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Tree Voles: an Evaluation of Their Distribution and Habitat Relationships Based on Recent and Historical Studies, Habitat Models, and Vegetation Change

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Cover photos: (Upper left) A red tree vole nest under construction. The nest, constructed of resin ducts, debarked twigs, and Douglas-fir cuttings, was built at the junction of three tops in a 35-year-old Douglas-fir tree. Photo by Jim Swingle. (Lower left) An adult captive red tree vole mechanically removing one of two unpalatable resin ducts in a Douglas-fir needle before eating the rest of the needle. Photo by Michael Durham. (Right) Eric Forsman examining a red tree vole nest in a dwarf mistletoe broom in the top of a western hemlock tree. Photo by Jim Swingle.

Abstract

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We describe the historical and current distribution of tree voles (*Arborimus longicaudus; A. pomo*) and compare the minimum density of trees with tree vole nests in different forest age-classes based on museum records, field notes of previous collectors, tree vole nest surveys conducted by federal agencies, and our field studies in Oregon and California. We conclude that tree voles are still fairly common in old forests within much of their historical range, but have become uncommon or rare in some areas as a result of fire and logging. Our analysis of food stored at red tree vole (*A. longicaudus*) nests in Oregon indicated that the vast majority of tree voles feed almost exclusively on needles of Douglas-fir (*Pseudotsuga menziesii*). However, tree voles in the Sitka spruce zone of northwestern Oregon feed primarily on western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*). Historical field notes from the California coastal region also documented occasional voles that feed on grand fir (*Abies grandis*), Monterey pine (*Pinus radiata)*, or Bishop pine (*P. muricata*). We used the program MaxEnt to develop predictive models of tree vole presence based on an a priori set of habitat, structure, and climate variables. Based on a comparison of potential vole habitat in historical and recent vegetation maps, we estimated that the geographic distribution of red tree voles in Oregon contracted by 23 percent in the period 1914–2013.

Keywords: Arboreal mammals, *Arborimus longicaudus, A. pomo*, Arvicolinae, California, forest management, Oregon, Northwest Forest Plan, red tree vole, Sonoma tree vole.

Contents

Chapter 1: Distribution and Habitat of Tree Voles Based on Historical and Recent Studies

Introduction

Because they are the only truly arboreal Arvicoline mammals in the world and are among the few mammals that feed primarily on needles and twigs of conifers, red tree voles (*Arborimus longicaudus*) and Sonoma tree voles (*A. pomo*) have long intrigued collectors and naturalists (Clifton 1960, Maser et al. 1981, Taylor 1915, Todd 1891, Walker 1928). The two species of tree voles are ecologically similar but geographically isolated (Murray 1995, Smith et al. 2003). Red tree voles occur in western Oregon and northwestern California, north of the Klamath River. Sonoma tree voles occur in coastal California from the Klamath River south to southern Sonoma County (Bellinger et al. 2005, Blois and Arbogast 2006, Murray 1995). Tree voles are a challenge to study because they spend most of their time in the forest canopy and are difficult to capture using conventional methods (Forsman et al. 2009b, Swingle 2005, Swingle et al. 2004). Until fairly recently, tree voles were somewhat of an enigma; they were studied by a few mammalogists but otherwise were largely ignored by forest managers and land management agencies (Todd 1891, True 1890, Verts and Carraway 1998). This began to change after the adoption of the Northwest Forest Plan in 1994 because, for the first time, federal land management agencies were required to search for and manage red tree voles and many other little-known species that were native to old forests in Washington, Oregon, and northwestern California (USDA and USDI 1994). The reason for this change was simple—forest managers, scientists, and the lay public were becoming more aware of the many unique inhabitants of the old forests of the Pacific Northwest, and were increasingly concerned that some of those species could be harmed if measures were not taken to protect them from habitat loss resulting from timber harvest, wildfire, and changes in land use. This increased awareness, coupled with a series of court cases that compelled federal management agencies to respond to concerns about unique native species, led the USDA Forest Service (Forest Service) and USDI Bureau of Land Management (BLM) to adopt new monitoring and research programs in the 1990s to better understand the distribution and abundance of little-known species that were thought to be dependent on old forests. The result was an explosion of information regarding many species, including tree voles. Some of this information has been published (e.g., Bellinger et al. 2005; Dunk and Hawley 2009; Forsman et al. 2004, 2009a, 2009b; Kelsey et al. 2009; Swingle and Forsman 2009; Swingle et al. 2010), but most of the new empirical information on distribution and habitat of tree voles remains unpublished.

Until fairly recently, tree voles were somewhat of an enigma; they were studied by a few mammalogists but otherwise were largely ignored by forest managers and land management agencies.

Our goal in this report is to summarize the historical and recent information on distribution and habitat of tree voles, and to provide managers with a new tool for assessing potential tree vole habitat. In chapter 1, we use historical and recent data to describe the current geographic distribution of tree voles. We also describe regional variation in habitat of tree voles, and compare the minimum density of trees with vole nests in different forest age-classes. In chapter 2, we describe regional variation in diets of red tree voles. In chapter 3, we describe an analysis based on maximum-entropy methods in which we used data on climate, forest structure, and forest tree species composition to predict the current distribution of potential red tree vole habitat in Oregon and northwestern California. In chapter 4, we examine changes that have occurred in the amount and distribution of potential tree vole habitat in western Oregon based on a comparison of forest cover maps generated in 1914 and 1936, and our modeled estimates of potential vole habitat in 2006. We believe this information will provide forest managers and policy makers with a better background and understanding of the distribution of tree voles and the kinds of habitat in which they occur, and will allow managers to better predict the consequences of various kinds of management on tree vole populations.

Study Area

Our study area included western Oregon and coastal northwestern California, from the Columbia River south to San Francisco Bay (fig. 1-1). With the exception of the Willamette Valley in Oregon and a few other interior valleys, this region is characterized by mountainous terrain and vegetation dominated by coniferous forests. Climate within the study area is characterized by warm, dry summers and cool, wet winters. Precipitation is highly variable depending on latitude and proximity to the ocean, ranging from very wet areas along the coast, to comparatively dry areas in the interior valleys of southwest Oregon. In areas below 800 m, most precipitation occurs as rain during the fall, winter, and early spring (October to April). At higher elevations in the Cascade Mountains, precipitation includes a mix of rain and snow, and the ground is often covered by snow for much of the winter (November to March).

In Oregon, species composition of forests differs among regions, with Douglas-fir[1] and western hemlock predominating in northwestern Oregon and mixed conifer or mixed evergreen forests predominating in southwestern Oregon (Franklin and

[1] See "Tree Species Mentioned in This Report" on page 90 for scientific names and authorities.

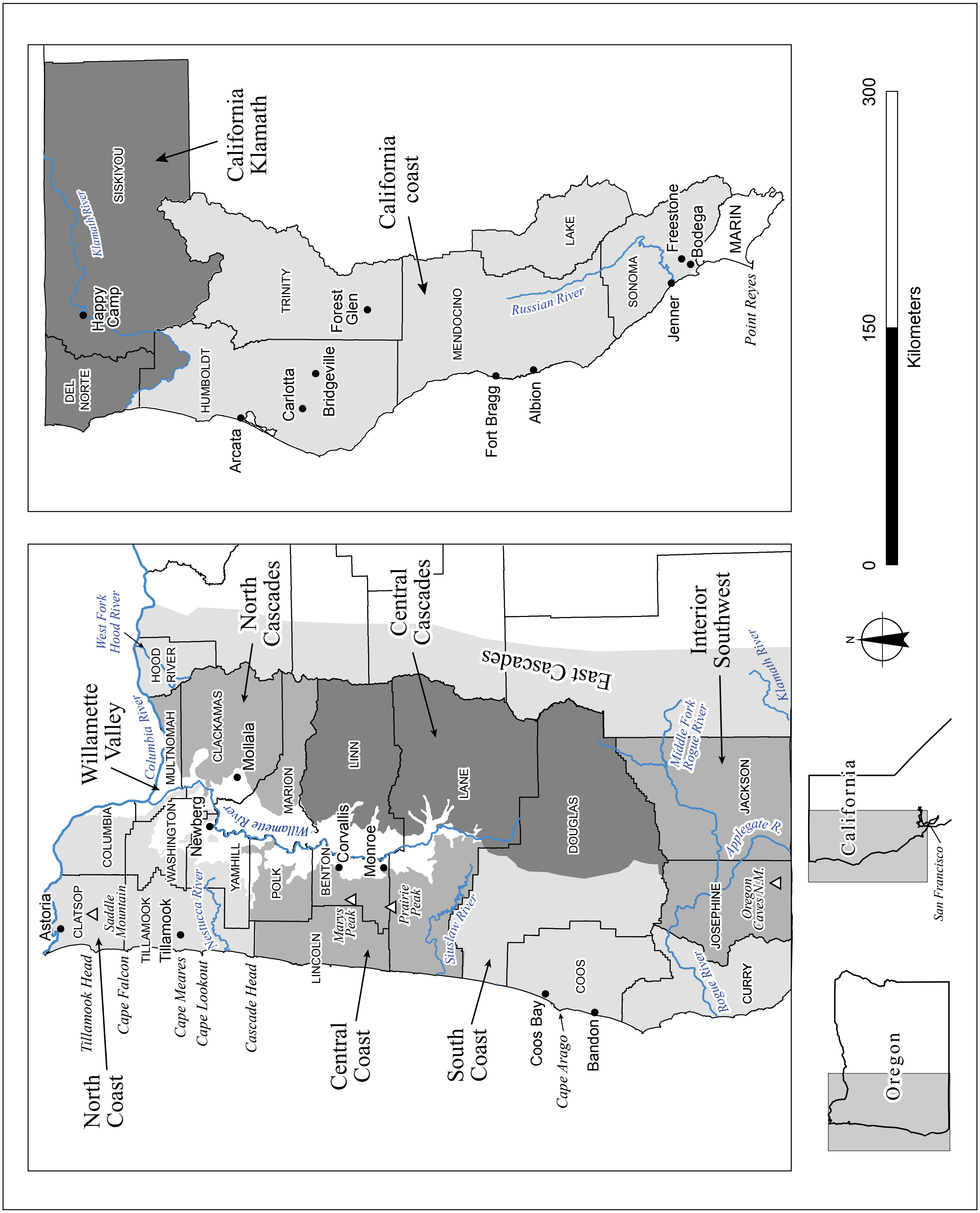

Figure 1-1—Geographic subregions and major geographic features used in analyses of the distribution and relative abundance of red tree voles and Sonoma tree voles in western Oregon and northwestern California. Study area is indicated by gray boxes in insert.

Dyrness 1973). A narrow belt of Sitka spruce and western hemlock is present along the coast. Mixed conifer and mixed evergreen forests typically include a diverse mix of species, including Douglas-fir, grand fir, western white pine, incense-cedar, Pacific madrone, California laurel, and tanoak. In California, forests are dominated by Douglas-fir or mixed-species stands of Douglas-fir, coast redwood and tanoak in the northern coastal region and by mixed-species stands of Douglas-fir, bishop pine, and grand fir in the coastal region between Fort Bragg and Bodega. Lumber production is a major industry throughout the study area, and landscapes typically include heterogeneous mixtures of forest age-classes that are the result of timber harvesting and fire. Private and state lands typically are dominated by young forests growing on harvested areas, whereas federal lands typically include a mixture of young forests growing on harvested areas and old forests growing on areas that have never been harvested.

Methods

We considered either specimens or nests as evidence of presence, because nests of tree voles rarely persist for more than a few years after they are last occupied and are easily identified based on the presence of tree vole fecal pellets, debarked twigs, and resin ducts from conifer needles.

Tree voles are the only animals that remove resin ducts from conifer needles, so any nest containing resin ducts can safely be classified as a tree vole nest.

Data sources used to document the range and habitat of tree voles included specimens collected from 1886 to 2013, tree vole specimens identified in pellets of northern spotted owls (*Strix occidentalis caurina*) and barred owls (*S. varia*), and field surveys of tree voles and their nests that we and many others conducted on federal, state, and private lands in Oregon and California from 1990 to 2013. We also examined field notes of previous researchers and resurveyed many historical collection locations to try to determine if tree voles were still present at or near those locations (app. 1). In California, we used a database compiled by Gordon Gould at the California Department of Fish and Game that included records of tree voles or tree vole nests located in California from 1984 to 2000 (Gould 2005). Data from these different sources differed in quality, but always consisted of unequivocal evidence of the presence of tree voles, whether in the form of museum specimens, skulls, or nests documented by tree climbers. We considered either specimens or nests as evidence of presence, because nests of tree voles rarely persist for more than a few years after they are last occupied and are easily identified based on the presence of tree vole fecal pellets, debarked twigs, and resin ducts from conifer needles (Maser 1966, Thompson and Diller 2002). Tree voles are the only animals that remove resin ducts from conifer needles, so any nest containing resin ducts can safely be classified as a tree vole nest. Methods associated with each of the above sources of data are described below. All means are reported as $\bar{x} \pm 1$ standard error (SE).

Data From Owl Pellets

Based on the percentage of occurrence of tree voles in the diets of northern spotted owls, Forsman et al. (2004) estimated the distribution of red tree voles in western Oregon and compared the relative abundance of red tree voles in owl diets in different subregions of the state. We reanalyzed the same data examined by Forsman et al. (2004), with the addition of 13,571 prey items and 268 owl territories that were not available when Forsman et al. (2004) conducted their analysis. The number of spotted owl territories in our sample was 1,386, and the number of prey items examined was 38,068, of which 3,991 were tree voles. Methods for this part of our study were as described in Forsman et al. (2004), but in short, were as follows:

- Regurgitated pellets were collected below northern spotted owl roosts and dissected in the laboratory.
- Individual prey items in pellets were identified to the lowest possible phylogenetic group, including 78 percent to species, 14 percent to genus, 4 percent to family, and 4 percent to order or class.
- Composition of the diet at each owl territory was calculated based on the percentage of numbers of each prey species in the total sample from the territory.

Of 38,068 prey items identified in pellets of spotted owls in Oregon, 3,991 were red tree voles.

We used the percentage of red tree voles in the diet at each territory as an index of red tree vole abundance in different geographic subregions (fig. 1-1) of Oregon. Obviously, owls do not sample prey in an unbiased way, and false negatives (no detections when the species is actually present) are possible with small samples of prey items. However, we reasoned that with the large number of owl territories in our sample, patterns in abundance of red tree voles in different geographic subregions should become apparent in spite of potential biases due to prey selection or small sample size.

We also obtained data on prey remains in pellets of spotted owls or barred owls from four areas in California, including samples from:

- 245 spotted owl territories on lands owned by the Green Diamond Resource Company in Del Norte, Humboldt, and Trinity Counties (Diller 2013).
- 79 spotted owl territories from the Northwestern California Study Area in Siskiyou, Trinity, Humboldt, and Mendocino Counties (Franklin 2015).
- 9 spotted owl and 2 barred owl territories in Redwood National and State Parks in Del Norte and Humboldt Counties (Schmidt 2013).
- 13 spotted owl territories in Point Reyes National Seashore in Marin County (Fehring 2013), and a sample from one spotted owl territory on private land near Bodega in Sonoma County (Moore 2013).

Museum Specimens and Archived Field Notes

We found 1,658 records of tree voles in museums, including 1,453 specimins and 205 additional visual records documented in archived field notes.

From 2004 to 2011, we searched museum catalogs and archived field notes and found 1,658 records of tree voles in museums, including 1,453 specimens and 205 visual observations of tree voles or their nests that were documented in field notes but not supported by specimens (apps. 2 and 3). Based on these sources, we compiled a database of all historical records of tree voles collected or observed in Oregon and California, including some specimens that had been lost or destroyed (app. 3). We visited 25 of the 35 museums that had tree voles in their collections and physically examined 1,426 (98 percent) of specimens in museums (app. 2). We also read and transcribed the archived field notes of Murray Johnson, Chris Maser, William Hamilton III, Don Roberts, and Seth Benson, who collected a large proportion (51 percent) of the tree voles in museums and who also raised many tree voles in captivity (Hamilton 1962, Johnson 1973, Johnson and George 1991) (app. 1). To evaluate potential biases inherent in different methods of capturing tree voles, we used χ^2 tests to compare sex ratios of museum specimens captured with different methods. We also assessed habitat associations by comparing the number of voles captured in four different forest age-classes, including early seral (0 to 15 years), young (16 to 79 years), mature (80 to 200 years), and old-growth (>200 years) forests. Museum specimens that were the result of captive breeding (n = 114) were included in some tables, but were not used to assess distribution.

Pre-Project and Strategic Surveys

After adopting the Northwest Forest Plan in 1994, the Forest Service and Bureau of Land Management initiated extensive surveys of red tree voles in western Oregon and northwestern California. For the most part, these surveys fell into three categories, which we will hereafter refer to as (1) pre-project surveys, (2) strategic surveys, and (3) the random plot study. Pre-project and strategic surveys were designed to determine if tree vole nests were present in areas proposed for management or in areas where there were few or no historical surveys. Pre-project surveyors followed an established protocol in which they visually searched for potential tree vole nests while walking transects in proposed project areas (Biswell et al. 2000, 2002; Huff et al. 2012). The survey protocol called for a minimum of 222 m of survey transect per hectare, with parallel transects spaced 40 to 46 m apart. Most (76 percent) trees containing potential nest structures detected from the ground were climbed to determine if the structures were built by red tree voles.

Strategic surveys were conducted using a variety of protocols, including the same protocol used in pre-project surveys (Biswell et al. 2002) as well as less formal protocols in which contract climbers searched for nests in non-random samples of large trees in old forest that had broken tops, dwarf mistletoe (*Arceuthobium* spp.) brooms, or large, epicormic branches. Size of pre-project and strategic survey polygons ranged from the immediate area around a single tree to 448 ha.

Tree vole nests detected in pre-project and strategic surveys were classified as "active" or "inactive" depending on physical evidence (Biswell et al. 2000, 2002; Huff et al. 2012). Nests with resin ducts, fecal pellets, or cuttings that were still green were classified as active, whereas nests with resin ducts or cuttings that were tan or brown were described as inactive. Cases in which resin ducts were found on the ground below nests that were not climbed were classified as "nest-status undetermined."

Survey results and plot locations from pre-project and strategic surveys were maintained in an ArcGIS® (Esri, Inc., Redlands, California)[2] geodatabase (geographic biotic observation or "GeoBOB") that we obtained from the BLM in February 2011. The GeoBOB database included polygon feature classes for each survey location, as well as information on forest size-class, land ownership, and number of trees with tree vole nests detected in each polygon.

We used data from pre-project surveys to estimate the minimum density of trees containing red tree vole nests per hectare as a function of forest size-class and elevation. The five forest size-classes were based on tree diameter-at-breast-height (dbh): (1) 2 to 13 cm dbh, (2) >13 to 23 cm dbh, (3) >23 to 53 cm dbh, (4) >53 to 81 cm dbh, and (5) >81 cm dbh. If a tree contained multiple nests, the status of the tree was based on the most recently used nest, which was determined based on evidence at each nest (Biswell et al. 2002). Lack of consistency in terms of tree climbing and mapping of polygons in some pre-project surveys caused considerable uncertainty regarding estimates of minimum nest tree density. To reduce this uncertainty, we restricted our assessment of distribution to 5,285 survey polygons that included data that were linked to mapped polygons. For comparisons of minimum density of nest trees among areas, we further restricted the analysis to 3,234 polygons that were ≥0.6 ha and in which ≥50 percent of potential nests were climbed to determine if they were tree vole nests. For comparisons of minimum nest tree density in different forest size-classes, we further restricted the analysis to 2,661 polygons for which field data sheets included information on the size of overstory trees. We excluded polygons that were <0.6 ha from our estimates of minimum density because many small polygons were surveyed after someone reported a possible nest and surveyors made a return visit to search the nest tree and a few adjacent trees. As a result,

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[2] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

estimates of minimum nest tree density based on polygons <0.6 ha were often based on one or two trees and were not representative of average conditions. Plots that fell outside the known range of tree voles were used to define the limits of the range, but estimates of minimum nest tree density were based only on plots that fell within the range of the species, as defined in this report. Because survey protocols in strategic surveys were not consistent, we used the strategic survey data to assess presence or absence but not density.

Random Plot Study

The random plot study was designed to assess the minimum density of red tree vole nests in different forest age-classes and land-use allocations on federal forest lands.

The random plot study was designed to assess the minimum density of red tree vole nests in different forest age-classes and land-use allocations on federal forest lands in Oregon and northwestern California in 2001–2004 (Dunk and Hawley 2009, Rittenhouse et al. 2002). The original sample for the random plot study was a stratified random sample of 400 1-ha plots selected from the grid of Current Vegetation Survey plots (CVS) and Forest Inventory and Analysis plots (FIA) in western Oregon and northwestern California (Bechtold and Patterson 2005; Max et al. 1996; Rittenhouse et al. 2002; USDA FS 2001, 2008). Stratification of the sample was based on forest age and management designations, with 70 percent of sampling plots classified as old forest and 80 percent of plots in reserved land use allocations under the Northwest Forest Plan (Rittenhouse et al. 2002, USDA and USDI 1994). Subsequent to implementation of surveys, a decision was made to double the plot size by adding a second 1-ha plot on the north side of each plot in the original sample of 400 plots. The decision to double the plot size at each location was controversial because vegetation in the north plot was not always the same as in the south plot and there was concern that the addition of a second plot would violate the assumption of independence of plots (Dunk and Hawley 2009). Because we did not want to discard data, we conducted one analysis with the original 1-ha plots and another analysis with the 2-ha plots. This allowed us to compare the results using both the original random sample and the entire sample.

Surveys of random plots were conducted by walking along linear transects and visually searching for potential vole nests in each plot (Dunk and Hawley 2009, Rittenhouse et al. 2002). Transects were spaced 25 m apart, with four 100-m transects in each 1-ha plot. All potential nests seen from the ground were examined by tree climbers to determine if they were vole nests. Vole nests were classified as inactive or active, using the same criteria as in pre-project and strategic surveys (Biswell et al. 2000, 2002). In 185 plots with complex tree canopies or in which few or no potential vole nests were detected on the terrestrial transects in old forest, surveyors climbed a stratified random sample of 1 to 6 large trees and searched for nests in the tree canopies (Dunk and Hawley 2009, Rittenhouse et al. 2002). The random plot survey data were partially summarized by Dunk and Hawley (2009), who limited their analysis to an assessment of minimum density of tree vole nests in different forest age-classes in the original sample of 1-ha plots. We used the entire sample to evaluate tree vole distribution, but we used only plots that fell within the range of the species, as defined in this report, to estimate minimum nest tree densities in different forest types and subregions.

After excluding plots that were not accessible because they were on nonfederal lands, had incomplete data, or had burned in recent wildfires, there were 350 1-ha plots in the original sample, 319 of which fell within the range of the red tree vole, and there were 317 2-ha plots, 302 of which fell within the range of the red tree vole. These were the samples we used in our analyses. However, the number of 2-ha plots used in the analysis of minimum nest tree density was further reduced to 207 because there were 95 cases in which forest age-classes in the north and south plots were different.

Retrospective and Targeted Surveys

During 1990–2013, we conducted a variety of field and laboratory studies on tree voles, including studies of home range and survival (Swingle and Forsman 2009, Swingle et al. 2010), distribution (Forsman et al. 2004, 2009a; Price et al. 2015), behavior (Forsman et al. 2009b), water consumption (Forsman and Price 2011), sampling methods (Swingle et al. 2004), and genetic relationships (Bellinger et al. 2005, Miller et al. 2006). During these studies we searched for tree voles at many locations in Oregon and California, including 44 surveys in which we attempted to determine if tree voles were still present in areas where they were found by earlier researchers (retrospective surveys). The primary survey method we used to locate voles in these studies was to walk or drive through forest areas, visually searching for arboreal nests and climbing trees to determine if nests were built by tree voles. In six areas in which we located no tree vole nests during ground surveys, we conducted follow-up surveys by climbing large trees and searching for nests in the canopy (Forsman et al. 2008). When trying to determine if tree voles were still present in areas where they had been found by earlier researchers, we began our searches as close as possible to the original locations, and then expanded the search outward from there, looking for nests in a 1- to 20-km radius around the historical location. The radius of the area searched depended on multiple factors, including the time available, distribution of potential habitat, and restrictions on access to private lands. We examined 96 percent of 2,229 potential vole nest structures by climbing trees and probing nests with our fingers or a piece of stiff wire to chase voles out of their nests (Swingle et al. 2004). We categorized the occupancy status of each nest as follows:

- Occupied—tree vole(s) captured or observed (n = 230).
- Likely occupied—nest not probed or dissected, but intact, with fresh green cuttings present, usually accompanied by green resin ducts, greenish fecal pellets, and debarked twigs (n = 206).
- Recent nest but not occupied—intact or predated nest, usually with some moderately old green cuttings present and variable amounts of faded green resin ducts. No tree vole detected when nest probed or dissected (n = 112).
- Old, unoccupied nest—no recent cuttings present. Debarked twigs usually present, along with old tan or brown resin ducts and decomposed fecal pellets (n = 491).
- Non-tree vole—nest or structure with no evidence of use by tree voles (n = 1,093).

