 | 0.030 $\pm$ 0.030 | 0.080 $\pm$ 0.029 |
| 15                     | 0.256 $\pm$ 0.126                          | 0.063 $\pm$ 0.035 | 0.029 $\pm$ 0.029 | 0.078 $\pm$ 0.029 |
| 20                     | 0.245 $\pm$ 0.120                          | 0.057 $\pm$ 0.032 | 0.028 $\pm$ 0.028 | 0.075 $\pm$ 0.027 |
| 25                     | 0.232 $\pm$ 0.114                          | 0.050 $\pm$ 0.028 | 0.027 $\pm$ 0.027 | 0.072 $\pm$ 0.026 |
| 30                     | 0.218 $\pm$ 0.107                          | 0.044 $\pm$ 0.025 | 0.025 $\pm$ 0.025 | 0.068 $\pm$ 0.025 |
| 35                     | 0.204 $\pm$ 0.100                          | 0.039 $\pm$ 0.022 | 0.024 $\pm$ 0.024 | 0.065 $\pm$ 0.024 |
| 40                     | 0.189 $\pm$ 0.093                          | 0.035 $\pm$ 0.020 | 0.022 $\pm$ 0.022 | 0.061 $\pm$ 0.022 |
| 45                     | 0.175 $\pm$ 0.086                          | 0.031 $\pm$ 0.017 | 0.021 $\pm$ 0.021 | 0.057 $\pm$ 0.021 |
| 49                     | 0.165 $\pm$ 0.081                          | 0.029 $\pm$ 0.016 | 0.020 $\pm$ 0.020 | 0.054 $\pm$ 0.020 |
| ESW ( $\bar{P}_a$ )    | 0.209 $\pm$ 0.103                          | 0.057 $\pm$ 0.032 | 0.025 $\pm$ 0.025 | 0.071 $\pm$ 0.026 |
| ESW (m)                | 30.0 $\pm$ 6.5                             | 19.7 $\pm$ 3.3    | 32.3 $\pm$ 10.2   | 25.5 $\pm$ 3.1    |

<sup>a</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

Table 3.24. Estimated density per ha ( $\pm SE$ ) of active red tree vole nest trees in different forest age classes in the Oregon Coast Range, April-October 2014.

| Forest age class <sup>a</sup> | Density          | 95% CI     | CV <sup>b</sup> | Proportion <sup>c</sup> |
|-------------------------------|------------------|------------|-----------------|-------------------------|
| Young                         | 5.50 $\pm$ 1.83  | 2.85-10.62 | 33.30           | 0.03                    |
| Mature                        | 11.93 $\pm$ 2.97 | 7.32-19.45 | 24.88           | 0.13                    |
| Old                           | 11.50 $\pm$ 5.63 | 4.48-29.53 | 48.95           | 0.16                    |
| All                           | 9.40 $\pm$ 1.81  | 6.45-13.71 | 19.27           | 0.09                    |

<sup>a</sup> Forest age classes were: Young (25-79 years), Mature (80-200 years), and Old (> 200 years).

<sup>b</sup> Coefficient of variation.

<sup>c</sup> Estimated proportion of total trees in the dominant canopy that contained  $\geq 1$  active tree vole nest.

## CHAPTER 4

### GENERAL SUMMARY AND CONCLUSIONS

Chad A. Marks-Fife

In this study, we investigated alternative methods for studying red tree vole (*Arborimus longicaudus*) population demographics including density and age structure of voles predated by spotted owls. New methods were necessary for studying this species since tree voles are difficult to capture (Swingle et al. 2004), making it impractical to use mark-recapture or other techniques traditionally used to estimate population density or age-structure in small mammals. We evaluated the age structure of tree voles predated by northern spotted owls (*Strix occidentalis caurina*) through analysis of teeth found in owl pellets collected at spotted owl territories in western Oregon. We used distance sampling techniques to estimate tree vole density through detection of their nests.

We found that measurements from lower M1 molars were a reliable indicator of tree vole age, especially with consideration to crown wear. Vole remains in owl pellets suggested a tree vole population dominated by young animals, with 47% of voles younger than six months and only 0.5% older than two years. However, because predation by owls was not an unbiased sampling method, we could not be certain that the age distribution of voles in owl pellets accurately reflected age distribution in the tree vole population. The proportion of juvenile tree voles in owl pellets varied among years, suggesting high annual variation in reproduction of tree voles. In one study area, annual variation in the proportion of juvenile tree voles in owl pellets was positively correlated with annual and seasonal precipitation, suggesting that annual productivity may be driven, at least in part, by availability of water in the forest canopy, whether as free water on foliage or as water contained in well-hydrated conifer needles.

Our study was the first to use multiple sampling techniques to estimate detection probabilities of tree vole nest trees and incorporate them into analyses of density. Using distance sampling, we estimated a minimum density of 1.91 voles/ha, which was nearly twice as high as any previous estimate. We found that detection probabilities of nest trees decreased with forest age, whereas density of nest trees increased in older forest. We estimated that detection probabilities of nest trees in mature forest (80-200 years) from the ground-based surveys described in the USDA protocol (Huff et al. 2012) were low (< 10%), even under optimal survey conditions with unlimited effort. To avoid false negative assessments of presence of tree voles, we provided estimates of the minimum

line-transect survey effort necessary to determine tree vole occupancy by detecting  $\geq 1$  tree vole nest. We also provided evidence that full-tree climbing searches were necessary to reduce false negative assessments of individual tree occupancy, and suggested several secondary methods for increasing nest tree detection.

Because of their association with old forests and their importance as a prey item for spotted owls and many other forest predators, tree voles are a growing conservation concern in western Oregon (Forsman et al. 2004a, 2004b, Graham and Mires 2005, Swingle et al. 2010). It is thought that tree vole abundance is declining as their preferred habitat becomes increasingly fragmented and converted to young, intensively managed forest (Huff et al. 1992, 2012). The U.S. Fish and Wildlife Service has already determined that the north coast population of tree voles in Oregon warrants listing as a threatened or endangered distinct population segment (USFWS 2011), and the extent of the species decline is currently unknown in other portions of the tree vole range. In addition, it is unknown what effect increased predation pressure from the recent population explosion of invasive barred owls (*Strix varia*) will ultimately have on tree vole populations. We presented new methods for quantifying tree vole distribution and density in our studies, but continued innovation will be necessary if we are to effectively manage forests in western Oregon to conserve habitat for tree voles.

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