We used 1984 as the cutoff for retrospective surveys because 1984 was the first year in which the Forest Service and BLM initiated numerous pitfall sampling studies of small mammals in the Pacific Northwest and northwestern California (Aubry et al. 1991; Corn and Bury 1986, 1991; Gilbert and Allwine 1991; Ralph et al. 1991; Raphael 1988). Many of our surveys were concentrated on private or state lands in the North Coast, Central Coast, and North Cascades Subregions of Oregon, where there had been few or no prior surveys of red tree voles. However, we also searched for tree voles in many other areas in Oregon and California where there were prior records of tree voles, including some areas on Forest Service or BLM lands where pre-project surveys had already been conducted.

Because the retrospective and targeted surveys included a mixture of different methods that were not appropriate for minimum density estimates, we summarized the data from these surveys based on the number of nests located per unit of survey effort (person-hours). For each area surveyed, we classified vegetation as old-growth forest (>200 years old), mature forest (80 to 200 years old), young forest (<80 years old), or rural-agricultural developments. Rural-agricultural developments consisted mainly of highly modified forest habitats intermixed with Christmas tree farms, pastures, vineyards, and residential developments.

California Department of Fish and Game Database

The California Department of Fish and Game tree vole database contained 448 records of tree vole specimens or nests located during surveys in 1973–2000 (Gould 2005). Because multiple tree voles or vole nests located in the same general area were lumped together as individual records in the database, we examined the original data and constructed a new database that included 1,323 records of individual nests or voles, including 49 records of red tree voles and 1,274 records of Sonoma tree voles. The majority of locations were on private (88.9 percent) or state (7.0 percent) lands, with the remainder on federal (3.7 percent), county (0.1 percent), or tribal lands (0.3 percent). Most locations (1,132) were documented during surveys in which private contractors or employees of private timber companies searched for vole nests while walking through proposed harvest areas on non-federal lands (Humboldt Redwood Company 2009, Thompson and Diller 2002, Wooster and Towne 2002). A small subset of the locations (n = 107) were documented by graduate students who studied tree voles (Meiselman and Doyle 1996, Murray 1995, Zentner 1977). The data consisted mainly of nest observations but also contained 39 records of tree voles captured in pitfall traps, 15 voles captured by climbers, and 10 voles observed by a private contractor who probed nests with a long pole.

Elevation and Tree Voles

We used logistic regression (Procedure GLIMMIX in SAS®; Cary, N.C.) to model relationships between presence of tree voles and elevation. For this analysis, we used the data from owl pellets, pre-project surveys, and random plot surveys. In the analysis of pellet data, the nominal variable was presence or absence of tree voles in the sample from each owl territory. In the analysis of pre-project and random plot surveys the nominal variable was presence or absence of tree vole nests in each polygon or plot that was surveyed. We also plotted the raw data from each data source to see if there were any obvious relationships between elevation and the proportion of tree voles in owl diets or minimum density of vole nest trees in survey plots.

Results

Oregon Pellet Data

Red tree voles occurred in the diet at 647 (47 percent) of 1,386 spotted owl territories examined in 1970–2012 (fig. 1-2). The average percentage of red tree voles in the diet was 7.1 ± 2.6 percent, based on the grand mean from the six subregions in which red tree voles were detected (table 1-1). Red tree voles were most common in owl diets in the Central Coast, South Coast, and Central Cascades Subregions, and were uncommon or absent in diets of most spotted owls in the North Coast, North Cascades, and East Cascades Subregions (fig. 1-2; table 1-1). In the Interior Southwest Subregion, tree voles were relatively common in owl diets in Josephine

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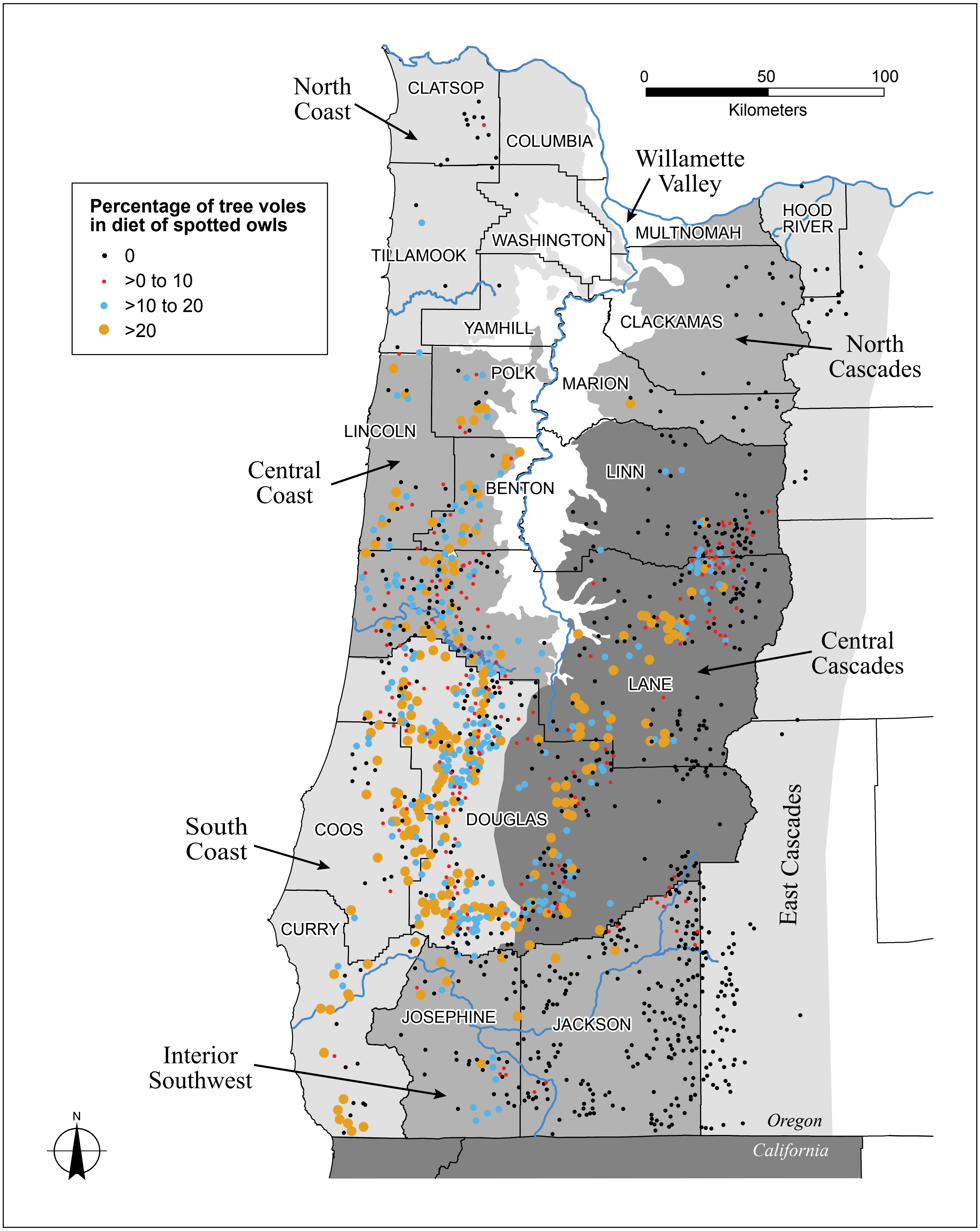

Figure 1-2—Percentage of red tree voles (percentage of prey numbers) in diets of northern spotted owls in Oregon. Size and color of circles indicates percentage of tree voles in the diet at each of 1,386 owl territories sampled in 1970–2009.

County, but were absent in owl diets in most of Jackson County except for the area north of the Rogue River and Middle Fork Rogue River (fig. 1-2). Although diets of spotted owls in the North Coast Subregion contained few tree voles, our sample from that area was small because there were few spotted owls in the young forests that covered much of that subregion (fig. 1-2) (Forsman 1988). For that reason, we did not feel that the pellet data adequately reflected tree vole distribution or relative abundance in the North Coast Subregion. In those subregions where they occurred, the percentage of red tree voles in the diet was highly variable among owl territories, suggesting high local variation in abundance of voles, or variation in prey selection among owls (table 1-1).

Table 1-1—Abundance of red tree voles in diets of northern spotted owls at 1,386 owl territories in Oregon, subdivided by geographic subregions, 1970–2009

Geographic subregion	Percentage of territories with tree voles in diet[a]	Percentage of tree voles in diet		
		$\bar{x}$ ± SE	Median	Range
North Coast	19	2.1 ± 1.1	0	0–18
Central Coast	66	12.3 ± 1.0	11.1	0–100
South Coast	73	16.6 ± 0.8	16.7	0–100
North Cascades	4	1.3 ± 1.3	0	0–33
Central Cascades	46	8.8 ± 0.7	0	0–100
East Cascades	0	0	0	0
Interior Southwest	13	2.1 ± 0.5	0	0–67
Grand mean ± SE[b]	37 ± 15	7.1 ± 2.6		

[a] The number of spotted owl territories sampled in each subregion was: North Coast (n = 21), Central Coast (n = 208), South Coast (n = 387), North Cascades (n = 25), Central Cascades (n = 409), East Cascades (n = 80), Interior Southwest (n = 256) . The mean percentage of prey numbers that were tree voles is indicated by $\bar{x}$ ± SE.

[b] Grand mean was estimated based on data from the six subregions in which tree voles occurred in the diet.

California Pellet Data

Of 245 spotted owl territories sampled in the Green Diamond Study Area in 1989–2004, 123 (50.2 percent) had tree voles in the diet (fig. 1-3) (Green Diamond Resource Company 2006). Of 3,056 prey items in the total sample, 497 (16.3 percent) were tree voles. The sample included owl territories both north and south of the Klamath River, the putative dividing line between the ranges of the red tree vole and Sonoma tree vole (fig. 1-3; Blois and Arbogast 2006, Murray 1995). The majority of owl territories in this sample were in relatively young forests regenerating on lands that had been clearcut during the previous century (Thome et al. 1999).

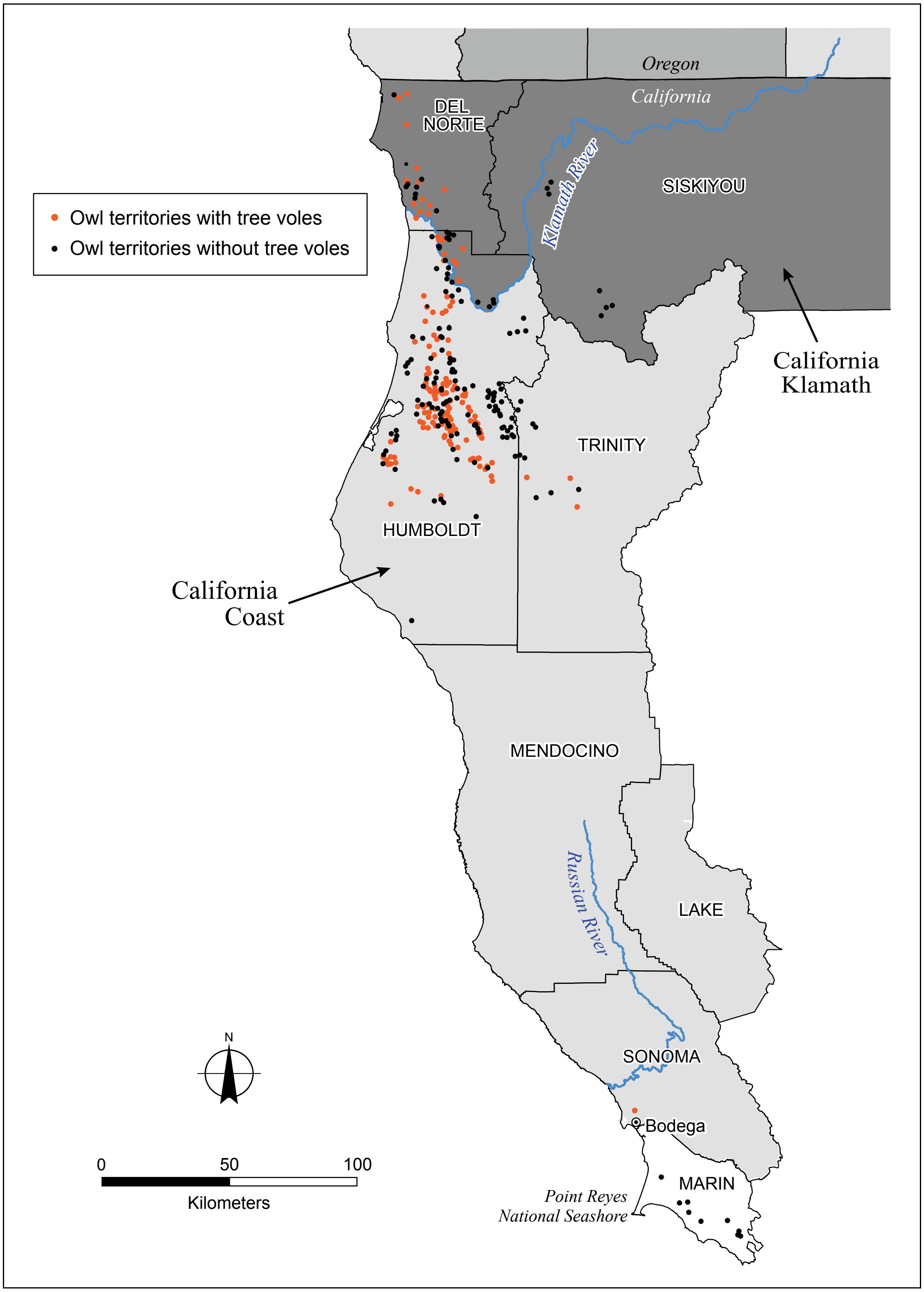

Figure 1-3—Distribution of tree voles in northwestern California based on occurrence in diets of northern spotted owls or barred owls, 1990–2010. Data courtesy of Lowell Diller at Green Diamond Resource Company; Alan Franklin at the National Wildlife Research Center, USDA Animal and Plant Inspection Service; Kristin Schmidt at Redwood National and State Parks; Katie Fehring at Point Reyes National Seashore; and Stan Moore at Bodega, California.

Pellets collected in the Northwestern California Study Area in 1987–2003 included 1,051 prey items, 70 (6.7 percent) of which were Sonoma tree voles. Tree voles were detected in the diet at 34 (43 percent) of the 79 spotted owl territories sampled (fig. 1-3). The average percentage of tree voles in the diet was 5.9 ± 1.0 percent. This sample extended the known range of the Sonoma tree vole 14 km east into central Trinity County (fig.1-3).

The pellet sample from Redwood National and State Parks was collected in 1997–2009 and included 37 prey items from three owl territories in Del Norte County and 77 prey items from eight owl territories in Humboldt County. Of 114 prey items in the combined sample, 16 (14.0 percent) were tree voles. Tree voles were detected in one (33.3 percent) of the territories in Del Norte County and five (62.5 percent) of the territories in Humboldt County (fig. 1-3). The average percentage of tree voles in the diet was 4.2 ± 4.2 percent in Del Norte County, and 17.1 ± 7.0 percent in Humboldt County. Ten of the 11 owl pairs surveyed inhabited mixed-species forests of mature or old-growth Douglas-fir, coast redwood, and western hemlock, and one pair inhabited a mixed-species forest of oak and Douglas-fir.

The pellet collection from southern Sonoma County included 29 prey items collected in 2010 from one spotted owl territory at Fay Creek, 2.6 km west and 1.6 km north of Bodega. Of 29 prey in the latter sample, two (7 percent) were Sonoma tree voles. This location was the southernmost record of a Sonoma tree vole in any of the data sources that we examined. The sample of pellets from spotted owls at Point Reyes National Seashore in Marin County included 357 prey items collected from 13 spotted owl territories in 2005. This area was approximately 30 km south of the known range of the Sonoma tree vole. As expected, the sample included no tree voles.

The southermost record of a tree vole in California was from an owl pellet at Fay Creek near Bodega.

Museum Specimens

Of 1,653 tree vole specimen records from museums or field notes of early collectors, most (68 percent) were collected or observed by biologists who climbed trees to chase voles from their nests (table 1-2; app. 3). The remainder were collected using a variety of methods, including capture by loggers (8 percent), capture in pitfall traps, live traps, or snap traps (11 percent), born in captivity to mothers that were pregnant at capture (3 percent), born to parents that were bred in captivity (7 percent), and unknown or miscellaneous methods (3 percent; table 1-2). The geographic distribution of museum specimens was non-uniform for both the red tree vole (fig. 1-4) and Sonoma tree vole (fig. 1-5). To some extent, this distribution reflected biased sampling efforts by collectors, who

Of 1,653 tree vole specimen records from museums or field notes of early collectors, most (68 percent) were collected or observed by biologists who climbed trees to chase voles from their nests.

Table 1-2—Number of tree vole specimens documented from museum specimens, field notes of collectors, or our captures

Age and collection method	Females	Males	Unknown sex
Adults and subadults			
Tree climbing[a]	545	248	55
Captured by loggers[b]	52	57	0
Pitfall traps	32	94	0
Other[c]	51	26	3
Juveniles			
Tree climbing[d]	149	165	79
Captured by loggers	6	3	1
Pitfall traps	1	6	1
Wildbred (born in captivity)[e]	21	24	14
Bred in captivity	49	57	8
Unknown capture method	4	1	0
Age unknown			
Tree climbing	9	10	21
Captured by loggers	3	1	0
Pitfall traps	2	7	20
Other[f]	0	0	10
Totals	924	699	212

[a] Included 595 specimens (424 female, 171 male) in museums, 63 specimens described in collector's field notes, and 190 specimens that we captured (85 female, 63 male) or observed but did not capture (n = 42) in 1990–2011.
[b] Collected from freshly felled trees except for two specimens that were killed when a hollow tree was blasted apart with dynamite.
[c] Included live traps (n = 2), roadkill (n = 4), visual sightings (n = 1), nests poked apart from the ground (n = 42), and unknown (n = 31).
[d] Included 370 specimens in museums or described in collector's notes (146 female, 163 male, 61 unknown sex) and 23 specimens that we captured or observed in nests (3 female, 2 male, 18 unknown sex) in 1990–2011.
[e] Born in captivity to mothers that were pregnant when captured.
[f] Included live traps (n = 2), owl pellets (n = 1), visual sightings (n = 3), and unknown (n = 4).

returned to places where they or earlier collectors found voles. This was especially the case regarding the large numbers of voles collected in Oregon near Tillamook, Molalla, Newburg, Corvallis, and Monroe. These locations were all favorite collection sites where Alex Walker (1928, 1930), Doug Bake (Forsman and Swingle 2010), Harry Schoenborn (Maser 1966, Olterman 1972), Stanley Jewett (1920, 1930), Percy Clifton (1960), Chris Maser (1966), and Murray Johnson (Johnson and George 1991, Johnson 1957–1985) focused their collection efforts. In California, the Harry Wilder Ranch near Carlotta in Humboldt County was a favorite collection site that was visited by many early collectors in 1913–1930, including Brazier Howell (1926), Joseph Mailliard (1923), and Seth Benson and Audry Borell (1931). Other popular collection sites in California

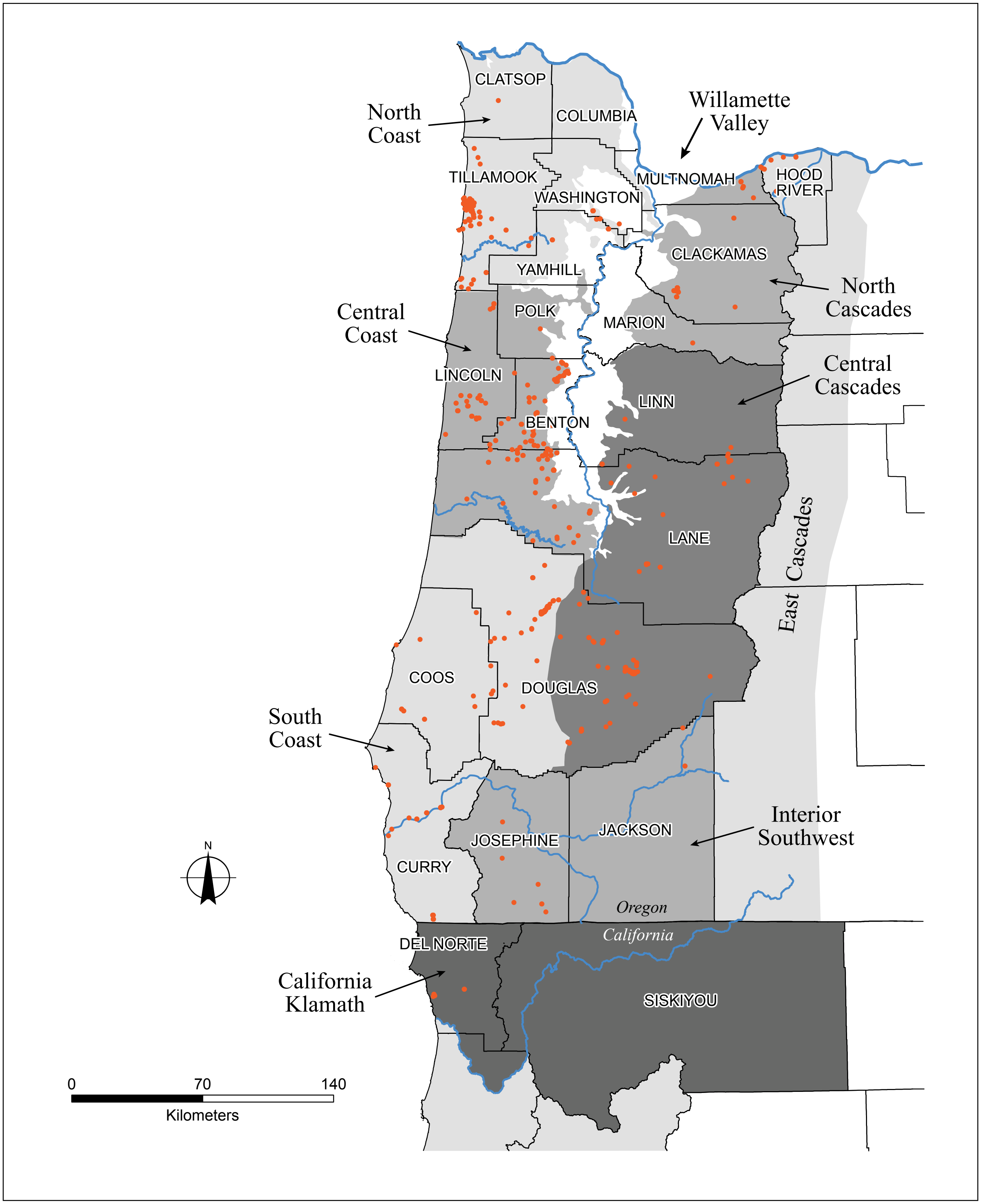

Figure 1-4—Distribution of red tree voles collected or observed in the wild. The sample included 686 museum specimens, 61 specimens described in collector's field notes, and 230 specimens that we captured or observed during studies conducted in Oregon in 1990–2013. Some locations had multiple voles collected at the same location.

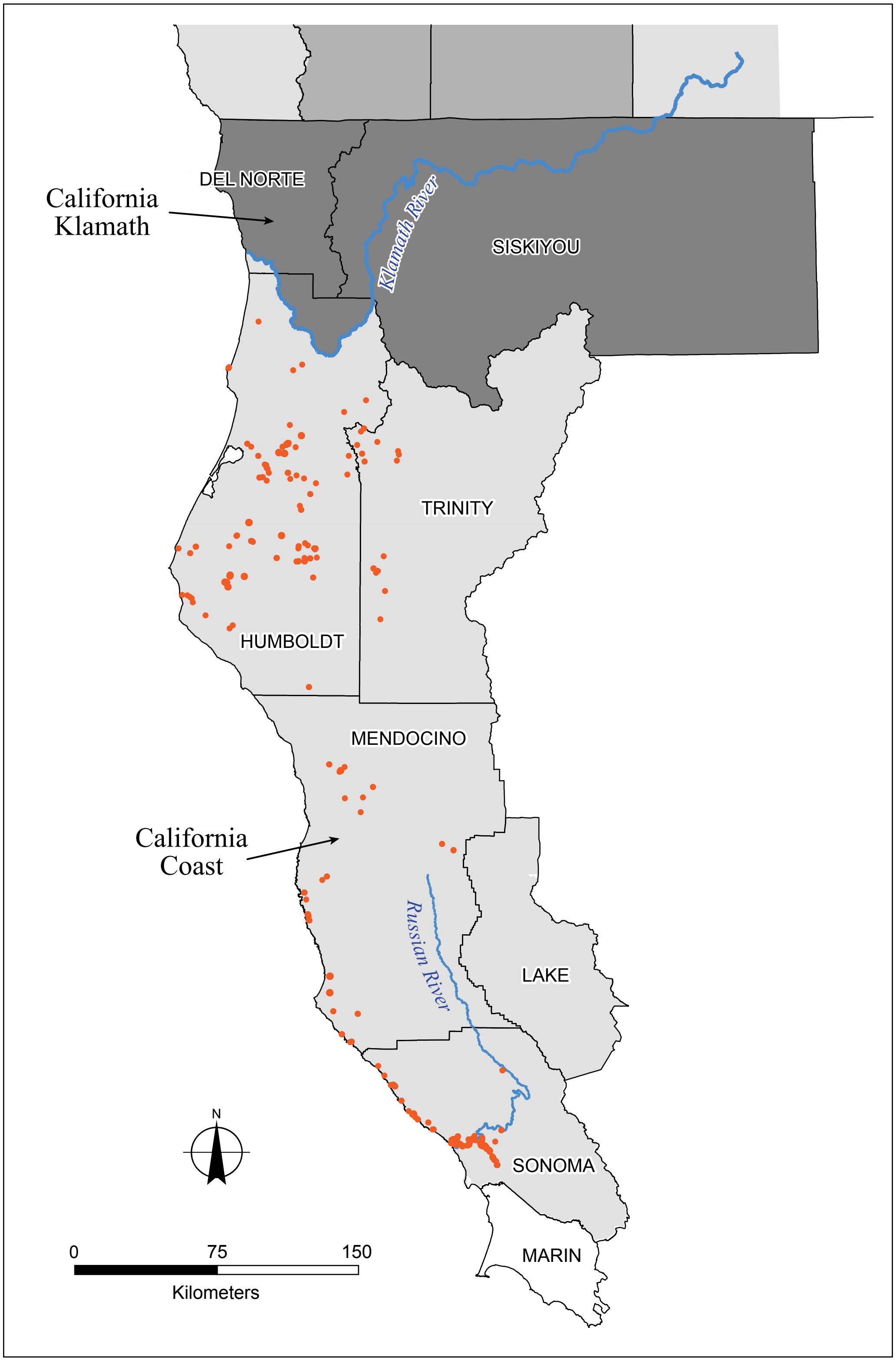

Figure 1-5—Distribution of Sonoma tree voles collected or observed in the wild. The sample included 738 museum specimens, 62 specimens described in collector's field notes, and 3 specimens that we captured and released during studies conducted in California in 2005–2007. Some locations had multiple voles collected at the same location.

Table 1-3—Percentage of tree vole museum specimens captured in different forest age-classes, subdivided by capture method[a]

	Tree climbing[c]	Logging[d]	Pitfall trap	Other[e]
Forest age-class[b]	**(n = 402)**	**(n = 115)**	**(n = 37)**	**(n = 3)**
Clearcut or early seral	0	0	3	0
Young forest	84	1	5	33
Mature forest	6	2	43	33
Old-growth forest	10	97	49	33

[a] Estimates do not include records in which forest age-class was unknown or specimens were captured as juveniles or born in captivity.
[b] Approximate forest age-classes in years were clearcut or early seral (0 to 15 years), young forest (>15 to 80 years), mature forest (>80 to 200 years), and old-growth forest (>200 years).
[c] Included 393 individuals captured by hand and 9 individuals captured when snap traps were placed on top of nests.
[d] Included 113 individuals captured by hand and 2 individuals captured when a hollow tree was blasted apart with dynamite.
[e] Included 2 voles captured in live traps on the ground, and 1 vole captured by hand inside a cabin.

were Arcata, Bridgeville, the lower Russian River, and the coastal headlands between Jenner and Fort Bragg. These areas were visited at different times by many early collectors, including Seth Benson, Audry Borell, Brazier Howell, Joseph Mailliard, Walter Dalquest, Don Roberts, William Hamilton III, Percy Clifton, and Murray Johnson. The most prolific and persistent collector at many of the California collection sites was Murray Johnson, who made annual collecting trips in 1969–1985 to collect Sonoma tree voles on the lower Russian River and many other areas in Sonoma and Mendocino Counties. Murray collected at least 150 tree voles on these trips (Johnson 1957–1985).

Some large areas in western Oregon and northwestern California had no museum records of tree voles, particularly in the North Coast Subregion of Oregon, where most locations were concentrated in southern Tillamook County and one small area in the Chehalem Mountains north of Newberg along the border of Washington and Yamhill Counties (fig. 1-4). We found only one historical record of a tree vole in Clatsop County, and no records in Columbia County, western Multnomah County, and most of Washington, Yamhill, and Polk Counties (fig. 1-4). It is unclear if the absence of historical records of tree voles in these areas was because tree voles were not present before the arrival of European settlers or because tree voles were eliminated from these areas before anyone was paying attention; we suspect the latter. Forests in Clatsop, Columbia, Washington and western Multnomah Counties were mostly harvested or burned in the late 1800s or early 1900s, long before any serious effort was made to document the mammalian fauna of the region (fig. 1-6).

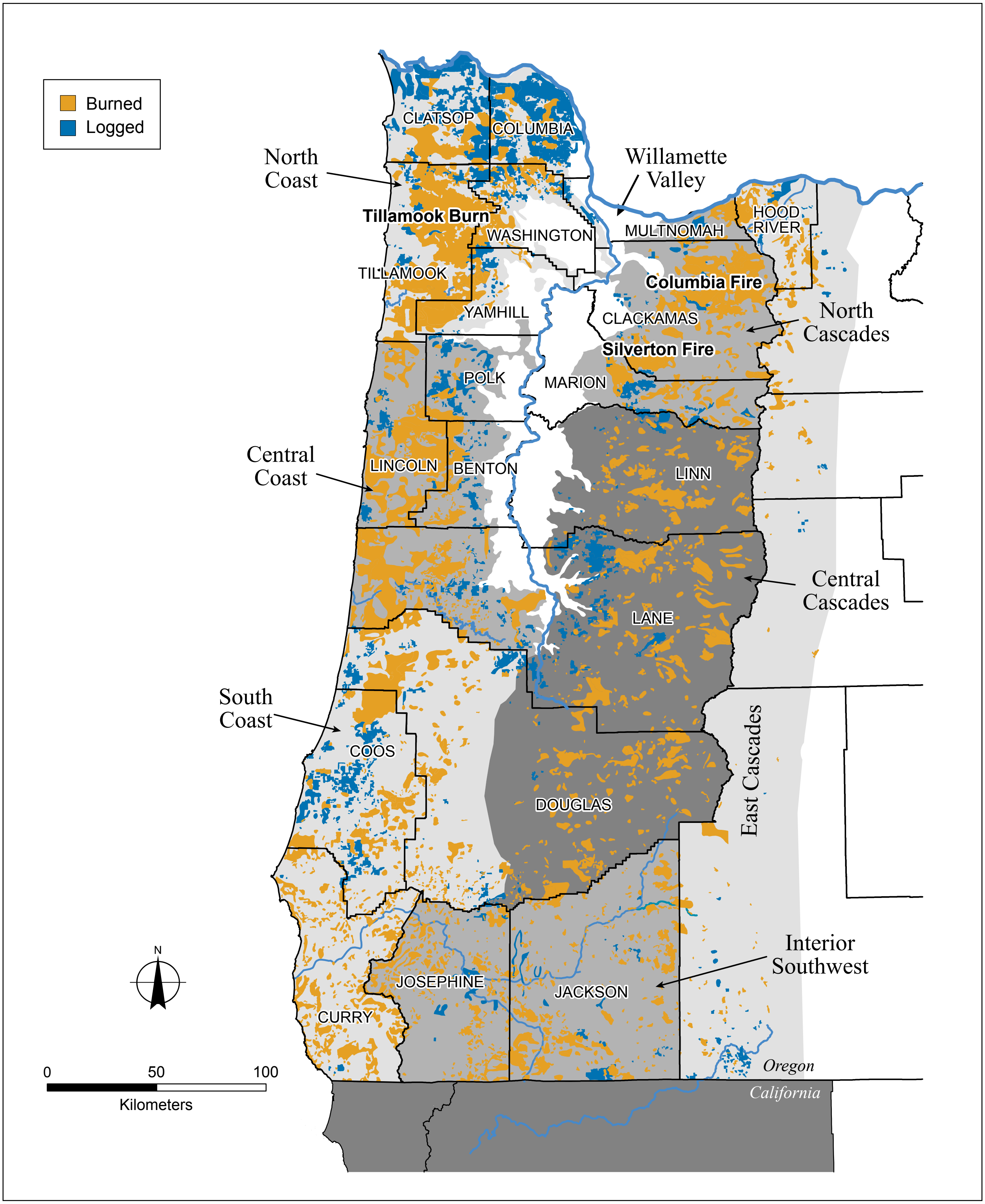

Figure 1-6—Areas logged or burned during the late 1800s to mid-1900s in western Oregon.

The relative number of non-juvenile males and females in museum samples varied with method of capture ($\chi^2 = 96.4$, df = 3, $P < 0.001$). Adult females predominated in collections from tree climbers, young males predominated in collections from pitfall traps, and sex ratios were nearly equal in samples collected by loggers (table 1-2). In contrast, relative numbers of juvenile males and females captured in nests or born to females that were pregnant at capture, did not differ, regardless of the method of capture ($\chi^2 = 4.6$, df = 3, $P = 0.220$, table 1-2). Another noticeable difference in samples collected using different methods was that the majority of specimens collected by climbers were in young forests whereas specimens from loggers and pitfall traps were mostly collected in mature and old-growth forests ($\chi^2 = 432$, df = 9, $P < 0.001$, table 1-3).

Pre-Project Surveys and Strategic Surveys

The distribution and minimum density of nest trees located in pre-project and strategic surveys indicated that red tree voles were most common in the Central Cascades, Central Coast, Interior Southwest, and South Coast Subregions, and were uncommon or rare in the North Coast, North Cascades, and California Klamath Subregions.

Red tree vole nests were found in 28 percent of 4,415 pre-project survey polygons (fig. 1-7) and 36 percent of 423 strategic survey polygons (fig. 1-8). When we excluded surveys in areas outside the range of the tree vole, the percentage of polygons in which surveyors detected ≥1 tree vole nest increased to 37 percent in 3,234 pre-project surveys and 43 percent in 348 strategic surveys. The distribution and minimum density of nest trees located in these surveys indicated that red tree voles were most common in the South Coast, Central Cascades, Central Coast, Interior Southwest, and South Coast Subregions, and were uncommon or rare in the North Coast, North Cascades, and California Klamath Subregions (fig. 1-7; table 1-4). All estimates of mean minimum nest tree density from pre-project surveys (table 1-5) were much lower than estimates from random plot surveys. In the Interior Southwest, the distribution of pre-project surveys in which vole nests were detected followed the same pattern as in the analyses of owl pellets and random plots, with the eastern and southern edge of the range roughly following the Applegate River north to the Rogue River, and then east along the north side of the Rogue River and Middle Fork of the Rogue River in northeastern Jackson County (figs. 1-7, 1-8). In the North Coast Subregion, no red tree vole nests were detected in any of the 87 pre-project surveys, suggesting that voles were absent from most areas. However, red tree voles were detected in 37 percent of 35 strategic-survey polygons that targeted old forests on BLM lands in the Nestucca River drainage, indicating that there were still local populations present in some areas in southern Tillamook County (fig. 1-8).

In the California Klamath Subregion, red tree vole nests were detected in only 14 (8 percent) of 167 pre-project surveys and 9 (19 percent) of 48 strategic surveys. The distribution of survey plots in which nests were detected indicated that the

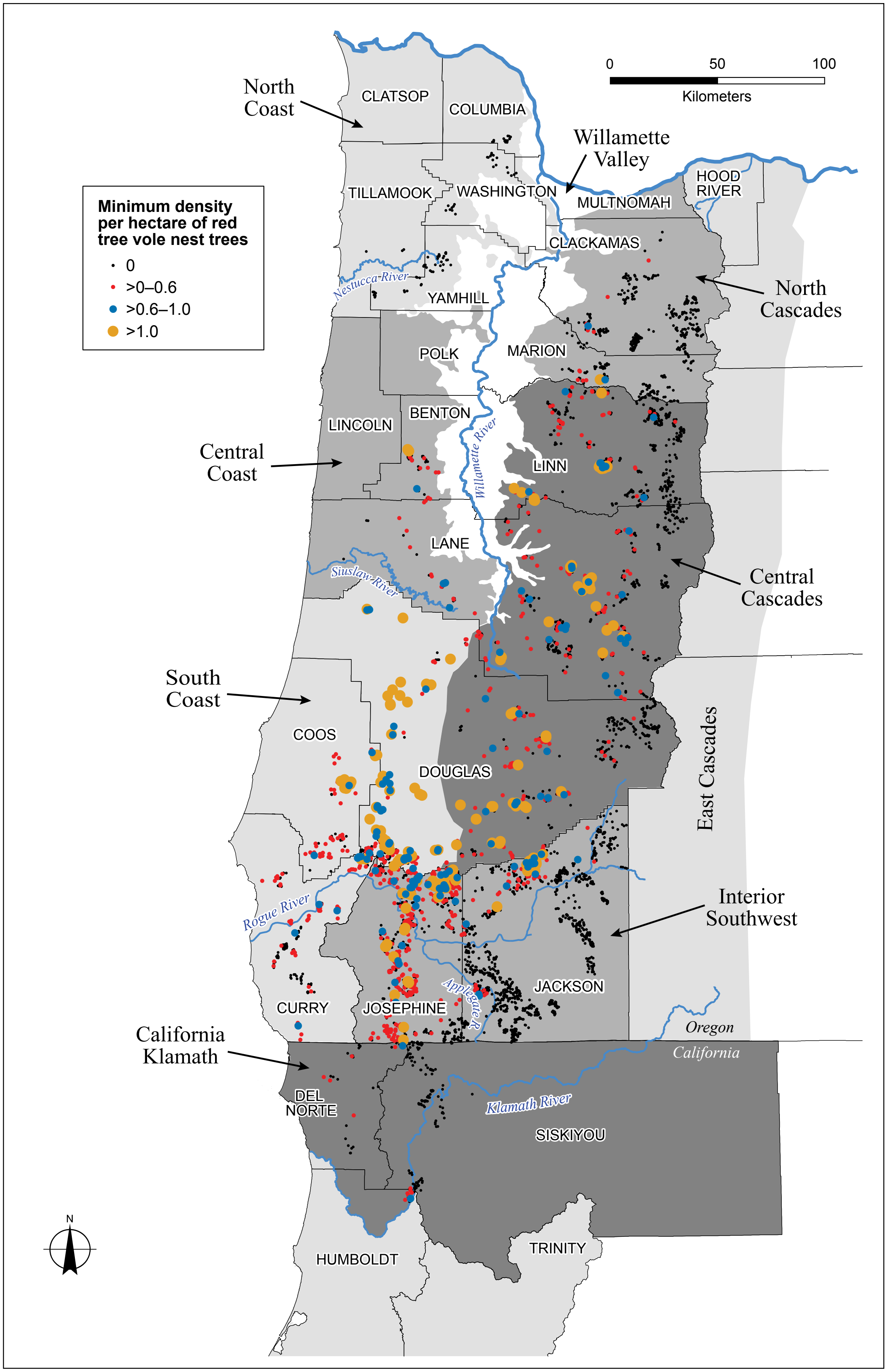

Figure 1-7—Distribution and relative abundance of red tree vole nest trees detected in 4,415 pre-project surveys in 1995−2010. Size and shade of symbols indicates the estimated minimum number of tree vole nest trees per hectare in each survey polygon. Estimates were based on all tree vole nest trees detected, regardless of nest occupancy status.

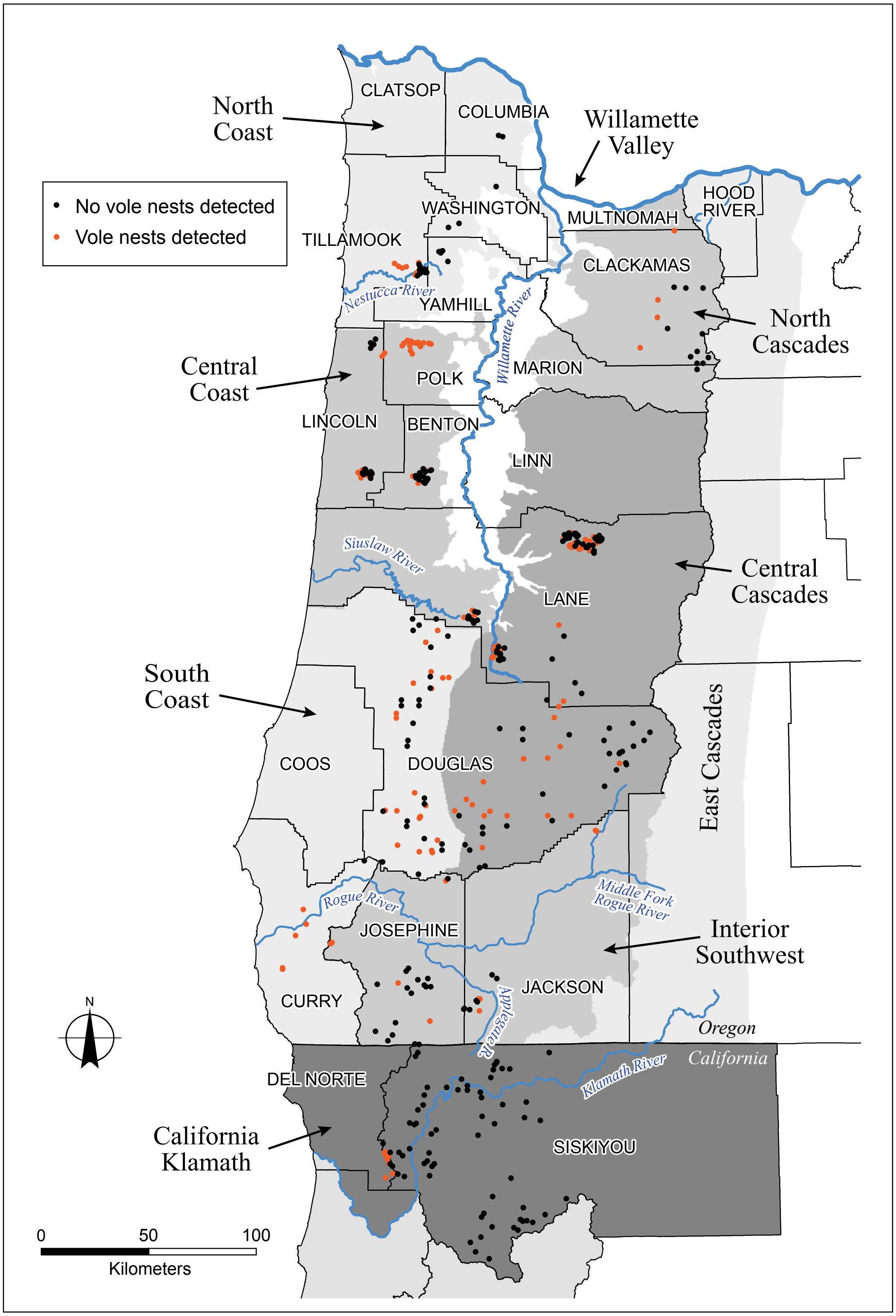

Figure 1-8—Locations of 423 red tree vole strategic survey sites in western Oregon and northwestern California, 1997–2006. Orange dots indicate sites with tree vole detections and black dots indicate sites without tree vole detections.

Table 1-4—Estimated mean minimum density of trees per hectare (ha) containing nests of red tree voles based on pre-project surveys in different geographic subregions of Oregon and California, 1995–2010[a]

		Trees per ha with tree vole nests ($\bar{x}$ ± SE)[a]		
Geographic subregion	**n[b]**	**Recent nests[c]**	**Old nests**	**All nests**
North Coast	86	0	0	0
Central Coast	64	0.11 ± 0.03	0.05 ± 0.01	0.17 ± 0.04
South Coast	430	0.13 ± 0.02	0.12 ± 0.02	0.28 ± 0.03
North Cascades	349	0.02 ± 0.01	0.01 ± 0.03	0.02 ± 0.01
Central Cascades	1,119	0.09 ± 0.01	0.10 ± 0.01	0.19 ± 0.02
Interior Southwest	1,135	0.07 ± 0.01	0.07 ± 0.01	0.17 ± 0.01
California Klamath	51	0.03 ± 0.01	0.02 ± 0.01	0.08 ± 0.02
Total	3,234	0.08 ± 0.01	0.08 ± 0.01	0.17 ± 0.01

[a] Estimates excluded surveys in which the survey polygon was <0.6 ha, or in which ≥50% of the potential nests were not climbed to confirm occupancy. If there were multiple nests in the same tree the count was based on the status of the most recently occupied nest.

[b] The number of pre-project surveys conducted in each subregion is indicted by n.

[c] Recent nests included occupied nests as well as nests that had been recently occupied, as evidenced by the presence of green cuttings or green resin ducts.

Table 1-5—Estimated mean minimum density of trees per hectare (ha) containing nests of red tree voles in different forest size-classes based on 2,661 pre-project surveys in western Oregon and northwestern California, 1995–2010

		Trees per ha with tree vole nests ($\bar{x}$ ± SE)[a]		
Forest size-class (dbh in cm)	**n[b]**	**Recent nests[c]**	**Old nests**	**All nests**
2–13	5	0	0	0
>13–23	17	0.11 ± 0.04	0.10 ± 0.06	0.21 ± 0.08
>23–53	711	0.05 ± 0.01	0.07 ± 0.01	0.12 ± 0.01
>53–81	1,239	0.07 ± 0.01	0.08 ± 0.01	0.17 ± 0.02
>81	689	0.15 ± 0.01	0.12 ± 0.01	0.29 ± 0.02

[a] If there were multiple vole nests in the same tree, count was based on the status of the most recently occupied nest.

[b] The number of plots sampled in each forest age-class is indicated by n. We excluded plots if they fell outside the range of the species or if surveyors did not report the forest size-class.

[c] Recent nests included occupied nests as well as nests that had been recently occupied, as evidenced by the presence of green cuttings or green resin ducts.

range of the red tree vole in this subregion included Del Norte and Humboldt Counties north of the Klamath River, and the western edge of Siskiyou County (fig. 1-8). When we restricted the sample to the latter area (58 pre-project polygons and 11 strategic polygons), the percentage of plots with ≥1 nest detected was 34 percent in pre-project surveys and 60 percent in strategic surveys. The high estimate from strategic surveys was inflated because 9 of the strategic survey locations were selected because they were in old forests where tree voles had previously been located by researchers from Humboldt State University (Biswell et al. 2004).

Random Plot Study

Of the random plots within the range of the red tree vole, 29 percent of 1-ha plots and 43 percent of 2-ha plots had ≥1 tree vole nest detected (fig. 1-9). The percentage of 1-ha plots and 2-ha plots with ≥1 nest tree detected was highest in the South Coast, Central Coast, and Central Cascades Subregions, and lowest in the California Klamath, North Coast, North Cascades, and Interior Southwest Subregions (table 1-6). In Oregon, the mean minimum density of trees containing tree vole nests was lowest in the North Cascades, Interior Southwest, and North Coast Subregions, and highest in the South Coast, Central Coast, and Central Cascades Subregions (table 1-7). Estimates of mean minimum nest tree density were similar regardless of whether we used 1-or 2-ha plots (table 1-7). Of 442 trees in which vole nests were detected in the combined sample of 1- and 2-ha plots, the majority (62 percent) contained old, apparently unoccupied nests, and the rest (38 percent) contained nests that were either occupied or recently occupied. The mean minimum density of trees containing red tree vole nests in the California Klamath Subregion was similar to the estimate from the adjacent Interior Southwest Subregion in Oregon (table 1-7).

There was a consistent pattern of increasing mean minimum nest tree density with increasing forest size-class, regardless of whether we used 1-ha or 2-ha plots (table 1-8). The mean minimum density of nest trees in old forests was typically 5 to 7 times higher than in young forests (table 1-8).

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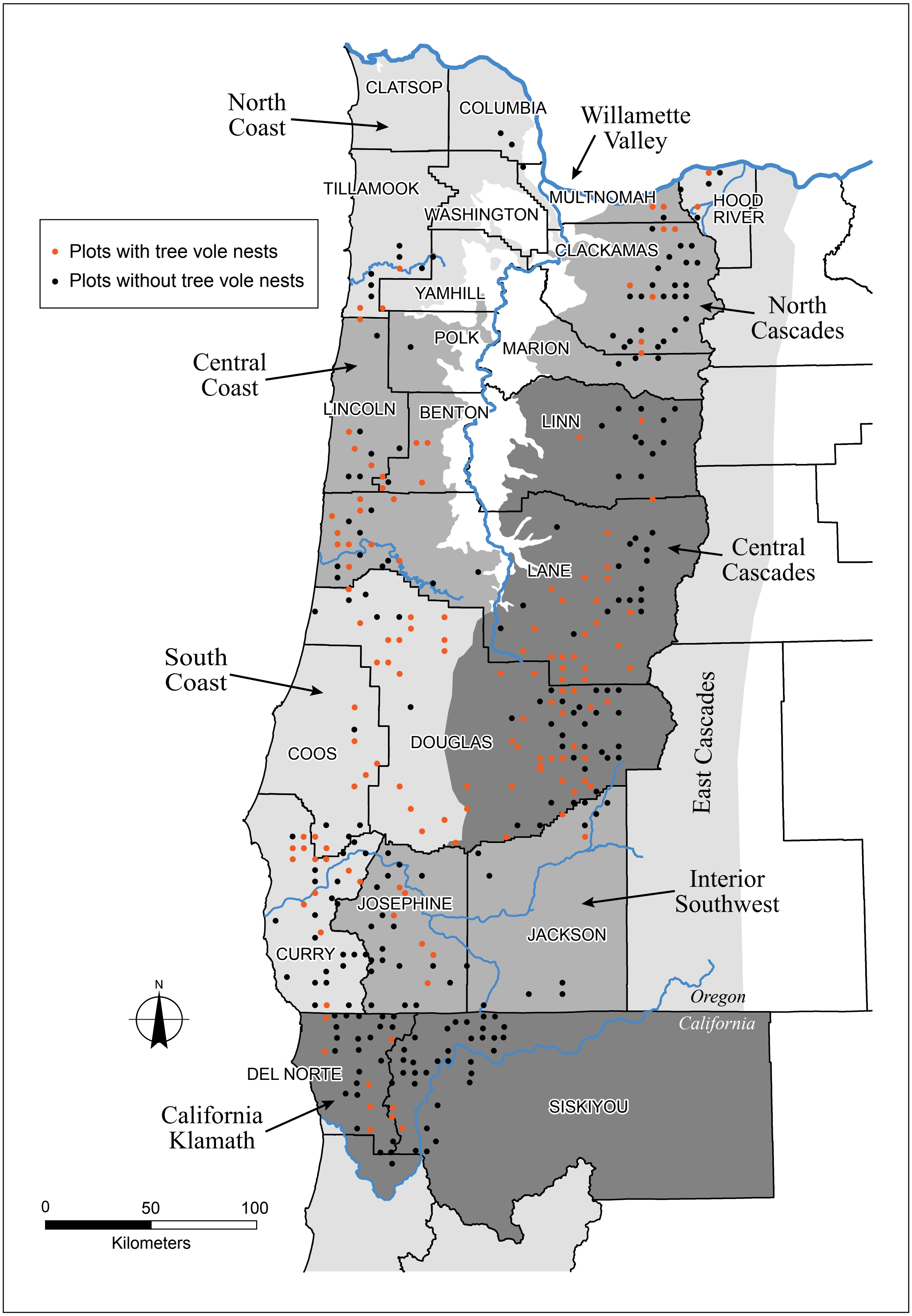

Figure 1-9—Distribution of red tree vole nests located in 354 random plot surveys in western Oregon and northwestern California, 2001–2004. Orange and black circles indicate plots with and without detections of tree vole nests, respectively.

Table 1-6—Number and percentage of 1-ha and 2-ha random survey plots in which red tree vole nests were detected in Oregon and northwestern California, 2001–2004

	1-ha plots		2-ha plots	
Geographic Subregion	Number	Percentage	Number	Percentage
North Coast	13	15	13	23
Central Coast	38	34	38	55
South Coast	61	49	61	57
North Cascades	41	17	41	24
Central Cascades	105	31	104	48
Interior Southwest	32	13	31	23
California Klamath	29	17	29	31
Grand mean ± SE	7	25 ± 5	7	37 ± 6

Table 1-7—Estimated mean minimum density of trees per ha containing nests of red tree voles in different subregions based on the random plot study in western Oregon and northwestern California, 2001–2004[a]

Plot size and geographic subregion	n[c]	Trees per ha with tree vole nests ($\bar{x}$ ± SE)[b]		
		Recent nests	Old nests	All nests
1-ha plots (n = 319):				
North Coast	13	0	0.62 ± 0.54	0.62 ± 0.54
Central Coast	38	0.32 ± 0.12	0.61 ± 0.19	0.92 ± 0.25
South Coast	61	0.54 ± 0.15	0.89 ± 0.23	1.43 ± 0.31
North Cascades	41	0.07 ± 0.05	0.32 ± 0.13	0.39 ± 0.16
Central Cascades	105	0.33 ± 0.08	0.36 ± 0.09	0.70 ± 0.15
Interior Southwest	32	0.09 ± 0.05	0.25 ± 0.13	0.34 ± 0.18
California Klamath	29	0.17 ± 0.11	0.17 ± 0.11	0.34 ± 0.21
Grand mean	7	0.22 ± 0.07	0.46 ± 0.10	0.68 ± 0.15
2-ha plots (n = 207):				
North Coast	9	0	0.17 ± 0.17	0.17 ± 0.17
Central Coast	26	0.23 ± 0.07	0.73 ± 0.20	0.96 ± 0.22
South Coast	34	0.53 ± 0.17	0.76 ± 0.24	1.29 ± 0.34
North Cascades	29	0.07 ± 0.05	0.28 ± 0.11	0.34 ± 0.13
Central Cascades	71	0.35 ± 0.10	0.51 ± 0.12	0.85 ± 0.20
Interior Southwest	21	0.05 ± 0.05	0.19 ± 0.14	0.24 ± 0.19
California Klamath	17	0.09 ± 0.05	0.06 ± 0.06	0.15 ± 0.07
Grand mean	7	0.19 ± 0.07	0.39 ± 0.11	0.57 ± 0.17

[a] Estimates were based on plots that fell within the geographic range of the species and were subdivided based on nest status and on 1-ha versus 2-ha plots.

[b] If there were multiple nests in the same tree the count was based on the status of the most recently occupied nest. Recent nests included occupied nests as well as nests that had been recently occupied, as evidenced by the presence of green cuttings or green resin ducts.

[c] The number of plots surveyed is indicted by n.

Table 1-8—Estimated mean minimum density of trees per ha containing nests of red tree voles in different forest size-classes based on the random plot study in western Oregon and northwestern California, 2001–2004a

Plot size and forest size class (*dbh in centimeters*)	n[c]	Trees per ha with tree vole nests ($\bar{x}$ ± SE)[b]		
		Recent nests	Old nests	All nests
1-ha plots (n = 319):				
2–13	12	0	0	0
>13–23	23	0	0.17 ± 0.17	0.17 ± 0.17
>23–53	70	0.16 ± 0.05	0.14 ± 0.08	0.30 ± 0.12
>53–81	110	0.29 ± 0.08	0.56 ± 0.14	0.85 ± 0.19
>81	104	0.46 ± 0.10	0.70 ± 0.12	1.16 ± 0.17
2-ha plots (n = 207):				
2–13	5	0	0	0
>13–23	10	0	0	0
>23–53	47	0.10 ± 0.03	0.06 ± 0.03	0.16 ± 0.05
>53–81	80	0.28 ± 0.08	0.59 ± 0.14	0.87 ± 0.20
>81	65	0.41 ± 0.12	0.69 ± 0.11	1.10 ± 0.18

[a] Estimates were based on plots that fell within the geographic range of the species and were subdivided based on nest status and on 1-ha versus 2-ha plots.
[b] If there were multiple vole nests in the same tree, count was based on the status of the most recently occupied nest. Recent nests included occupied nests as well as nests that had been recently occupied, as evidenced by the presence of green cuttings or green resin ducts.
[c] The number of plots surveyed is indicted by n.

Retrospective and Targeted Surveys

During 1990–2013, we spent 4,913 hours searching for tree voles at 261 different locations in Oregon and California, including 44 historical locations and 217 targeted locations where there were no historical records of tree voles (table 1-9). The mean number of hours spent searching for and climbing to potential nests in the retrospective and targeted areas was 18.8 ± 2.0 hours (range = 1 to 397 hours). In our retrospective surveys of historical sites, we found evidence of tree voles at or near 66 percent of sites surveyed in the range of the red tree vole (fig. 1-10) and 44 percent of the sites surveyed within the range of the Sonoma tree vole (fig. 1-11). At targeted sites we found evidence of tree voles at 44 percent of 210 sites surveyed in Oregon and 43 percent of 7 sites surveyed in California (table 1-9). In general, the number of nests located per hour of effort during retrospective and targeted surveys was lowest in the North Cascades and North Coast Subregions (table 1-9).

In the North Coast Subregion, most tree vole nests (56 percent) were in remnant patches of old forest or mixed-age stands of young and old forest (38 percent), and most nests were in state parks (31 percent), or on other state or federal lands (63 percent).

In the North Coast Subregion, most tree vole nests (56 percent) were in remnant patches of old forest or mixed-age stands of young and old forest (38 percent), and most nests were in state parks (31 percent), or on other state or federal lands (63 percent). In this subregion we found vole nests at only one of five sites examined on

Table 1-9—Mean number of red tree vole nests located per hour of survey effort during retrospective and targeted surveys of tree voles in western Oregon and California, 1990–2013[a]

Geographic subregion	Retrospective surveys					Targeted surveys				
	n	$\bar{x} \pm$ SE	Median	Effort	Percent with vole nests	n	$\bar{x} \pm$ SE	Median	Effort	Percent with vole nests
North Coast	8	0.09 ± 0.04	0.03	528	50	102	0.03 ± 0.01	0	1,206	12
North Cascades	2	0.15 ± 0.15	0.15	95	50	16	0.14 ± 0.06	0.02	276	50
East Cascades	1	0.29	0.29	21	100	12	0.11 ± 0.03	0.11	200	58
Central Coast	12	0.18 ± 0.07	0.09	422	75	34	0.31 ± 0.06	0.17	707	71
Central Cascades	5	0.22 ± 0.20	0	42	40	30	0.50 ± 0.07	0.42	424	93
South Coast	6	0.64 ± 0.17	0.75	18	83	7	0.43 ± 0.12	0.29	496	100
Interior Southwest	1	0.33	0.33	6	100	9	0.18 ± 0.11	0.09	340	67
California	9	0.21 ± 0.09	0	66	44	7	0.34 ± 0.18	0	66	43
Totals	44	0.25 ± 0.05	0.10	1,198	61	217	0.20 ± 0.02	0	3,715	44

[a] Data are subdivided by geographic subregion in Oregon. Retrospective surveys were conducted at approximate locations where tree voles were observed or collected prior to 1986. Targeted surveys were conducted at non-random locations that we selected to determine if tree voles were present in specific areas. Sample size (n) indicates number of areas surveyed and "Effort" indicates number of person hours spent conducting surveys and climbing trees to examine nests.

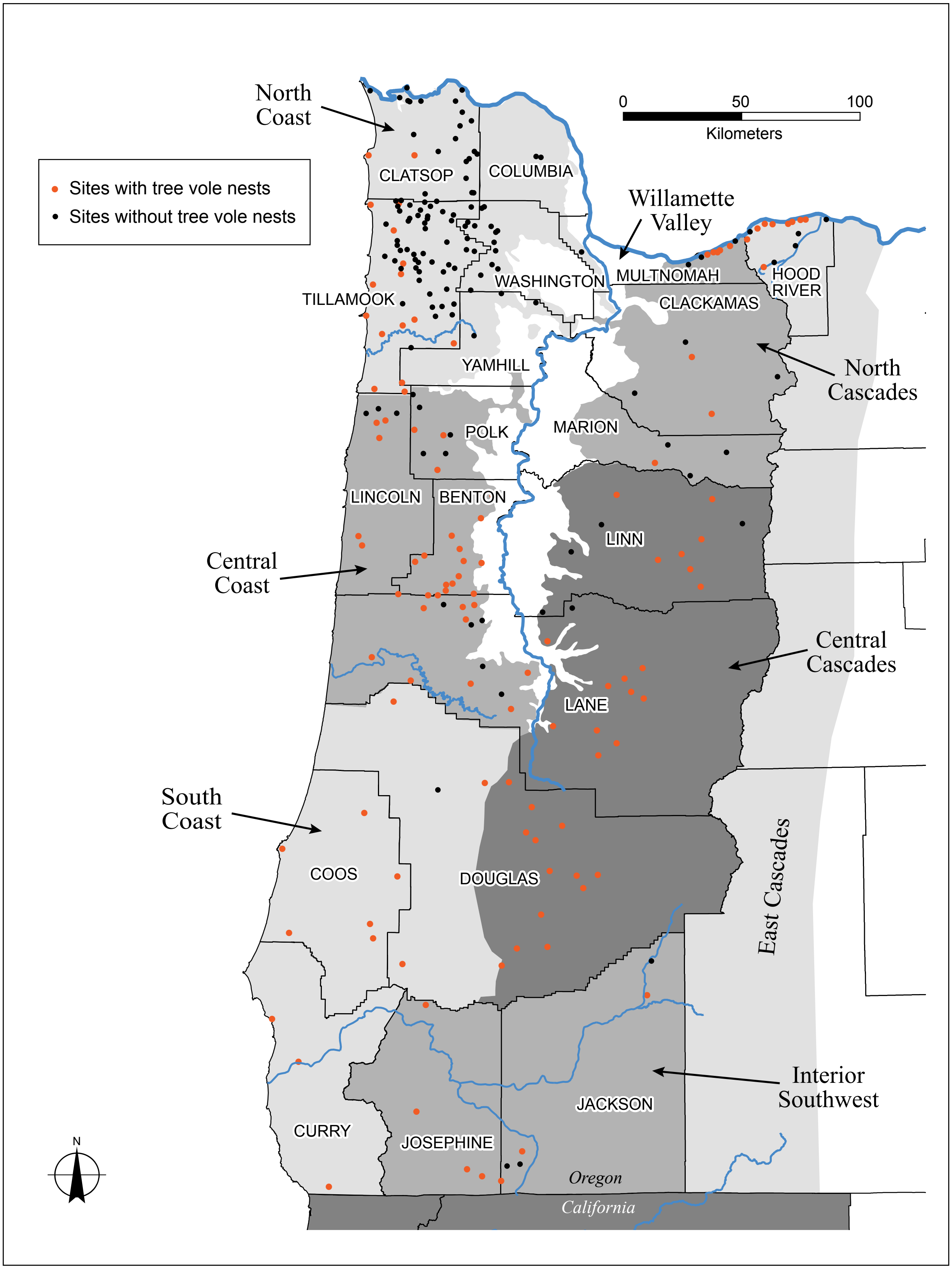

Figure 1-10—Results of retrospective and targeted surveys of red tree voles in Oregon, 2000–2013. Orange and black dots indicate sites with and without vole nest detections, respectively.

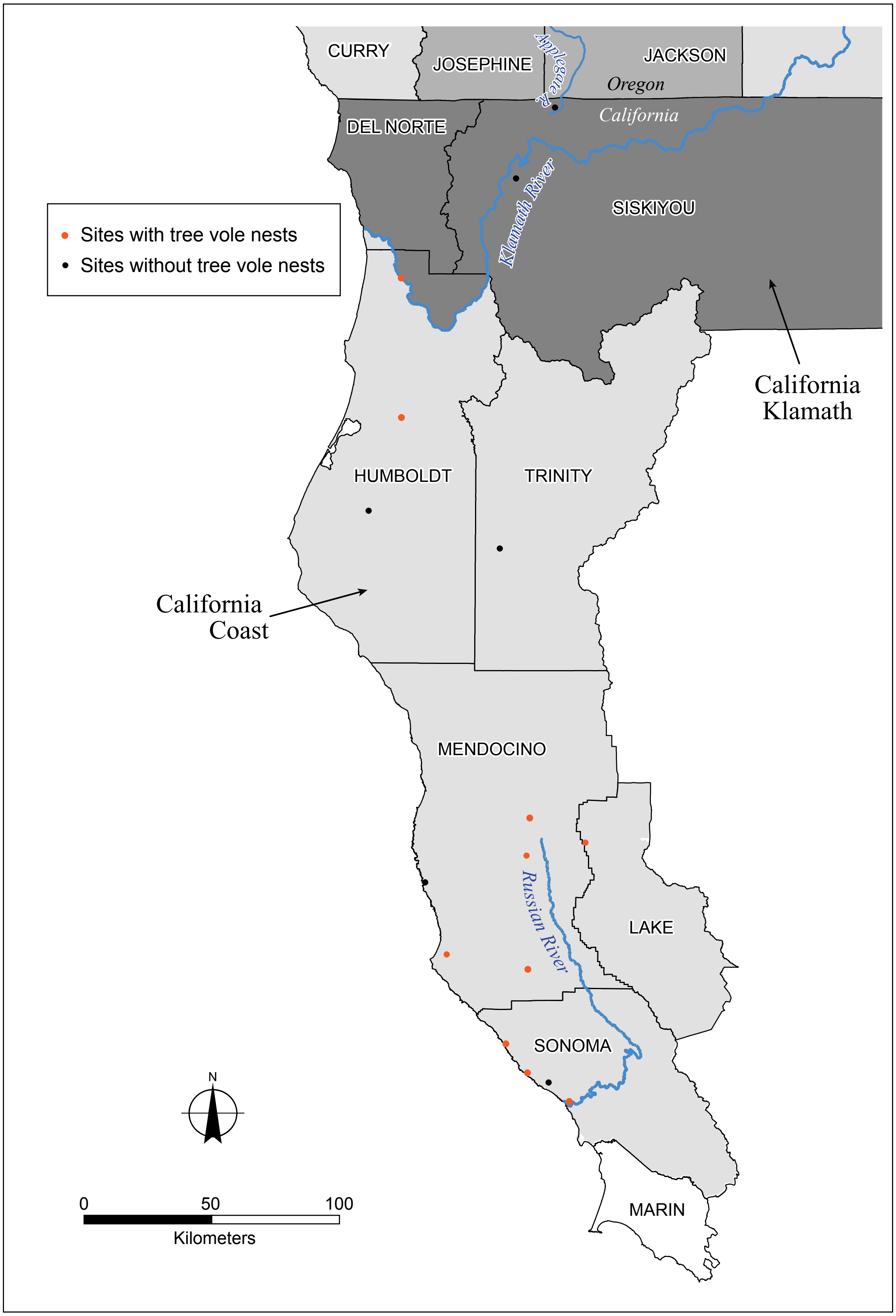

Figure 1-11—Retrospective and targeted surveys of red tree voles and Sonoma tree voles in California, 2005–2010. Locations with and without detections of tree voles or their nests are indicated by orange and black dots, respectively.

private lands, and the 94 locations where we found no evidence of voles included nine locations in old forest and 85 locations in young forest or recently harvested areas (fig. 1-10).

In the Northern Cascades Subregion, we found tree vole nests in most of the drainages in the Columbia River Gorge between Portland and Hood River, and in the headwaters of Lake Branch, a tributary of the West Fork of Hood River (Forsman et al. 2009a) (fig. 1-10). Although the Lake Branch location technically fell on the east slope of the Cascades, vegetation in the upper Lake Branch drainage was predominantly western hemlock and Douglas-fir forest, typical of red tree vole habitat on the west slope of the Cascades. At other locations surveyed in the North Cascades, we found evidence of red tree voles at only 50 percent of the areas surveyed, and the number of nests located per hour of survey effort was considerably lower than in most other subregions except for the North Coast and East Cascades (fig. 1-10; table 1-9). At the only location in the North Cascades where large numbers of red tree voles were collected prior to 1984 (Schoenborn Ranch south of Molalla), we found no evidence of tree voles (fig. 1-10). Most of the Schoenborn Ranch area had been harvested and converted to young forest and rural residential property after tree voles were collected there in 1954–1965 (Maser 1966, Olterman 1972).

In the Central Coast Subregion, we found tree vole nests at 75 percent of the historical sites and 71 percent of the targeted sites surveyed (fig. 1-10; table 1-9). Most of the retrospective and targeted surveys with evidence of red tree voles in the Central Coast Subregion were in tracts of old forest (62 percent) or in young forests adjacent to older forest (38 percent). Occupancy of some locations in young forest appeared to be highly ephemeral. For example, we found four occupied nests in a 35-year-old plantation of Douglas-fir in Benton County in 2004, but we found no occupied nests when we resurveyed the same area on four different occasions in 2007–2011.

One of the more interesting retrospective surveys in the Central Coast Subregion was a resurvey of the study area where Chris Maser (1966) conducted a population density study of red tree voles. The original Maser study plot was a 12.4-ha forest of 14- to 49-year-old Douglas-fir and Oregon white oak adjacent to a pasture on Nichols Creek, 7.2 km southwest of Monroe in Benton County. The forest on Maser's study plot was the result of natural reseeding of an area that had been cleared for pasture in 1918. Maser (1966) estimated the minimum number of tree voles present (12 adults, 28 juveniles) by visually searching all trees in the plot, climbing every tree in which a nest was detected, and dissecting each nest to capture any voles that were present. We visited the same area in 2006 and found that the plot sampled by Maser had been clearcut in about 1988 and was covered by an even-aged stand of 15-year-old Douglas-fir. In addition, the pasture adjacent to Maser's old study plot had been planted with Douglas-fir in 1969 and was covered by a stand of 36-year-old trees that had been commercially thinned in 2005, a year before our resurvey. We found no vole nests in the 15-year-old trees on the old study plot, but we did find one occupied nest and several unoccupied nests in the recently thinned stand that was growing on the old pasture site. When we resurveyed this area in 2011 and 2013, we found no evidence of tree voles, and the stand was clearcut in 2016.

Another area where Maser (1966) and others (Brown 1964, Johnson and George 1991, Wight 1925) found concentrations of red tree voles in the Central Coast Subregion was the McDonald-Dunn Research Forest 7.6 km northwest of Corvallis in Benton County. We conducted numerous surveys on this area in 1990–2012 and found tree voles or their nests at 16 of 20 locations surveyed, including 13 locations in old forest and four locations in young forests. Vole nests on McDonald-Dunn Forest were concentrated in a few widely spaced locations, suggesting that distribution of voles on the 4550-ha forest was not uniform.

In the South Coast Subregion of Oregon we found evidence of red tree voles at five of six historical sites and all seven of the targeted sites surveyed (fig. 1-10; table 1-9). The 12 sites where we found voles were in mixed-age stands of old and young forest. The only location where we found no evidence of voles was in a 30-year-old Douglas-fir stand growing on a site where the original homesteader had reported seeing tree voles when he cleared the land for pasture in 1973.

The largest targeted survey conducted in the South Coast Subregion was a survey that we conducted on the Weyerhaeuser Millicoma Tree Farm 25 km east of Coos Bay in 2010. This tree farm was an intensively managed area dominated by a mosaic of recent clearcuts and young Douglas-fir forests that were 15–49 years old. In this study we surveyed 176 km of transect by visually searching for nests as we drove or walked along logging roads. We found 23 tree vole nests, including 20 unoccupied nests and three occupied nests. The three occupied nests were in 32- to 38-year-old stands of Douglas-fir. The number of nests found per person hour in this survey (0.07) was near the lowest value observed in all areas surveyed in Oregon except for the North Coast Subregion (table 1-9).

In the Interior Southwest Subregion we found tree vole nests at six of nine targeted sites and at the one retrospective site surveyed (Oregon Caves National Monument) (fig. 1-10; table 1-9). Tree vole presence at Oregon Caves was not surprising given that old forest in the monument had changed little since Roest (1951) collected a tree vole there in 1949. All nine targeted sites surveyed were in mixed-age forests on federal lands. Of the seven sites where we found voles or vole nests in this subregion, all were in stands dominated by Douglas-fir.

In the Central Cascades Subregion we found evidence of tree voles at 40 percent of historical sites and 93 percent of targeted sites (fig. 1-10; table 1-9). All of the historical sites surveyed were in foothills near the Willamette Valley and had been heavily affected by timber harvesting since the original collections. The high percentage of locations with vole nests in targeted surveys in the Central Cascades was expected because most of our surveys in that region were conducted during a genetic study in which we targeted areas where tree vole nests had already been documented during pre-project surveys in 2001–2006 (Bellinger et al. 2005, Miller et al. 2006).

In California we found Sonoma tree vole nests at 44 percent of historical sites and 43 percent of targeted sites surveyed south of the Klamath River, and no red tree vole nests at one targeted site on the Applegate River just south of the Oregon border in Siskiyou County (fig. 1-11; table 1-9). At the five historical sites where we found no evidence of Sonoma tree voles we conducted fairly extensive surveys at two areas (Elk Creek south of Happy Camp, Wilder Ranch east of Carlotta), and very limited surveys at three areas (Forest Glen, Albion, Russian Gulch northwest of Jenner). Absence of detections at the Elk Creek location was particularly interesting because that historical location was over 25 km east of the known range of the species, and was based on a single report by Zentner (1977), who claimed that he found tree vole nests about 10 km south of Happy Camp in Siskiyou County. Zentner (1977) did not say how he confirmed that the nests he observed were tree vole nests, and all subsequent surveys in the Happy Camp area have been negative (figs. 1-7 through 1-9).

California Department of Fish and Game Database

The distribution of Sonoma tree vole locations indicated that they were found in forested areas throughout most of Humboldt County and in locations scattered throughout the western portions of Mendocino and Sonoma Counties, at least as far south as Bodega and Freestone in Sonoma County.

The California Department of Fish and Game tree vole database included 1,274 records of Sonoma tree voles (1,222 nest locations, 52 specimen locations) and 49 records of red tree voles (38 nest locations, 11 specimen locations). Most (68 percent) of the specimen records were voles collected during pitfall sampling studies in 1993–1995. Of the 1,323 records in the database, 89 percent were on private lands, 4 percent were on federal lands, and 7 percent were on state or county lands (fig. 1-12). The 49 red tree vole locations were mostly in western Del Norte County, and were mostly on private lands (73 percent). The distribution of Sonoma tree vole locations indicated that they were found in forested areas throughout most of Humboldt County and in locations scattered throughout the western portions of Mendocino and Sonoma Counties, at least as far south as Bodega and Freestone in Sonoma County (fig. 1-12). The data also included several records of tree vole nests in Siskiyou and Trinity Counties, all but one of which were reported by Zentner (1977) and were outside the known range of either the red tree vole or Sonoma tree vole.

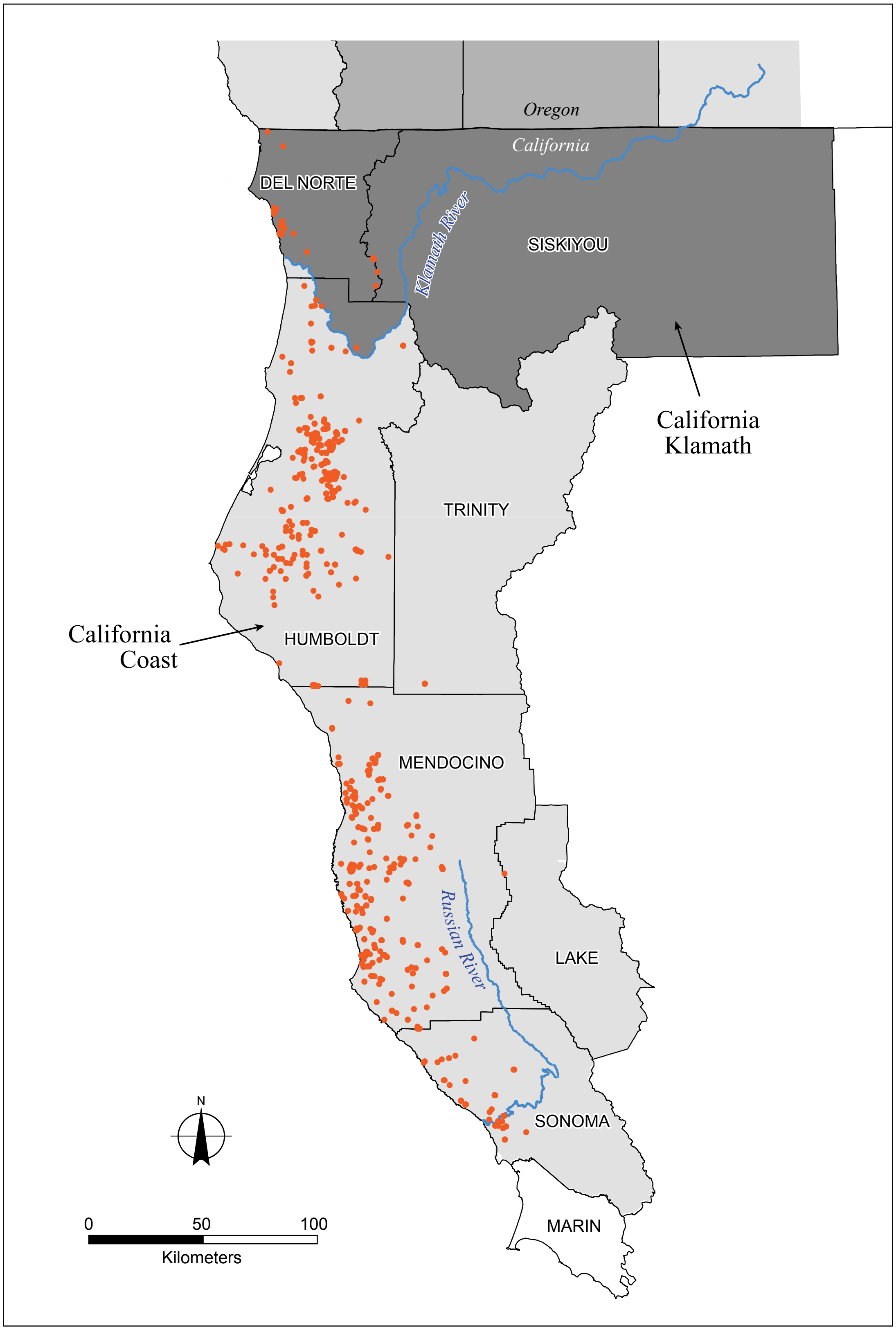

Figure 1-12—Distribution of 1,274 locations where tree voles or their nests were reported in the California Department of Fish and Game database, 1984–2000. Locations reported by Zentner (1977) were excluded because many of his unconfirmed locations were outside the confirmed range of either species of tree vole.

Elevation Limits

Our logistic regression analyses indicated that the odds of tree vole presence in owl pellet samples, pre-project survey polygons, and random plots declined with increasing elevation (table 1-10; figs. 1-13, 1-14a, and 1-14b). Results from all three analyses were similar, indicating that the odds of tree vole presence decreased by factors of 0.775 to 0.867 for every 100-m increase in elevation. In general, tree voles were uncommon in samples above 1200 m, and rare in samples above 1400 m. The highest elevations at which tree voles were detected in pellet samples were 1390 m in the Central Cascades and 1435 m in the Interior Southwest Subregion. In pre-project and random plot surveys, the highest elevations at which vole nests were detected were 1585 m in the Interior Southwest Subregion, 1432 m in the Central Cascades Subregion, and 1159 m in the North Cascades Subregion. Upper elevation limits where we found tree vole nests during targeted surveys in the Coast Ranges were 778 m on Marys Peak and 975 m on Prairie Peak. The lowest elevations where we found nests were on coastal lowlands and headlands only a few meters above sea level. Elevations of 2,232 Sonoma tree vole nests in the California Department of Fish and Game database and other sources (museum records, our surveys) ranged from 6 to 1555 m.

Table 1-10—Results of logistic regression analyses of elevation and red tree vole presence in northern spotted owl pellets, random plot surveys, and pre-project surveys in Oregon

	Intercept			Elevation (m)		
Model	Estimate	SE	*P*	Estimate	SE	*P*
Owl pellets	1.5006	0.1192	< 0.0001	-0.0026	0.0002	< 0.0001
Random plot surveys	0.1106	0.2710	= 0.6835	-0.0014	0.0003	< 0.0001
Pre-project surveys	0.7206	0.0978	< 0.0001	-0.0021	0.0001	< 0.0001

Discussion

We concluded that tree voles in Oregon are most abundant and most evenly distributed in the central and southwestern portion of western Oregon and are uncommon or rare in the northern Coast Ranges and northern Cascades.

Historical and Current Distribution

Based on the data from all sources examined, we concluded that tree voles in Oregon are most abundant and most evenly distributed in the central and southwestern portion of western Oregon and are uncommon or rare in the northern Coast Ranges and northern Cascades, where they are mostly restricted to isolated populations in remnant stands of old forest on federal and state lands (Forsman et al. 2008, 2009; Price et al. 2015). The fact that tree voles still occur in some local areas in the northern Coast Ranges and northern Cascades suggests that the species probably occurred in old forests throughout this region prior to the arrival of European

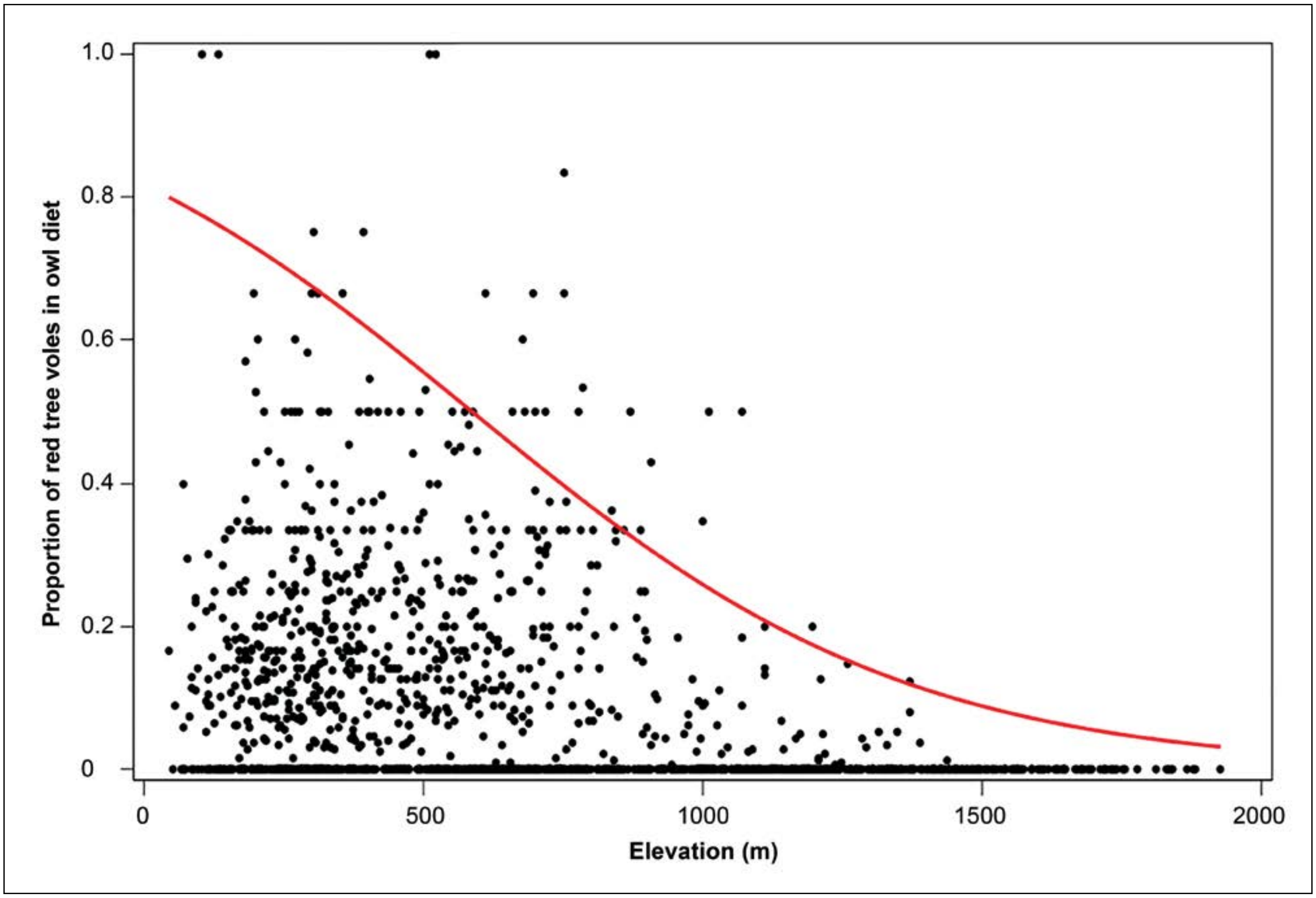

Figure 1-13—Proportion of red tree voles in diets (of total prey numbers) of northern spotted owls in Oregon, plotted relative to elevation at the owl territory center. Sample included 1,386 owl territories sampled in 1970–2009. The curved line indicates the modeled relationship based on logistic regression analysis of presence or absence of tree voles in the diet.

settlers in the early 1800s. However, few people were paying any attention to tree voles in the 1800s or early 1900s, so the exact limits of tree vole distribution prior to European settlement are unknown.

Elimination of red tree voles from many lowland forest areas in northwestern Oregon was suggested by the fact that we found few or no tree voles in many areas they once inhabited, including the Chehalem Mountains near Newberg (Clifton 1960; Hubbard 1940, 1941), Schoenborn Ranch near Molalla (Maser 1966, Olterman 1972), Cape Meares near Tillamook (Forsman and Swingle 2010), most of the area surrounding Saddle Mountain in Clatsop County, and several historical sites adjacent to the southern Willamette Valley (Maser 1966). Since the original observations were made, virtually all of these areas had been harvested, burned, or both, and then converted to nonforest use or intensively managed young forest. Our retrospective survey of the Maser (1966) population study area near Monroe was probably typical of the recent history of many private forest

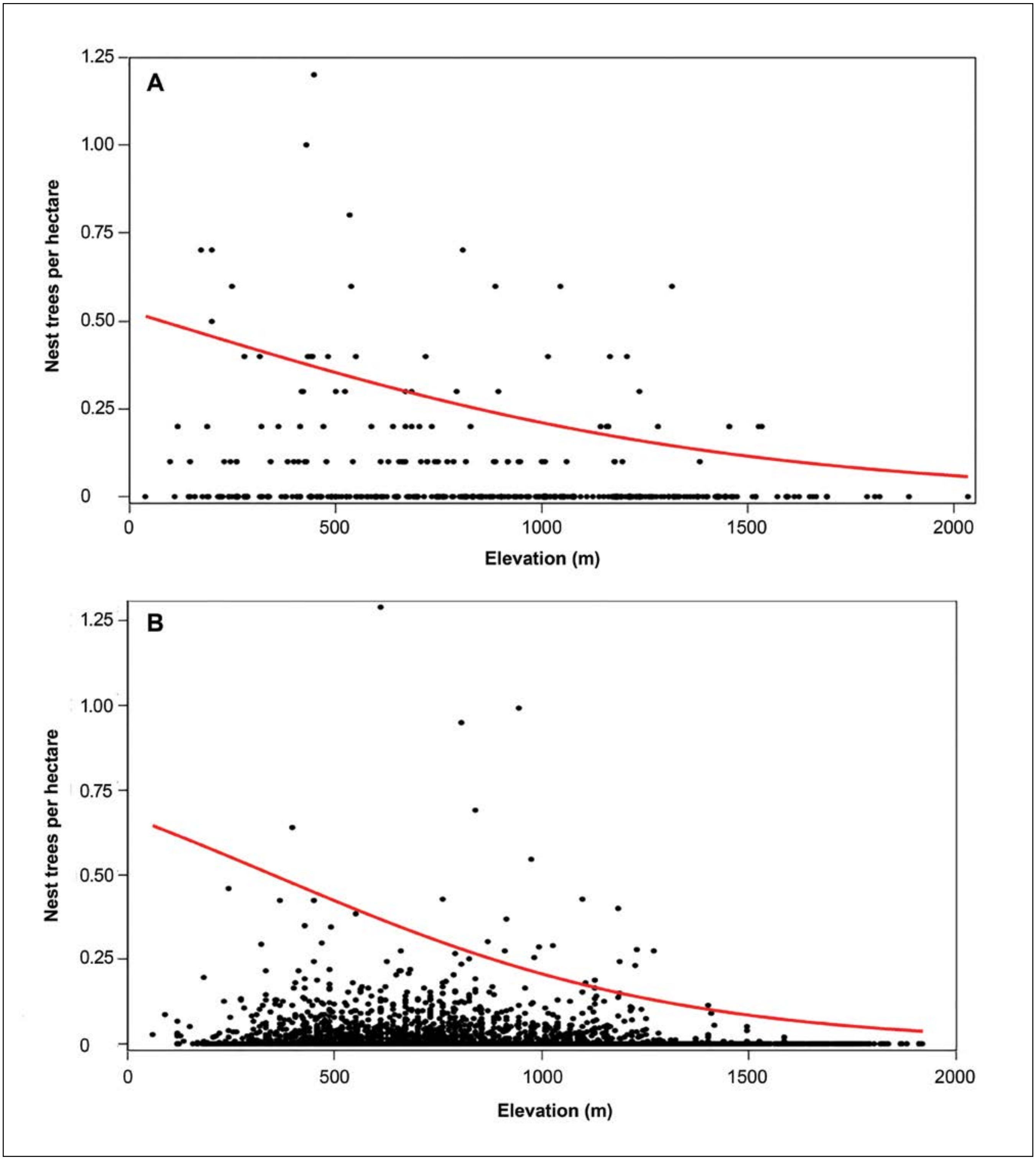

Figure 1-14—Estimated minimum density of red tree vole nest trees at different elevations in 354 random plots (A) and 4,415 pre-project survey polygons (B) in western Oregon and northern California. Estimates were based on all tree vole nest trees detected, regardless of occupancy status. Curved lines indicate modeled relationships based on logistic regression analyses of presence or absence.

lands in western Oregon. In 1965, Maser found fairly high densities of tree voles (approximately one adult per hectare) in a young stand of Douglas-fir and Oregon white oak that had regenerated on an area that had been clearcut and converted to pasture in the early 1900s. When we resurveyed the site in 2006, we found that the study plot had been clearcut again, and we found no tree vole nests in the young trees regenerating on the study plot. This scenario of repeated heavy disturbance does not bode well for red tree voles on private lands in western Oregon. Tree voles may be able to reinvade harvested areas from adjacent refugia for the first few rotations, but the comparative rarity of tree voles in young stands does not instill much hope that they will be able to persist in areas where trees are managed on short rotations with frequent thinning.

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Although our surveys indicate that tree voles have been largely eliminated from the Tillamook and Clatsop State Forests in the Northern Coast Subregion (Price et al. 2015), data from the strategic surveys and targeted surveys clearly revealed that some tree voles were still present in the old forests at the western edge of Tillamook State Forest, and on Forest Service and BLM lands adjacent to Tillamook State Forest in southern Tillamook County (figs. 1-7 through 1-10). It seems possible, therefore, that tree voles could eventually recolonize the Tillamook State Forest if the Oregon Department of Forestry actively managed forests to produce habitat for tree voles. To date, efforts to manage for old forests on state forest lands have met strong resistance from some stakeholders who have argued that the primary goal on state forests should be to produce revenue for schools and counties, as described by Wells (1999).

Other areas in western Oregon where there were few historical or recent records of red tree voles included much of the western half of Coos County and the central portion of Lincoln County. These areas were mostly in private ownership where virtually all old forests had been harvested or burned and replaced by young forests. Our limited data from these areas indicated that tree voles were still present but were comparatively rare. These results need to be better documented by additional surveys on other nonfederal lands in Lincoln, Lane, Douglas, and Coos Counties, which will require the cooperation of private landowners.

The combined data from all sources indicated that in most of western Oregon, the eastern edge of the range of the red tree vole in the Cascades Mountains corresponds with the transition zone between forests of Douglas-fir and high-elevation forests of mountain hemlock, Pacific silver fir (*Abies amabilis* (Douglas ex Loudon) Douglas ex Forbes), and noble fir. However, in southwestern Oregon, the eastern edge of the range follows the Applegate River north from California to the Rogue River, and then east on the north side of the Rogue River and Middle Fork of the

Rogue River (figs. 1-2, 1-4, and 1-7 through 1-10). In this area, summers are much hotter and dryer than in the rest of the range of the red tree vole in Oregon, and range limits appear to be determined by climate and the gradual transition to landscapes dominated by pine and oak woodlands.

All sources of data examined in our analysis indicate that red tree voles do not occur east of the crest of the Cascades except in the eastern Columbia River Gorge and in a small area at the northern end of the Cascades in Hood River County, where forests of Douglas-fir and western hemlock extend east over the crest of the Cascades along the Columbia River Gorge and into the headwaters of the Lake Branch tributary of the Hood River (figs. 1-4, 1-9, and 1-10) (Forsman et al. 2009a). More surveys are needed in the latter area to determine if tree voles occur in the area south of Lake Branch, where other tributaries of the Hood River also include forests of Douglas-fir and western hemlock.

Data from California indicate that the current range of the red tree vole includes Del Norte County, the western edge of Siskiyou County, and all of Humboldt County north of the Klamath River (figs. 1-3, 1-4, 1-7, 1-8, 1-9, 1-11, and 1-12). The range of the Sonoma tree vole includes the coastal forest extending from the Klamath River in Humboldt and Mendocino Counties and the western edge of Trinity County south to Freestone and Bodega in southern Sonoma County (figs. 1-3, 1-5, 1-11, and 1-12). The large expanse of open grasslands, bays, and marshes south of Freestone and Bodega apparently represents an impassable barrier to Sonoma tree voles, as indicated by the absence of historical and recent records of tree voles farther south.

In contrast to the red tree vole, the range of the Sonoma tree vole is primarily on private lands. Our retrospective and targeted surveys, and surveys reported in the California Department of Fish and Game database (Gould 2005), indicate that tree voles are still present on many of these lands, but we found relatively few occupied nests compared to some of the earlier collectors who easily collected large numbers of Sonoma tree voles. In some cases, the numbers of voles acquired by early collectors seem almost unbelievable today. For example, Harry Wilder and Irvin Clay claimed to have captured more than 50 Sonoma tree voles in two mornings of collecting on the Wilder Ranch near Carlotta in 1913 (Howell 1926: 43). When we visited the same area in 2008, we found that the forested hillsides had all been harvested and converted to young saplings with no evidence of tree voles. Our overall impression, therefore, is that Sonoma tree voles are still present in much of their historical range in California, but that numbers have declined appreciably from levels encountered by earlier collectors.

Zentner (1977) claimed to have found tree vole nests outside the known range of the red tree vole and Sonoma tree vole at several locations in California, including locations in eastern Trinity County and western Siskiyou County east of the Klamath River. In subsequent surveys in those areas, we found no evidence of tree voles, but did document large numbers of nests built by squirrels (*Glaucomys sabrinus, Tamiasciurus douglasii, Sciurus griseus*) and woodrats (*Neotoma* spp.; fig. 1-11). In addition, no tree vole nests were found during numerous pre-project surveys, random plot surveys, and strategic surveys in areas around the historical Zentner locations east of the Klamath River in Siskiyou County (figs. 1-7 through 1-9), and no tree voles were found in owl pellets collected in this area (fig. 1-3). We think it is unlikely that tree voles were present but undetected during all of these surveys. We suspect, therefore, that Zentner (1977) may have incorrectly labeled nests of squirrels or woodrats as tree vole nests. We are especially suspicious of his data because he reported that the central mass of the nests he identified as tree vole nests consisted mainly of stripped bark as opposed to resin ducts (Zentner 1977: 35). We consider this issue unresolved until more surveys are conducted in the areas where Zentner claimed to have found tree voles, but until then, we think his data should be considered skeptically.

Although our targeted surveys, retrospective surveys, and owl pellet analyses indicate that tree voles are absent in some portions of their historical range, there are some important qualifications on these results. First, as already mentioned, detection rates of tree vole nests are never 100 percent, so it is certain that many nests were not detected during ground-based surveys (Swingle 2005, Swingle and Forsman 2009). Second, a retrospective survey is likely to find a population decline because the number of historical sites that are still occupied cannot exceed 100 percent. However, the retrospective surveys that we conducted were not limited to the historical nest groves in which voles were collected. Instead, we searched large areas around each historical collection site, and if we found tree voles or their nests anywhere in the survey area we considered the site as still occupied, regardless of the distance from the historical nest location and regardless of whether nests were occupied. If anything, therefore, we think that our retrospective surveys overestimated the proportion of historical sites still occupied by tree voles.

The occurrence of tree voles in a large sample of owl diets was a useful indicator of tree vole presence in different geographic areas, but several factors limited the inferences that could be drawn from the data. Most importantly, the sample size of prey remains from many owl territories was small and this undoubtedly resulted in many false negatives (no detections of tree voles when the species was actually present). We could have reduced the odds of false negatives by limiting the analysis to owl territories with large samples of prey items, but this would have excluded a large number of owl territories in which tree voles were detected. We decided that retention of all of the distributional data was more important than trying to reduce the proportion of false negatives by setting artificial limits on sample size.

Other concerns with data from owl pellets were that: (1) regional variation in prey diversity could cause diets to vary in ways that were unrelated to the density of tree voles, or (2) the results would not apply to areas where spotted owls had been eliminated by the removal of old forests. These are valid concerns, but the fact that the owl pellet data were in close agreement with regional patterns in tree vole abundance based on pre-project surveys, strategic surveys, targeted surveys, and random plot surveys led us to conclude that the owl pellet data provided a good indication of regional patterns of tree vole abundance and distribution. In regard to the concern that owl pellet data could not be used to assess vole distribution in areas where owls did not occur, we emphasized this in the results, and fig. 1-2 makes it obvious where those areas were.

Although most sources of data that we examined were not selected randomly, we feel that our results are generally representative of the distribution and relative abundance of tree voles on federal and state lands in Oregon and California. Many thousands of forest stands and over a thousand different owl territories were sampled. The scope of the effort was so extensive that we felt that concerns about the lack of random sampling were overwhelmed by the sheer amount of data from throughout the range of the red tree vole. That being said, there were definitely some areas that were not covered by our surveys where more data are needed, especially within the range of the Sonoma tree vole, where the majority of the population is on private lands.

Habitat Relationships

Density of tree voles in old forests is disproportionately underestimated based on ground transects because many nests are located high above ground or inside cavities where they cannot be detected from the ground.

Based on all sources of data in our analysis, we concluded that red tree voles were most abundant in old forests, and were often rare or absent in areas that had been harvested or burned and converted to young, intensively managed forests. Although similar conclusions have been reached by others (e.g., Aubry et al. 1991, Corn and Bury 1986, Dunk and Hawley 2009), imperfect detection of tree voles and their nests makes all comparisons among forest age-classes suspect. If anything, density of tree voles in old forests is disproportionately underestimated based on ground transects because many nests are located high above ground or inside cavities where they cannot be detected from the ground (Swingle 2005, Walker 1928). As a result, the high numbers of tree vole nests found in old forests probably underestimates the differences between old and young forests.

Even in young forests, many tree vole nests are difficult to detect from the ground. For example, Swingle and Forsman (2009) estimated that only 48 percent of nests used by radio-marked tree voles in predominantly young forests were detectable from the ground. The only way to evaluate and correct for this source of bias would be to conduct studies in which large numbers of trees were inspected from the ground and then climbed to determine the number of nests actually present and to determine if those nests were actually occupied by tree voles. Any estimates that do not include correction for imperfect detection should be considered estimates of minimum density. We recommend that future population studies of tree voles include assessments of detection probabilities. This will not be easy or inexpensive, but is badly needed.

Although nest detectability is imperfect, our experience leads us to conclude that the odds that no tree vole nests will be detected in an area where tree voles actually occur (false negatives) are low, especially when survey plots are large. Even when survey plots are relatively small, as in the random plot study, the evidence suggests that false negatives are uncommon. For example, Dunk and Hawley (2009) estimated that the rate of false negatives in the random plot survey was only 6 percent based on a comparison of nest detections from ground transects and nest detections in trees surveyed by climbers.

Although nest detectability is imperfect, our experience leads us to conclude that the odds that no tree vole nests will be detected in an area where tree voles actually occur (false negatives) are low, especially when survey plots are large.

The fact that tree vole nests were detected in only 27 percent of 1-ha random plot surveys and 28 percent of pre-project survey plots indicated that red tree voles were uncommon or absent in many areas, particularly in the northern Coast Ranges and northern Cascades. This result is even more significant given that most (80 percent) of the random plot surveys were in old forest, where tree voles are most abundant (Corn and Bury 1986, 1991; Dunk and Hawley 2009; Forsman et al. 2009a).

Particularly noticeable was the absence of red tree vole detections in the northern Coast Ranges (Price et al. 2015) in the extensive areas that burned during the Tillamook Burn fires of 1933–1951 (Holbrook 1943, Kemp 1967, Lucia 1983, Wells 1999), and the 1902 Columbia and 1865 Silverton fires in the north Cascades (fig. 1-6). Apparently, red tree voles were almost completely eradicated during these huge fires and the extensive salvage logging that followed. Tree voles have been unable to recolonize the burned areas, either because the regenerating young forests are too far from a population source or because management of the burned areas has maintained conditions unsuitable for tree voles, or both. Subsequent to the Tillamook Burn fires, much of the region was salvage-logged and replanted with Douglas-fir, which has subsequently been intensively managed to the present day (ODF 2010, Wells 1999). At the time of our surveys, forests in the burned area were predominantly young stands that were being managed on short rotations with periodic thinning to reduce crown density (ODF 2010). The thinned stands typically had low crown closure and were largely lacking in the kinds of canopy structures that provide sturdy foundations for tree vole nests, including broken tops, forked trunks, cavities, epicormic branching, dwarf mistletoe brooms, and heavy accumulations of moss and lichens (Forsman et al. 2008, Maser 1966, Swingle 2005). Without management to produce or retain such structures, there is little likelihood that tree voles will re-establish a presence in the areas burned during the Tillamook Burn. Though the red tree vole is listed as an Oregon Sensitive Species (ODFW 2008), the most recent management plan for state forests in western Oregon (ODF 2010) did not address the habitat needs of tree voles. Forests in the areas that burned in the 1902 Columbia and 1865 Silverton fires in the northern Cascades were considerably older than the forests in the Tillamook Burn, but the absence of tree voles even in those mature forests suggests that it may take centuries for tree voles to reinvade areas that burn during very large, hot fires.

Although the data from random plot surveys, pre-project surveys, and pitfall trapping studies indicated that tree voles were most abundant in old forests, the vast majority of tree voles captured by tree climbers were captured in young forests. This apparent contradiction was almost certainly due to sampling bias. Most specimen collectors tended to search for tree voles in young forests where nests were easy to see from the ground and trees were easy to climb. Few of the early collectors had the technical ability to climb old-growth trees (Bailey 1915, Jobanek 1988), so old-growth forests went largely unsurveyed, except by mammalogists who used pitfall traps, and a few loggers who captured voles in recently felled trees (Bailey 1915, Forsman and Swingle 2010, Walker 1928). Many mammalogists who used pitfall traps to sample tree voles (Corn and Bury 1986, 1991; Gilbert and Allwine 1991; Gomez and Anthony 1998; Gomez et al. 1997; Manning and Maguire 1999; Martin and McComb 2002; Ralph et al. 1991; Raphael 1988) sampled a cross-section of forest age-classes, so the results from pitfall traps in table 1-3 probably provide a more accurate picture of the relative abundance of tree voles in different forest age-classes than do results from tree climbing. However, even pitfall data may be biased if differences in tree spacing and canopy interconnectivity cause tree voles to travel on the ground more frequently in some forest age-classes than in others.

Although the results from the random plot study, pre-project surveys, and strategic surveys indicated that tree vole nests were most abundant in old forests, all of these different sources also indicated that tree voles occurred at lower densities in young forests. This indicated that tree voles began to colonize young stands at a fairly early age (15 to 25 years). However, the fact that few or no tree vole nests were found in most young stands suggested that such stands were mostly not suitable for tree voles or were located too far from the nearest source population to be rapidly recolonized.

When we did find tree voles in young forests, they were often in regenerating stands adjacent to mature or old-growth forest. Recolonization of these young stands was likely dependent on the presence of source populations in adjacent old forests. It is important, therefore, that forest managers be cognizant of the fact that remnant patches of old forest may be important as refugia for tree voles and that young forests may facilitate dispersal and gene flow between these remnant patches. Even very small patches of old forest may be important as refugia where they occur in landscapes that are otherwise dominated by young forests.

When we did find tree voles in young forests, they were often in regenerating stands adjacent to mature or old-growth forest. Recolonization of these young stands was likely dependent on the presence of source populations in adjacent old forests.

Elevation Limits

Based on data from all sources, the range of the red tree vole in Oregon extends from a few meters above sea level up to and including the lower edge of the transition zone where forests of Douglas-fir intergrade with forests of true fir and mountain hemlock. Although our surveys indicate that tree voles are now absent or uncommon in many of the young forests regenerating on harvested areas at low elevations along the coast, we also found that tree voles still occurred at sites near sea level in some locations, including Tillamook Head, Cape Falcon, Cape Meares, Cape Lookout, Cascade Head, Cape Arago, and Bandon.

Based on data from all sources, the range of the red tree vole in Oregon extends from a few meters above sea level up to and including the lower edge of the transition zone where forests of Douglas-fir intergrade with forests of true fir and mountain hemlock.

In the Coast Ranges and Cascades of western Oregon, red tree voles were uncommon above 1000 m elevation, although they were occasionally found up to 1059 m in the north Cascades, 1475 m in the central Cascades, 1437 m in the southern Cascades, and 1585 m at Sturgis Creek in the Klamath Mountains just north of the Oregon-California border. Although Manning and Maguire (1999) reported a tree vole captured at 1600 m in the central Cascades, Manning (2012) subsequently informed us that they had plotted the location incorrectly, and that the elevation at the capture site was actually 1475 m.

Hamilton (1962) suggested that tree voles may not occur at high elevations because their small, exposed nests do not provide adequate insulation during winter. Another possibility is that it may be difficult for tree voles to forage at high elevations during winter because limbs of trees are often covered by layers of snow and ice for long periods of time. We suspect that both of the above hypotheses may be true, albeit difficult to test. Another obvious hypothesis is that, in most areas, the upper limits of tree vole distribution could be determined by the upper elevation limits of Douglas-fir, the primary food source of tree voles in most areas.

This seems unlikely given that tree voles have learned to feed on other species of conifers such as Sitka spruce, western hemlock, grand fir, Monterey pine, and bishop pine in many low-elevation areas (Benson and Borell 1931, Clifton 1960, Jewett 1920, Kelsey et al. 2009, Taylor 1915, Vrieze 1980, Wooster and Town 2002, this study). However, there are no records of tree voles feeding on mountain hemlock, Pacific silver fir, or noble fir, and we cannot rule out the possibility that these high-elevation species are unacceptable as a substitute for Douglas-fir as a food source.

Sex Ratios

We found that the sex ratio of tree voles captured by loggers was nearly 50:50. This result was probably most reflective of the actual sex ratio of tree voles, as there is good reason to believe that sex ratios from other sampling methods (pitfall traps, tree climbing) are biased. The predominance of females in samples collected by tree climbers probably results from the higher detectability of large female brood nests (Swingle 2005), whereas the predominance of males in samples from pitfall traps likely reflects higher levels of terrestrial movement by males searching their home ranges for potential mates (Swingle and Forsman 2009). We found no evidence that disproportionate sex ratios in samples collected by tree climbing and pitfall trapping were a result of ground nesting by males. In addition, Swingle and Forsman (2009) found that radio-collared male tree voles nested exclusively in trees, but regularly descended to the ground to move between trees. Thus, we think that ground nesting by tree voles (Bailey 1936, Howell 1926, Maser 1966, Thompson and Diller 2002) is a rare occurrence and that opinions to the contrary (Anthony 1928, Howell 1926, Maser 1966, Nowak and Paradiso 1983, Phillips and Chrostowski 1981) are incorrect.

Population Density and Regulation

Although tree voles occur in coniferous forests throughout much of western Oregon and northwestern California, there was no evidence from our surveys or any of the historical data that they ever occurred at the high densities sometimes reported for other voles (e.g., Cornely and Verts 1988, Smolen and Keller 1987, Verts and Carraway 1987). Instead, they typically occurred at low densities, with clusters of nests distributed in a very patchy pattern at the landscape scale. Tree voles defend their nests in the wild and adults infrequently occupy the same nests at the same time except for brief periods when males visit female nests to breed (Forsman et al. 2009b, Swingle 2005). Although there have been a few cases where two occupied nests were found in the same tree at the same time (Benson and Borell 1931, Taylor 1915, Johnson 1957–1985, this study), this appears to be the exception rather than the rule, especially in young forests (Swingle and Forsman 2009). Based on the multiple sources of data described in this report, and observations of adult behavior in other studies (Forsman et al. 2009b, Swingle and Forsman 2009), we believe that tree vole populations are naturally maintained at low densities because of adult territoriality, a low reproductive rate (Clifton 1960, Forsman et al. 2009b, Hamilton 1962), high rate of predation (Swingle et al. 2010), and the comparatively low density of trees with good structures for nest support (i.e., habitat).

Management Implications

Our analyses suggest that tree voles are still present throughout much of their historical range, but have become rare or absent in some areas that have been converted to young, intensively managed forests. In western Oregon and northwestern California, red tree voles will likely continue to thrive in the extensive areas of old forest on federal lands that are currently protected by the Northwest Forest Plan (USDA and USDI 1994). Where federal lands are lacking, however, there is a high likelihood that tree voles will gradually disappear unless managers actively manage for at least some old forests. This is especially true in the North Coast Subregion of Oregon where there is little federal forest land. In California, Sonoma tree voles occur primarily on private and state lands, where landowners are required to follow state forestry regulations, but are not specifically required to protect tree voles or their habitat (http://calfire.ca.gov/resource_mgt/downloads/2013_FP_Rulebook_with_Tech_RuleNo1.pdf). Thus, the persistence of Sonoma tree voles in many areas is in doubt. However, the continued persistence of Sonoma tree voles in small tracts of forest as far south as Freestone and Bodega does suggest that Sonoma tree voles may persist in highly fragmented forest landscapes, as long as some areas of tree vole habitat are retained. Ultimately, persistence of both species of tree voles will depend on the willingness of humans to protect mature and old-growth forests, which provide stable, high-quality habitat for tree voles and serve as refugia for recolonization of adjacent areas that have been harvested or burned.

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Chapter 2: Diet

Introduction

Although they may feed on other items in captivity (Benson and Borell 1931, Clifton 1960), tree voles (*Arborimus pomo, A. longicaudus*) in the wild feed primarily on needles and twigs of conifers (Forsman et al. 2009b, Maser 1966). To obtain food they harvest conifer branch tips (hereafter cuttings) at night and store them on or inside their nests. Cuttings harvested by tree voles are easily identified based on their small size (typically 8 to 25 cm) and the chisel-shaped bite marks on the base of each twig (Forsman et al. 2009b). In addition, cuttings harvested by tree voles are almost always found in association with tree vole fecal pellets, debarked twigs, and discarded resin ducts, which the voles remove from the edges of each needle (Kelsey et al. 2009, Maser 1966). In this chapter, we describe and compare diets of tree voles in different parts of their range based on the composition of cuttings found in tree vole nests that we examined in western Oregon and northwestern California in 2000–2013.

Methods

We estimated diets based on the ratio of cuttings from different tree species that were stored in the nests of 421 red tree voles (*A. longicaudus*) nests and 10 Sonoma tree voles (*A. pomo*). In most cases (63 percent), we actually counted cuttings, but at a few nests with large numbers of cuttings we estimated the species ratio of cuttings based on what was visible on top of the nest because we did not want to tear the nests apart. The sample of nests examined was not selected randomly, and no attempt was made to sample equal numbers of nests in different regions. Instead we used all cases in which we climbed to nests and recorded the composition of cuttings in the nest.

Results

Of 421 nests examined within the range of the red tree vole, 362 (86 percent) contained exclusively Douglas-fir cuttings.

Of 421 nests examined within the range of the red tree vole, 362 (86 percent) contained exclusively Douglas-fir[1] cuttings (table 2-1). At the other 59 nests, cuttings were grand fir (0.5 percent), western hemlock (7.6 percent), Sitka spruce (3.1 percent), or mixtures of western hemlock and Sitka spruce (2.1 percent), or western hemlock and Douglas-fir (0.7 percent) (table 2-1). The only area where red tree voles did not feed primarily on Douglas-fir was in the narrow zone of Sitka spruce and western hemlock along the coast of northwestern Oregon. In the Sitka spruce zone, where 88 percent of the tree vole nests examined had exclusively western hemlock or Sitka spruce cuttings, voles rarely used Douglas-fir, even when it was present (fig. 2-1). There was an apparent latitudinal difference in food preference in the Sitka spruce zone with 53 of 54 nests

Table 2-1—Number of occupied and recently occupied nests of red tree voles in Oregon, subdivided by the species of conifer cuttings that were being used for food

Species of cuttings in nest	Number of nests
Douglas-fir	362
Grand fir	2
Western hemlock	32
Western hemlock and Douglas-fir	3
Western hemlock and Sitka spruce	9
Sitka spruce	13

(98 percent) in the North Coast Subregion containing western hemlock or Sitka spruce cuttings, but only 6 of 13 nests (46 percent) in the Sitka spruce zone in the Central and South Coast Subregions containing western hemlock or Sitka spruce cuttings (fig. 2-1).

Of 27 Sonoma tree vole nests examined in California, 23 (85 percent) contained Douglas-fir cuttings or resin ducts, and 4 (15 percent) contained cuttings or resin ducts from Monterey pine. The latter nests were in Monterey pine trees that were planted near the Green Diamond Resource Company office in Korbel, 10 km east of Arcata in Humboldt County. Many of the resin ducts from Monterey pine needles were over 9 cm long, much longer than Douglas-fir (3 cm), and all were from the outer edges of the needles. Monterey pine does not normally occur within the range of the Sonoma tree vole except where it is planted as an ornamental (McDonald and Laacke 1990).

Discussion

In most of their range, red tree voles were limited primarily to forests of Douglas-fir, which was their primary food source. The main exception was the Sitka spruce zone (Franklin and Dyrness 1973) of coastal northwestern Oregon, where red tree voles lived primarily in forests of western hemlock or Sitka spruce, and largely avoided Douglas-fir, even when it was present. A good example of this behavior was an occupied nest that we found on Cape Meares in Tillamook County. The nest was in a Douglas-fir, but the cuttings and resin ducts in the nest were entirely western hemlock, which the vole had harvested from adjacent western hemlocks that had branches that were in contact with the nest tree. Tree voles that fed on western hemlock and Sitka spruce had to handle needles differently than voles that fed on Douglas-fir (Kelsey et al. 2009). When feeding on Douglas-fir, tree voles remove the resin ducts from the outer edges of each needle and eat the middle portion of

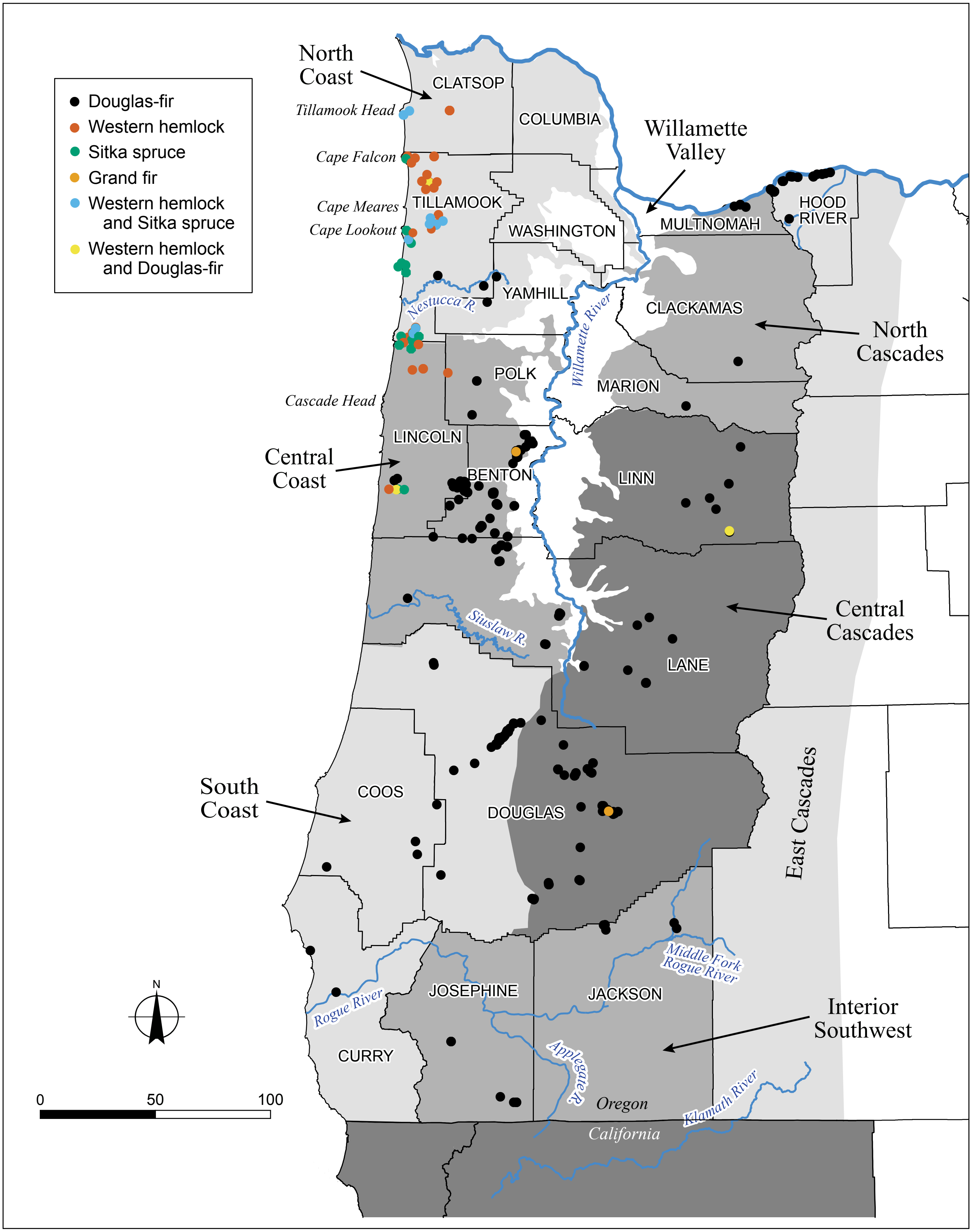

Figure 2-1—Species of cuttings documented in red tree vole nests in Oregon.

the needle (Benson and Borell 1931, Kelsey et al. 2009, Maser 1966, this study). In contrast, western hemlock has a single resin duct that runs down the center of the needle, and tree voles that feed on western hemlock eat the edges of the needle and discard the center of the needle (fig. 2-2) (Kelsey et al. 2009, this study).

In nests of red tree voles that were feeding on Sitka spruce, we did not find any resin ducts, but we did find some spruce needles that had the apical half eaten, apparently whole. Resin ducts in Sitka spruce needles may be difficult to remove because they are located midway between the edge of the needle and the midrib (fig. 2-2). In addition, the location of resin ducts in needles of Sitka spruce is unpredictable because they are discontinuous, varying in length and location within the needle (Kelsey et al. 2009, Weng and Jackson 2000). Some Sitka spruce needles have no ducts, whereas some have ducts on only one side of the needle and others have ducts concentrated in the basal half of the needle (fig. 2-2). Thus, it appears that tree voles that feed on spruce may avoid the resin ducts by only eating a portion of each needle. This calls for further investigation with captive voles, as our sample of vole nests in spruce trees was small.

Some researchers (Clifton 1960, Johnson 1957–1985, Walker 1930) found that when red tree voles that were used to feeding on Sitka spruce or western hemlock were switched to a diet of Douglas-fir, they lost weight and died within a few days. Apparently these voles were unable to switch from one type of food to another, possibly because of the different techniques required to remove resin ducts of different species. We suspect that food-handling procedures are learned from the mother, and are not easily changed without considerable time to experiment with a novel food. An alternative hypothesis that could explain why tree voles cannot easily switch between alternative food types is that the intestinal flora needed to digest or neutralize leaf toxins is specific to certain plant species and is passed maternally when juveniles consume their mother's fecal pellets (Clifton 1960, Hamilton 1962).

Tree voles also feed on other species of conifers, including grand fir (Benson and Borell 1931, Johnson 1957–1985, Taylor 1915, Vrieze 1980, this study), bishop pine (Wooster and Town 2002), and Monterey pine (this study). Feeding on these alternative species occurs primarily in California, but we did document a few cases of voles feeding on grand fir in Oregon. Grand fir and pine trees have resin ducts that are located near the edges of the needle, much like Douglas-fir. It is possible, therefore, that tree voles that are used to feeding on Douglas-fir may find it easier to switch to grand fir or pine than to western hemlock or Sitka spruce. Again, this hypothesis is in need of experimental testing with captive voles.

Observations of nests where Sonoma tree voles were feeding on Monterey pine or bishop pine (Wooster and Town 2002, this study) suggest that future researchers need to conduct surveys for Sonoma tree voles in bishop pine forests as well as forests of Douglas-fir. This may prove difficult because branches of bishop pine are commonly covered by dense mats of fallen needles that are difficult to distinguish from tree vole nests when viewed from the ground (Wooster and Town 2002). Thus, unless resin ducts are found on the ground, the only way to effectively document tree vole nests in forests of bishop pine is to climb the trees to examine the mats of needles.

In California and coastal southern Oregon, tree voles often occurred in mixed species stands of coast redwoods and other conifers. In these stands tree voles appeared to ignore the redwoods and feed on Douglas-fir, grand fir, western hemlock, or bishop pine. Apparently, the structure or chemical composition of redwood needles made them unpalatable. The same was true of western redcedar and incense-cedar, both of which were common conifers in our study areas but were never eaten.

Most tree vole nests that we examined contained the remains of conifer twigs that had the bark removed (fig. 2-3). These twigs looked like tiny toothpicks and were easy to miss without close inspection. Maser (1966) suggested that debarked twigs in tree vole nests were the result of voles removing the bark to feed on the cambium layer and the woody pith inside twigs. It remains unclear if the voles also eat the bark as well as the underlying cambium. This needs further investigation.

Management Implications

In most of their range, tree voles depend on Douglas-fir as their primary food source, and are likely to benefit from management that retains mature or old forests of Douglas-fir. The exception is the Sitka spruce zone, where tree voles feed primarily on western hemlock and Sitka spruce and are likely to benefit from management that retains mature forests of hemlock and spruce. In all forest types, old trees with deep crowns likely provide a more stable food supply than do small trees with shallow crowns. Thinning that disrupts arboreal connections between tree limbs is likely to be particularly disruptive in young stands, where tree voles need to move between multiple trees to obtain food (Swingle 2005).

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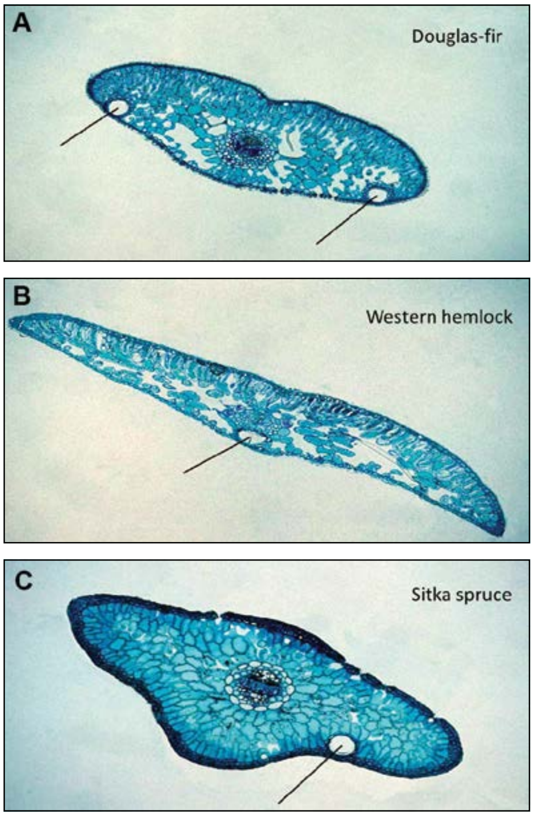

Figure 2-2—Location of resin ducts in three different species of conifers used as food by tree voles. Douglas-fir has two resin ducts located near the lateral edges of the needle. Western hemlock has a single resin duct located in the center of the needle. Sitka spruce has two resin ducts located halfway between the center and the edge of the needle, but the ducts are often incomplete or missing entirely.

Figure 2-3—Debarked twigs from a tree vole nest. These twigs look like tiny toothpicks. Also note the angled bite marks on the ends of the twigs.

Chapter 3: Current Status of Potential Red Tree Vole Habitat Based on Species Distribution Models

Introduction

An integral part of the Northwest Forest Plan (NWFP) is the monitoring of status and trends of habitat for species associated with late-successional and old-growth forests (Lint et al. 1999, Madsen et al. 1999). To meet NWFP monitoring requirements, the USDA Forest Service (Forest Service) and USDI Bureau of Land Management (BLM) developed satellite-based maps of forest composition and structure for assessing the distribution of different forest types and age-classes within the region covered by the NWFP (Moeur et al. 2005, 2011). The primary reason for development of these maps was to allow managers and researchers to monitor trends in forest vegetation over time and to assess the amount of late-successional and old-growth forest available to species that inhabit old forests, such as the northern spotted owl (*Strix occidentalis caurina*), marbled murrelet (*Brachyramphus marmoratus*), and red tree vole (*Arborimus longicaudus*).

There have been several recent studies that used NWFP satellite maps and sophisticated models to predict distributions of habitat for northern spotted owls and marbled murrelets based on biotic and abiotic conditions (Davis et al. 2011, Huff et al. 2006, Lint 2005, Raphael et al. 2011). In this chapter, we use the NWFP satellite maps to predict the amount and distribution of potential habitat of the red tree vole in western Oregon and northwestern California (fig. 3-1). Our objective is to provide forest managers, wildlife biologists, and the public with a better understanding of the areas where red tree voles may be expected to occur in western Oregon and northwestern California.

Methods

Vegetation Data

We obtained vegetation data (app. 4) from satellite maps produced by the NWFP late-successional and old-growth monitoring program (Moeur et al. 2011). These landscape-scale data were produced with "gradient nearest neighbor" (GNN) models developed by the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA) group at Oregon State University (http://lemma.forestry.oregonstate.edu/) using a method that combined direct gradient analysis (Gauch 1982, ter Braak 1986) and nearest-neighbor imputation (Moeur and Stage 1995). These methods were described in detail by Ohmann and Gregory (2002). In general, the method used to develop GNN layers was to assign detailed forest vegetation data from forest inventory plots to every pixel in a geographic information system (GIS) raster map based on modeled relationships between plot data and a combination of spatial predictor variables

Figure 3-1—Modeling regions used in the development of habitat suitability models for red tree voles in western Oregon and northwestern California.

derived from Landsat satellite imagery, climate variables, topographic variables, and soil parent materials. The assumption behind the GNN methods was that two locations with similar combined spatial signatures should also have similar forest structure and composition. Plot data were from the Forest Inventory and Analysis program (FIA) (USDA FS 2003) and Forest Service Current Vegetation Survey program (CVS) (Max et al. 1996). The GNN data used in our analysis included the entire range of the red tree vole. Satellite imagery from which GNN layers were created covered the time period through 2006 in Oregon and 2007 in California. On-the-ground plot data used to create the vegetation layers were collected during 2001–2007.

Accuracy assessments for GNN continuous variables were based on the correlation of observed plot values against predicted (modeled) values. Ohmann and Gregory (2002) used a modified leave-one-out cross-validation approach that yielded results similar to those of a true cross-validation approach, but probably slightly underestimated true accuracy. Accuracy assessments were based on pooled plots for each modeling region.

Our selection of GNN variables was based on: (1) information on habitat relationships from literature and expert knowledge, (2) on-the-ground plot accuracies of vegetation variables, and (3) correlations between modeling covariates. We chose not to use any vegetation data measured on a continuous scale that had plot accuracies with Pearson correlation (r) < 0.5, which equates to moderate agreement between the GNN map prediction and the plot. The accuracy assessment for GNN species composition variables was based on Cohen's Kappa coefficient, which is a measure of agreement between predicted and actual conditions (in this case, dominant tree species), taking into consideration agreement occurring by chance (Cohen 1960). For species composition, we chose not to include any variables that had Cohen's Kappa values < 0.2 (poor agreement) for individual species or < 0.3 (fair agreement) for estimates that were averaged for several species in a group category (e.g., "subalpine conifers"). In cases in which variables were highly correlated (r > 0.7), we dropped the variable with the lowest plot accuracy.

We dropped mean diameter-at-breast-height (dbh) of conifers, mean stand height, mean stand age, and basal area of conifers from our initial list of GNN variables because they were highly correlated with other GNN variables and had the lowest plot accuracies. We selected a consistent set of four variables for forest-stand structure that we included in all of our modeling regions. From least to most accurate (plot accuracy ± SD) these variables were density per hectare of large conifers (≥75 cm dbh; 0.63 ± 0.06), percentage of hardwood cover (0.63 ± 0.05), diameter diversity index (0.71 ± 0.05), and percentage of conifer cover (0.74 ± 0.07). We also developed six variables of forest-species composition based on the percentage of total basal area in a stand composed of six focal tree species or groups of tree species. The latter variables were included as appropriate for each modeling region where tree voles occurred. The average Cohen's Kappas for the tree-species groups or forest-type variables listed in order from lowest to highest accuracy were coast redwoods, (0.31); pines (0.37 ± 0.10); food-source trees (0.37 ± 0.09); subalpine forest (0.40 ± 0.10); and white fir or grand fir (0.43 ± 0.02). The food-source tree group variable consisted of the four tree species that red tree voles used for food, including Douglas-fir, western hemlock, Sitka spruce, and grand fir. Species composition of the four food-source tree species varied among regions with Douglas-fir and western hemlock predominate in the western Cascades and Coast Ranges, Sitka spruce and western hemlock predominate along the coast, and Douglas-fir and grand fir predominate in southwest Oregon.

Abiotic Data

To a considerable extent, patterns of forest vegetation expressed in the GNN maps, especially tree species, reflected the underlying patterns of climate and topography. Therefore, we limited our inclusion of abiotic environmental variables (app. 4) to those that had potentially important influences on tree vole distribution, outside of vegetative patterns.

Because Johnson (1973) suggested that red tree voles are adapted to a regime of moderate temperatures and high rainfall, we used temperature and precipitation variables in our models. We chose these abiotic features because tree voles obtain water from needles they consume (Forsman and Price 2011), and captive voles have been observed licking water from needles (Benson and Borell 1931, Clifton 1960, Maser 1966). Hamilton (1962: 503) stated that "The humid coastal belt, bathed regularly by summer fogs, is effective both in maintaining fresh foliage and providing water to be licked from the needles. The habitat which in less humid zones annually becomes a virtual desert provides a full measure of moisture except in the driest months of early fall." Thus, it seemed reasonable to assess whether precipitation, temperature, and the amount of water contained in needles are important factors influencing the distribution of tree voles, particularly in late summer (July to September).

To model the possible influence of temperature and precipitation on the distribution of red tree voles, we initially considered average annual precipitation, average maximum temperature in August, and summer-moisture stress (the ratio of summer temperature and precipitation) for inclusion in our models. However, the latter two variables were highly correlated ($r > 0.7$), so we dropped moisture stress and replaced it with an index of summer fog that was not highly correlated with summer temperature (*r* = -0.55–0.17). We developed the summer fog index from parameter-elevation regression on independent slope models (PRISM; http://www.prism.oregonstate.edu/) following a multi-step procedure in which we used dew point (DEWPT) and minimum temperature (MINT) grids for the months of July and August. Using ArcGIS (Esri, Inc., Redlands, Calif.), we combined July and August estimates into summer average DEWPT and MINT. The original PRISM maps were produced in 4-km^2 resolution, which was too coarse to capture the variation of DEWPT and MINT at the spatial scale of our habitat modeling, so we downscaled our DEWPT and MINT maps to 100-m^2 resolution and then used statistical software (SAS Institute, Inc., Cary, N.C.) to regress dependent variables against a 100-m^2 resolution digital elevation model (DEM) (Zimmermann and Roberts 2001). The predicted values of the regression were then used to generate smoothed 100-m^2 grids of summer average DEWPT and MINT. We then used ArcGIS to calculate the difference between DEWPT and MINT. As ambient air temperature approaches the dew point temperature, the air becomes saturated and fog or moisture condensation on vegetation can occur. Thus, our summer fog layer (fig. 3-2) represents the average difference between MINT and DEWPT; the lower the value, the higher the potential that fog or condensation will occur during the summer period.

They are thought to be poorly adapted to high-elevation areas characterized by low winter temperatures (Hamilton 1962). Thus another abiotic variable considered was winter minimum temperature, but this was dropped because it was highly correlated (*r* = 0.863) with the summer fog variable in the Cascade Mountains Region. We also included a variable for solar radiation. Southerly aspects in the northern hemisphere receive more annual solar radiation and are relatively warmer and drier than northerly aspects. We used this variable to evaluate whether tree voles tend to place their nests where they will be exposed to higher solar radiation (Meiselman and Doyle 1996, Swingle 2005). We used the potential relative radiation (PRR) index (Pierce et al. 2005) as a more realistic measure for solar radiation than simple aspect.

Data on Presence of Red Tree Voles

Red tree vole presence data used to train and test our habitat models came from nest tree locations found during the random plot study, strategic surveys, and pre-project surveys described in chapter 1. From the random plot study data, plots with red tree vole nests were denoted using a single point in the center of the 1-ha plot, or a single point in the center of the mid-line separating paired plots. To reduce spatial autocorrelation and other modeling issues arising from biased strategic and pre-project survey data (Fourcade et al. 2014), we generated a 2.4 × 2.4-km sampling grid across the range of the red tree vole and randomly selected one nest tree location from each grid cell.

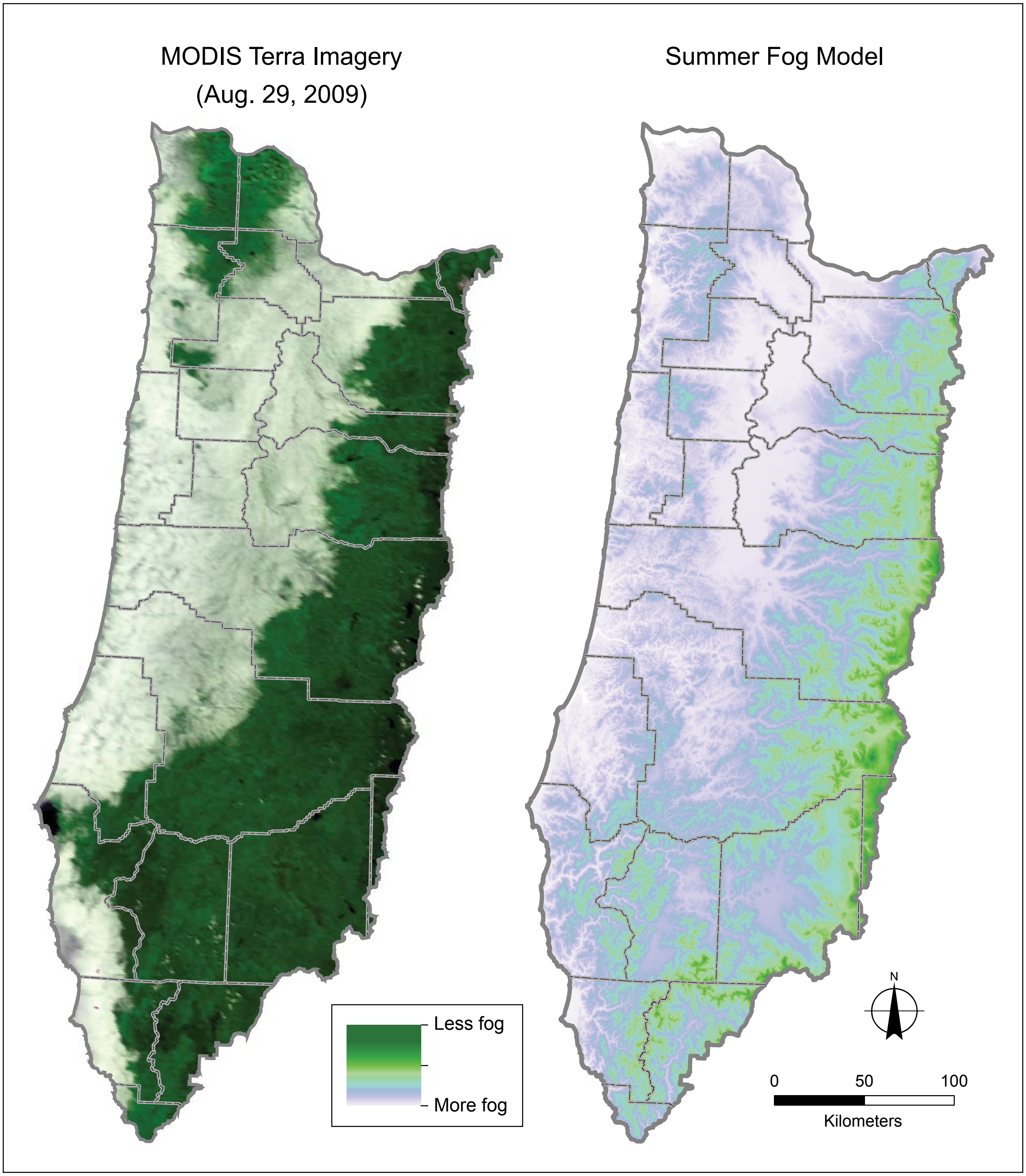

Figure 3-2—2009 National Aeronautics and Space Administration (NASA) moderate resolution imaging spectoradiometer (MODIS) image of summer fog in western Oregon and northwestern California (left) compared to the summer fog index model used in our analysis of habitat suitability for red tree voles (right).

Habitat Modeling Regions

Because of variation in habitat relationships of tree voles in different parts of their range, we split the range into four modeling regions (fig. 3-1). These divisions were based on large-scale geographic provincial boundaries that conformed to the existing GNN modeling regions (http://lemma.forestry.oregonstate.edu/data/structure-maps), and allowed us to maintain a consistent set of variables for each modeling region based on geographic breaks that we thought were warranted, while also obtaining an adequate number of red tree vole locations within each region to conduct model training and testing.

The largest modeling region was the Cascade Mountains Modeling Region (fig. 3-1). This region encompassed about 3.3 million ha, contained about 2.6 million ha of forested land, and included 212 (44 percent) of the 484 red tree vole nest tree locations used in development of our habitat models. Forests in this region primarily consisted of Douglas-fir and western hemlock at lower elevations and Pacific silver fir, mountain hemlock, and subalpine fir at higher elevations. In the southern portion of this region, forests of Douglas-fir and western hemlock were gradually replaced by forests of white fir, Shasta red fir, sugar pine, western white pine, and ponderosa pine. About 68 percent of the forest land in this modeling region was managed by federal agencies.

The second largest modeling region (2.2 million ha) was the North Coast Modeling Region, which included the area west of the Willamette River and north of the line separating Lane and Douglas Counties (fig. 3-1). This region included about 1.6 million ha of forested land and 20 percent ($n = 96$) of the red tree vole locations used in model development. Forests in this region were dominated by Douglas-fir, western hemlock, and western redcedar. Other important forest types in this region included a narrow zone of Sitka spruce and western hemlock along the coast and mixed stands of Douglas-fir, grand fir, bigleaf maple, and Oregon white oak in the foothills adjacent to the Willamette Valley. Forest lands in this modeling region were managed by private owners (61 percent), federal agencies (24 percent), and the Oregon Department of Forestry (15 percent).

The Klamath Mountains Modeling Region (1.8 million ha) contained approximately 1.6 million ha of forest land and 24 percent (n = 118) of the tree vole locations used to develop our models (fig. 3-1). It conformed to the GNN Oregon and California Klamath Mountains Modeling Region, which included portions of the Klamath physiographic provinces of Oregon and California. Forest vegetation was dominated by a diverse array of mixed conifer and mixed conifer/hardwood forests, including Douglas-fir mixed with a variety of other species, including white fir, grand fir, ponderosa pine, sugar pine, western white pine, tanoak, Pacific madrone, canyon live oak, and California laurel. About 73 percent of the forest land in this region was managed by federal agencies.

The South Coast Modeling Region (1.1 million ha) included the southern half of the GNN Oregon Coast Modeling Region (fig. 3-1). It contained about 1.0 million ha of forested land and 12 percent (n = 58) of the red tree vole locations that we used in model development. Forests in this region were mostly dominated by Douglas-fir, with a narrow belt of Sitka spruce and western hemlock along the coast (McCain and Diaz 2002). Forests at the southern edge of this region gradually transitioned into tanoak and coast redwood forests near the Oregon-California border. Most forests in the South Coast Modeling Region were managed by private landowners (65 percent). The other 35 percent were managed by federal agencies (31 percent), or the Oregon Department of Forestry (4 percent).

The division of the North and South Coast Range Modeling Regions was based on a distinct north/south genetic discontinuity of red tree voles (Miller et al. 2006) and ecological differences that indicated a distinct population segment of red tree voles in the northern Coast Ranges of Oregon, north of the Siuslaw River (USFWS 2011).

Habitat Modeling and Model Evaluation

We used the software application MaxEnt (http://www.cs.princeton.edu/~schapire/maxent/) to produce habitat models and maps for red tree vole distribution. MaxEnt uses a machine-learning process and a suite of potential response functions to estimate the most uniform maximum entropy probability distribution of the "average" environmental conditions at known species locations compared to what is available across the modeled area (Phillips and Dudík 2008, Phillips et al. 2006). It produces a prediction for each pixel in a grid map that represents the relative habitat suitability of each pixel for species presence based on the relationship of the pixel's environmental conditions to those pixels with species presence, and its difference from the surrounding background environmental conditions within the modeling region (Phillips and Dudík 2008).

The modeling process fits model-training data (red tree vole nest tree locations) to environmental covariates using various combinations of linear, quadratic, product, hinge, and threshold response functions (features). The use of all feature types may lead to model overfitting depending on the sample size of the training data (Phillips et al. 2006). However, the "auto feature" setting in MaxEnt restricts the model to simpler linear, quadratic, and hinge features for small sample sizes (Elith et al. 2011). Modeling with just the hinge feature produces models with simpler or smoother functions and is generally a useful simplification that can reduce overfitting (Phillips 2013). Our selection of features included a combination of linear, product, and hinge features because our hypothesized variable responses fit these choices. We used the "auto feature" option, further limiting the subset of response features selected, and the model retained only those features with some effect. We also used the "regularization multiplier" (RM) in program MaxEnt to avoid overfitting the data. The RM feature performs a function similar to Akaike's information criterion (Akaike 1974) by penalizing the complexity of the model.

We produced 10 bootstrapped random replicates for each modeling region using 25 percent of the red tree vole location data held out to test the model. We evaluated the contribution that each variable made to the overall model by reviewing the jackknife graphs produced by MaxEnt for mean test gain and area under the receiving curve (AUC) from the bootstrap replicates (Phillips et al. 2006). Based on these graphs, we dropped variables that decreased mean test gain and AUC.

Once the final list of modeling variables was selected, we evaluated and calibrated each habitat model. Model evaluation consisted of three steps. First, we used model test gain to evaluate predictions from our habitat models (Phillips et al. 2006). Test gain scores indicated how different the testing data were from the background data, and were similar to "deviance" in generalized linear modeling. Higher gains indicate larger differences between environmental conditions at locations with tree vole presences and average background environmental conditions. The exponent of gain produces the mean probability value of predicted species presences compared to a random location selected from the background. In addition, differences between model test gain and regularized training gain can be useful for controlling model overfitting, as a large difference is an indication of model overfitting (Phillips 2013).

Second, we used the AUC statistic to evaluate model accuracy and fit to the testing data (Fielding and Bell 1997). The AUC statistic is a measure of the model's predictive accuracy, and produces an index ranging from 0.5 to 1.0, with values close to 0.5 indicating no discrimination and a value of 1.0 indicating perfect predictions. We interpreted the AUC statistic as follows:

- >0.9–1.0 = excellent model.
- >0.8–0.9 = good model,
- >0.7–0.8 = fair model.
- >0.6–0.7 = poor model.
- 0.5–0.6 = model that did not predict much better than a random guess.

Examples of this interpretation in the field of niche-based species-distribution models can be found in Araújo et al. (2005) and Randin et al. (2006). In our analysis, we used 10,000 randomly selected background locations (map pixels) instead of true absence data, so it was not possible to achieve an AUC statistic of 1.0 (Wiley et al. 2003). Specific to our case, AUC statistics represented the percentage of times a location with red tree vole presence would have a higher habitat suitability value than a randomly selected background location without tree vole presence.

Third, we measured model performance based on the continuous Boyce index (CBI), which was designed specifically for testing habitat models produced from presence only data (Boyce et al. 2002, Hirzel et al. 2006). The CBI is based on the Spearman rank correlation coefficient (r_s), which compares the ranks of modeled species presence with the area available to "binned" modeled prediction ranks. A good model predicts an increasing ratio of the percentage of species presence based on testing data to the percentage of the modeled landscape in each model bin as the bin values increase (Hirzel et al. 2006).

Our evaluation process was iterative. We ran the first habitat model using the default RM setting of 1.0 to determine which model variables to use, as described in the previous section. Once variables were selected, we then increased the RM setting by increments of 0.25 or 0.50 while observing changes in test gain and AUC, the difference between test gain and regularized training gain, and CBI, including the shape of the predicted/expected (P/E) curve. Our final calibrated model was the one that had the highest test gain, AUC, and CBI, when means and confidence intervals of the test and regularized training gain were similar and overlapped.

Habitat Map Development

In addition to being useful for model evaluation, the P/E curve also provides information that can be used to reclassify outputs of continuous habitat models into discrete habitat classes (Hirzel et al. 2006). The point along the model-prediction axis (x-axis) where the curve crosses P/E= 1 along the y-axis (fig. 3-3) is the threshold where species presence predicted by the model is higher than would be expected if habitat use was random. This threshold is often used to classify habitat models into binary maps, where logistic probability values greater than the P/E = 1 threshold represent "suitable" habitat (Hirzel et al. 2006). We further divided the continuous scale of probability of occurrence from our habitat models into four habitat classes that ranged from the least to the most suitable habitat conditions, as follows:

- **Unsuitable**—MaxEnt logistic output from zero to the value where the 95-percent confidence interval is below the P/E = 1 threshold. This habitat class represents the lowest suitability class and the model predicts that the species does not occur.
- **Marginal**—MaxEnt logistic output where the 95-percent confidence interval fluctuates along and encompasses the P/E = 1 threshold. This habitat class represents a condition near the low end of where the species may be present.

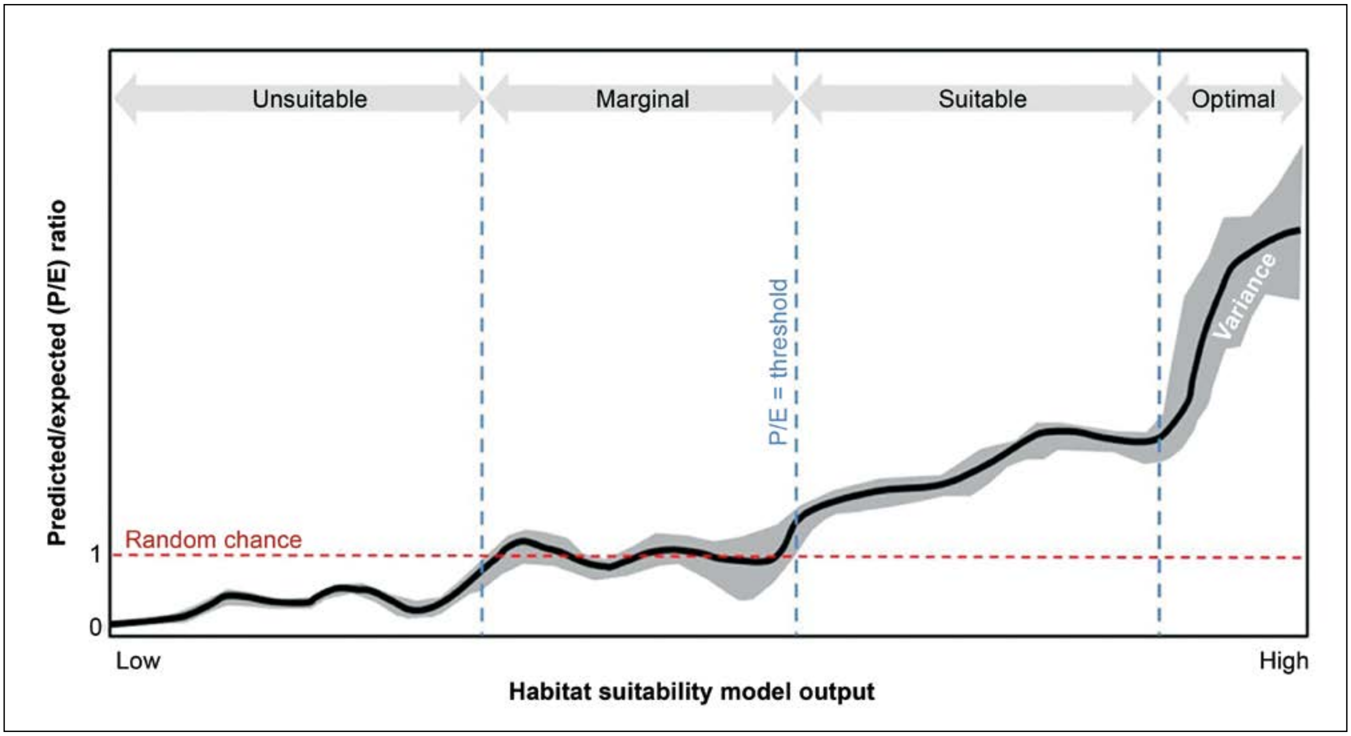

Figure 3-3—Curve illustrating the predicted versus expected ratio (P/E) used to classify continuous outputs from Program MaxEnt habitat models into discrete classes of habitat suitability for red tree voles in western Oregon and northwestern California (modified from fig. 6 in Hirzel et al. 2006: 150). Shaded area bracketing the line indicates 95-percent confidence intervals.

- **Suitable**—MaxEnt logistic output in which the 95-percent confidence interval departs from the P/E = 1 threshold to the logistic output of 0.5. A MaxEnt logistic output value of 0.5 represents the "average" environmental condition associated with the training data. This habitat class represents habitat conditions where the model predicts that the probability of red tree vole presence is higher than expected by random chance, up to average conditions associated with tree vole presence.
- **Highly Suitable**—MaxEnt logistic output ranging from >0.5 to the highest output from the habitat model. This habitat class represents the most suitable, or "above average," conditions and the model predicts red tree vole presence.

We combined the suitable and highly suitable habitat classes into one map class that we termed "potential habitat," which represented areas in which tree voles were likely to occur. Potential habitat maps were based on the average habitat model from 10 bootstrap replicates. We used the standard deviation grids to calculate a 95-percent confidence interval for each grid cell and produced maps based on upper and lower confidence intervals. Summary maps were then used to generate histograms of model-area predictions for each model region and for the entire range-wide modeling area.

We combined the suitable and highly suitable habitat classes into one map class that we termed "potential habitat," which represented areas in which tree voles were likely to occur.

Using Owl Pellet Data to Evaluate Habitat Maps

In addition to the map evaluations discussed above, we conducted independent tests of maps with the spotted owl diet data described in chapter 1. For this test, we defined each spotted owl location as the area within a 1900-m radius around the center of activity of the owls (usually a nest site). To reduce the likelihood of concluding that tree voles were absent when they were actually present (false negatives), we limited the analysis to spotted owl locations where ≥10 individual prey items were identified in pellets. To better represent the timeframe of our map, we also limited data to pellets collected in 2000–2008. We used Mann-Whitney *U*-tests (Mann and Whitney 1947) to assess whether mean habitat suitability values from the models and the mean percentages of potential habitat within owl territories were higher in territories with tree voles in the diet than in territories without tree voles in the diet. Our hypothesis was that average habitat suitability would be higher in spotted owl territories where tree voles were found in owl pellets than in spotted owl territories where tree voles were not found in pellets. Likewise, we expected higher amounts of potential habitat within territories where tree voles were found in pellets than in territories without tree voles in pellets. We also examined correlations between the percentage of tree voles in each pellet collection, and mean habitat suitability, and amounts of potential habitat within each owl territory. We expected positive Pearson correlation coefficients between habitat suitability and amounts of potential habitat with increasing percentage of tree voles in the diet.

Results

Suitability increased logarithmically as density of large conifers increased.

Stand-structure variables were the most informative explanatory variables in our analysis, contributing 42 to 81 percent of the information on which the final model was based (table 3-1). Tree species composition and abiotic variables contributed 9 to 31 percent (table 3-2) and 11 to 27 percent (table 3-3), respectively. In terms of stand structure, density of large conifers (≥75 cm dbh) was the strongest variable, with habitat suitability increasing logarithmically as density of large conifers increased (app. 4, fig. A4-1). On average, the next most informative variable was diameter-diversity index, which was a measure of stand structural diversity. Habitat suitability increased sigmoidally as diameter-diversity index increased (app. 4, fig. A4-2). The third most important variable was percentage of conifer cover, which also had a positive sigmoidal relationship with habitat suitability (app. 4, fig. 4A-3). However, habitat suitability decreased as conifer cover approached 100 percent, indicating that some canopy opening was desirable. On average, hardwood cover contributed about 4 percent of the information that produced the habitat models, and in general had a negative relationship with habitat suitability (app. 4, fig. 4A-4).

Table 3-1—Percentage of contribution of stand structure variables to the final models in the analysis of habitat suitability for red tree voles in Oregon

Modeling region	Density of large conifers[a]	Diameter diversity index[b]	Conifer cover	Hardwood cover
Cascade Mountains	21.0	8.5	8.3	4.3
Klamath Mountains	24.7	14.2	18.3	1.4
North Coast	48.2	12.3	16.5	3.5
South Coast	24.6	33.5	2.9	6.2

[a] Density of large conifers lowered gain the most when removed from models in the North Coast Modeling Region.
[b] Diameter diversity index had the highest gain by itself for each modeling region and lowered gain the most when removed for only the South Coast Modeling Region.

Table 3-2—Percentage of contribution of forest species composition variables to the final models in the analysis of habitat suitability for red tree voles in Oregon

Modeling regions	Food[a]	Subalpine[b]	White fir	Redwood	Pine
Cascade Mountains	11.5	12.2	3.5		4.0
Klamath Mountains	11.2	0.7	1.9		1.6
North Coast	8.1				1.4
South Coast	5.9			2.0	0.8

[a] The “Food” variable included the group of tree species used as food by tree voles: Douglas-fir, Sitka spruce, western hemlock, and grand fir.
[b] High-elevation conifers such as Pacific silver fir, noble fir, subalpine fir, and mountain hemlock.

Table 3-3—Percentage of contribution of abiotic environmental variables to the final models in the analysis of habitat suitability for red tree voles in Oregon

Modeling region	Summer fog[a]	Average maximum summer temperature	Average annual precipitation[b]	Solar radiation
Cascade Mountains	9.7	10.0	4.4	2.5
Klamath Mountains	3.8	3.4	13.1	5.8
North Coast	5.9	1.4	2.0	1.7
South Coast	13.8	8.0	1.7	0.8

[a] Summer fog lowered gain the most when removed for the Cascade Mountains Modeling Region.
[b] Average annual precipitation lowered gain the most when removed from models in the Klamath Mountains Modeling Region.

In terms of forest tree-species composition, the strongest variable was the percentage of total stand basal area composed of food-source trees, which was primarily Douglas-fir, but also included grand fir, and western hemlock and Sitka spruce in the North Coast Modeling Region (table 3-2). The relationship between food-source tree species and habitat suitability was mostly linear, where habitat suitability increased as percentage of basal area of food-source trees increased (app. 4, fig. 4A-5). The rest of the tree-species variables showed negative exponential or linear relationships with habitat

Summer fog was the most important abiotic variable, followed by summer maximum temperature, average annual precipitation, and solar radiation.

suitability (apps. 4, fig. 4A-6 through 4A-9). Habitat suitability decreased rapidly as percentage of basal area of subalpine conifers (app. 4, fig. 4A-6), white fir (app. 4, fig. 4A-7), coast redwood (app. 4, fig. 4A-8), and pine (app. 4, fig. 4A-9) increased, suggesting that red tree voles were less likely to be present at higher elevations and in forests dominated by coastal redwoods and pines. On average, summer fog (app. 4, fig. 4A-10) was the most important abiotic variable, followed by summer maximum temperature (app. 4, fig. 4A-11), average annual precipitation (app. 4, fig. 4A-12), and solar radiation (table 3-3).

Our final models had mean test AUCs that ranged from 0.82 to 0.85 and CBIs that ranged from 0.996 to 0.999 ($P < 0.001$). These test statistics indicate that our models produced moderate to good predictions of red tree vole presence. The independent evaluation of the modeled habitat map based on owl pellet data produced similar results. At the rangewide scale, amounts of potential habitat ($U = 6251.0$, $P < 0.001$) and mean habitat suitability (fig. 3-4; $U = 6368.5$, $P < 0.001$) within owl territories where tree voles were found in owl pellets (n = 81) were higher than in owl territories where tree voles were not found in pellets (n = 92). There was fair to moderate correlation between the percentage of tree voles in owl pellets and mean habitat suitability ($r = 0.546$, $P < 0.001$) and amount of potential habitat ($r = 0.506$, $P < 0.001$) within owl territories (fig. 3-5).

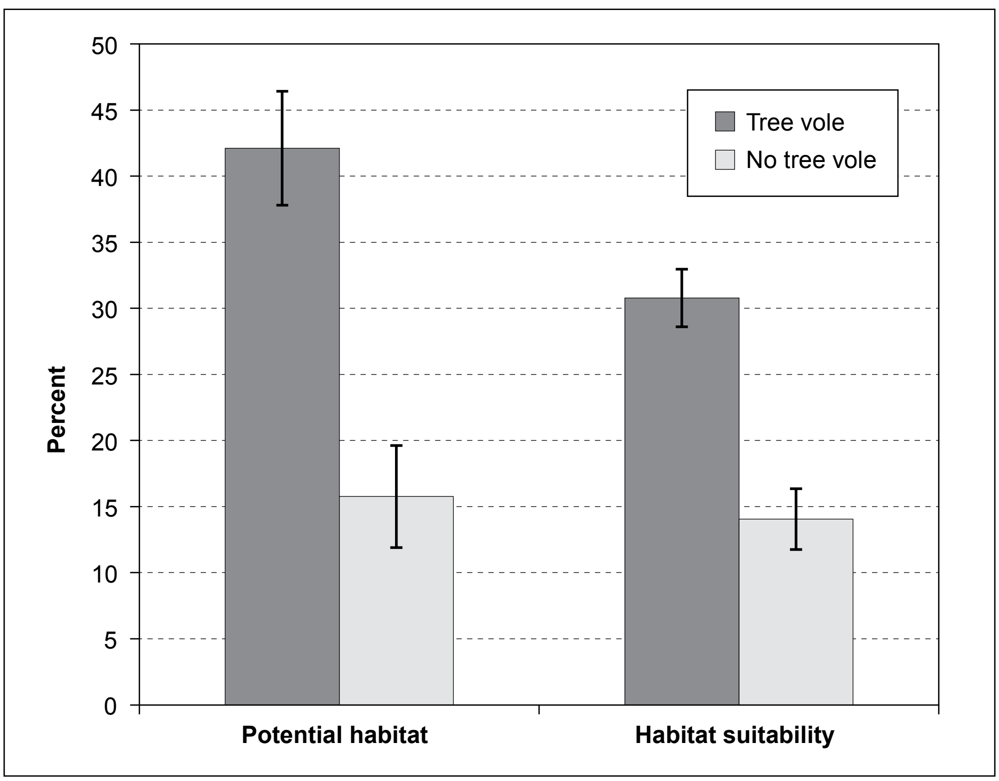

Figure 3-4—Mean amount of potential habitat and mean habitat suitability for red tree voles in northern spotted owl territories in which tree voles were found in owl pellets (tree vole) versus spotted owl territories in which tree voles were not found in pellets (no tree vole). Error bars indicate 95-percent confidence intervals.

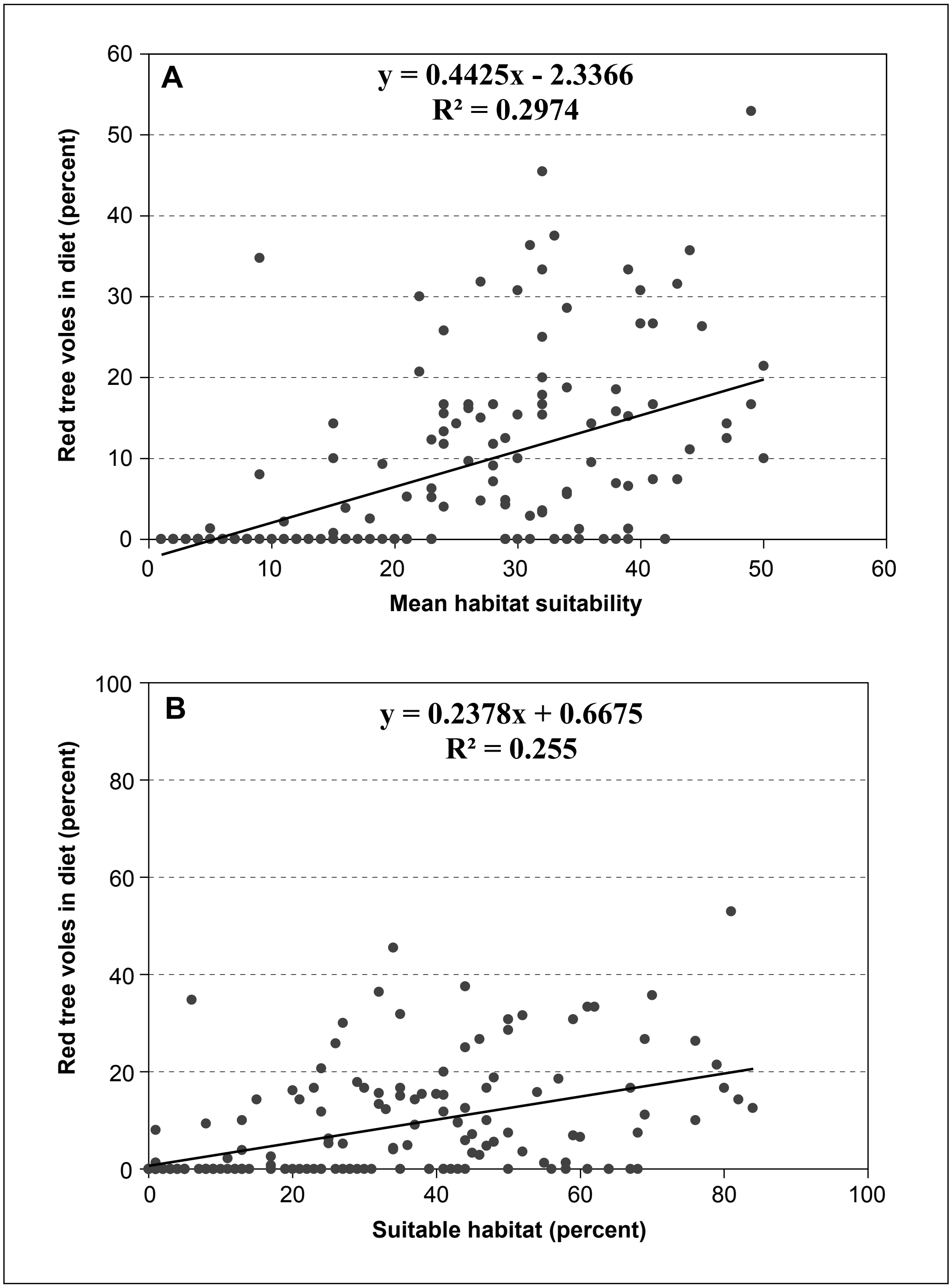

Figure 3-5—Linear correlations between percentage of red tree voles in diets of northern spotted owls (percentage of prey numbers) and mean habitat suitability within the owl territories in which pellets were collected (A), and the percentage of potential habitat within owl territories (B). Owl territories were defined as the area within 1900 m of the owl nest site or center of activity.

Based on the summary statistic maps produced during bootstrapping, we estimated that there was a total of 1.6 million ha of red tree vole habitat within the range of the red tree vole as of 2006–2007 (fig. 3-6). Of this, about 1.1 million ha occurred on federal lands (Forest Service, BLM, and National Park Service), and 0.5 million ha was on nonfederal lands (state, county, or private). Of the 1.1 million ha of habitat on federal lands, at least 59 percent was in reserve land-use allocations designated in the NWFP (USDA and USDI 1994). We could not estimate the total amount of tree vole habitat in NWFP reserves because Riparian Reserve allocations designated in the NWFP were never mapped. Aside from a few state parks, none of the 0.5 million ha of red tree vole habitat on nonfederal lands had any restrictions on harvest to protect tree voles.

The majority of potential tree vole habitat was located in the Cascade Mountains Modeling Region (fig. 3-6). In this modeling region, potential habitat was concentrated on federal lands in the central Cascades in eastern Lane and Douglas Counties. In the Cascade Mountains north of Lane County potential habitat was concentrated along the major river valleys of the Santiam, Clackamas, and Bull Run Rivers and their tributaries in Marion and Linn Counties. These concentrations of potential habitat appeared to be somewhat isolated from each other except where the headwaters converged between river drainages (fig. 3-6). South of the Rogue River in Jackson County, our models predicted little potential habitat in the Cascades Monitoring Region (fig. 3-6).

In the Klamath Mountains Modeling Region, potential tree vole habitat appeared to be fairly well distributed from north to south, but occurred in smaller blocks and patches than in the Cascade Mountains Modeling Region (fig. 3-6). This was expected because of the checkerboard pattern of land ownership, where square-mile sections of private land alternated with square-mile sections managed by the Bureau of Land Management. The largest, most contiguous area of potential habitat in the Klamath Modeling Region occurred in the forests separating the Umpqua and Rogue Valleys in Douglas and Josephine Counties (fig. 3-6). The small amount of potential habitat in Jackson County was mainly located north of the Rogue River and west of the Applegate River (fig. 3-6). Although the model predicted a large area of potential habitat in western Siskiyou County in California (fig. 3-6), no tree voles have been documented in that area, despite numerous surveys (Dunk and Hawley 2009, chapter 1). Thus, that area appears to be outside the range of the red tree vole.

Although our models predicted large areas of potential habitat on the Tillamook and Clatsop State Forests in the four northernmost counties in the Oregon Coast Ranges, recent surveys indicate that tree voles were absent from most of those areas.

Potential habitat within the two coastal modeling regions mostly occurred on BLM and Forest Service lands (fig. 3-7). Although our models predicted large areas of potential habitat on the Tillamook and Clatsop State Forests in the four northernmost counties in the Oregon Coast Ranges (fig. 3-6), recent surveys indicate that tree voles were absent from most of those areas (Price et al. 2015, chapter 1).

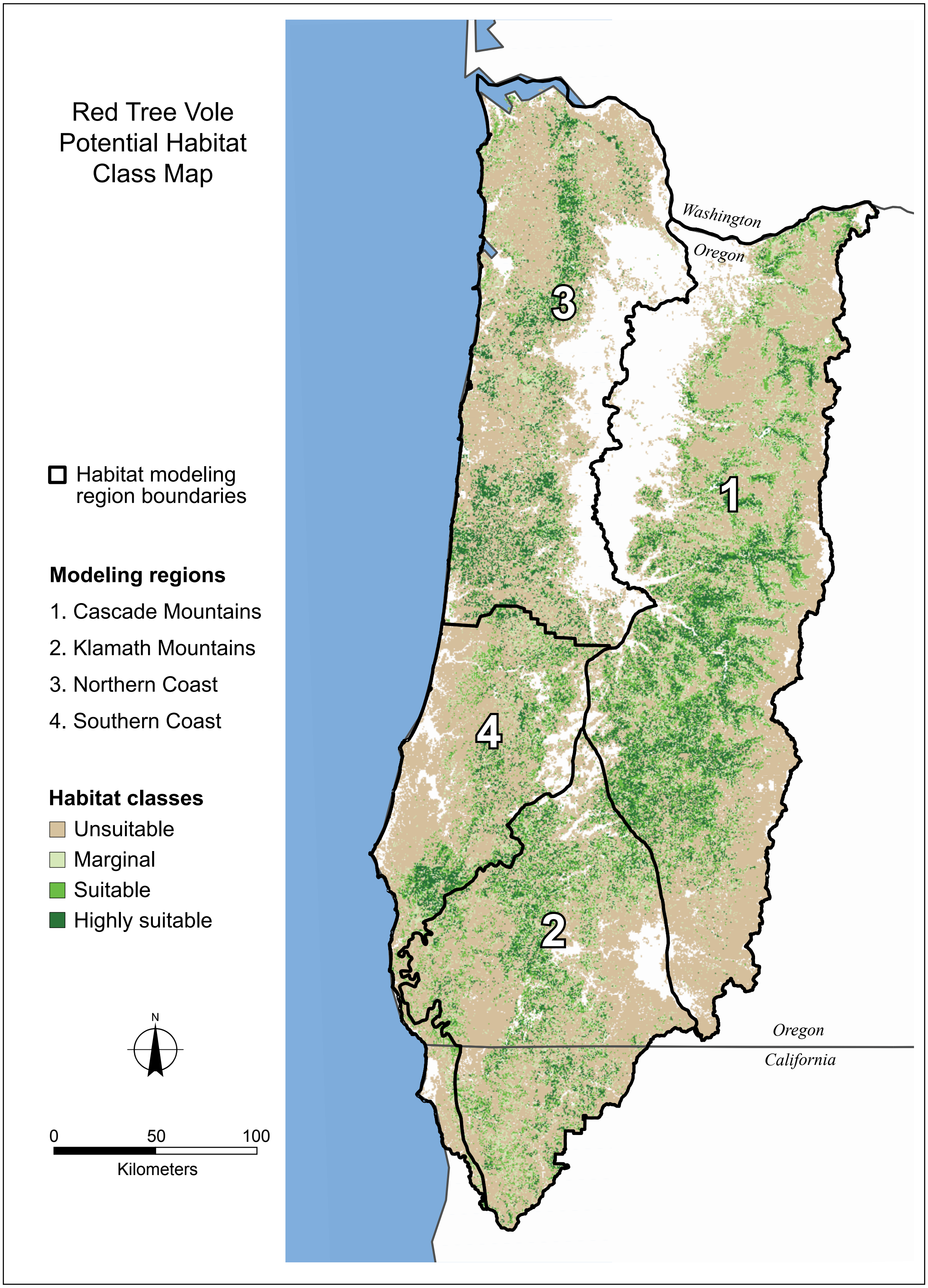

Figure 3-6—Predicted map of habitat suitability for red tree voles based on forest conditions in 2006 (Oregon) and 2007 (California).

Discussion

Our habitat modeling and mapping results provide a spatial representation of potential red tree vole habitat. Although obviously related, this should not be confused with maps of current red tree vole distribution developed from actual vole locations in chapter 1. Habitat models work well for producing maps that reflect the fundamental niche of the animal, but it is the realized niche that matters most for species occurrence. Although our map shows where forest structure, tree-species composition, and climate-based environmental gradients combine to produce conditions likely to be suitable for red tree voles, the analysis did not account for other factors, such as the history of natural- and human-caused forest disturbances, that can have long-lasting effects on the distribution of an arboreal species like the red tree vole. For example, the absence of tree voles from most of the apparently suitable habitat within the Tillamook and Clatsop State Forests (Price et al. 2015) is probably the result of the entire area being almost completely logged or burned or both between 1880 and 1960, leaving few refugia for tree voles, and thus few sources of nearby colonizers. Subsequent management of the area with a focus on thinning of young stands and short rotations (Wells 1999) has probably made recolonization by tree voles even less likely. For an arboreal species that normally disperses only tens or hundreds of meters from its natal site (Swingle 2005), rapid and sustained reductions in habitat quality over tens or hundreds of thousands of hectares will likely have very long-term consequences on distribution.

The absence of tree voles from most of the apparently suitable habitat within the Tillamook and Clatsop State Forests is probably the result of the entire area being almost completely logged or burned or both between 1880 and 1960.

Similarly, although our habitat models classified some of the forests of western Siskiyou County in northern California as potential habitat for tree voles, few vole nests were found in that area. Whether this was due to abiotic factors or a physical barrier created by high-elevation forests of true fir in the Siskiyou Mountains to the north and west was unclear.

As with all models, there is considerable uncertainty regarding our map of potential habitat (fig. 3-7). This uncertainty comes from a variety of sources, including accuracy of the GNN data and uncertainty in the climate models that we used to produce maps of precipitation and temperature. Nevertheless, we think our models are useful for estimating the approximate distribution of red tree vole habitat within the millions of hectares that compose the geographic range of the red tree vole. In addition, our models allowed us to investigate relationships between the presence of tree voles and various environmental conditions.

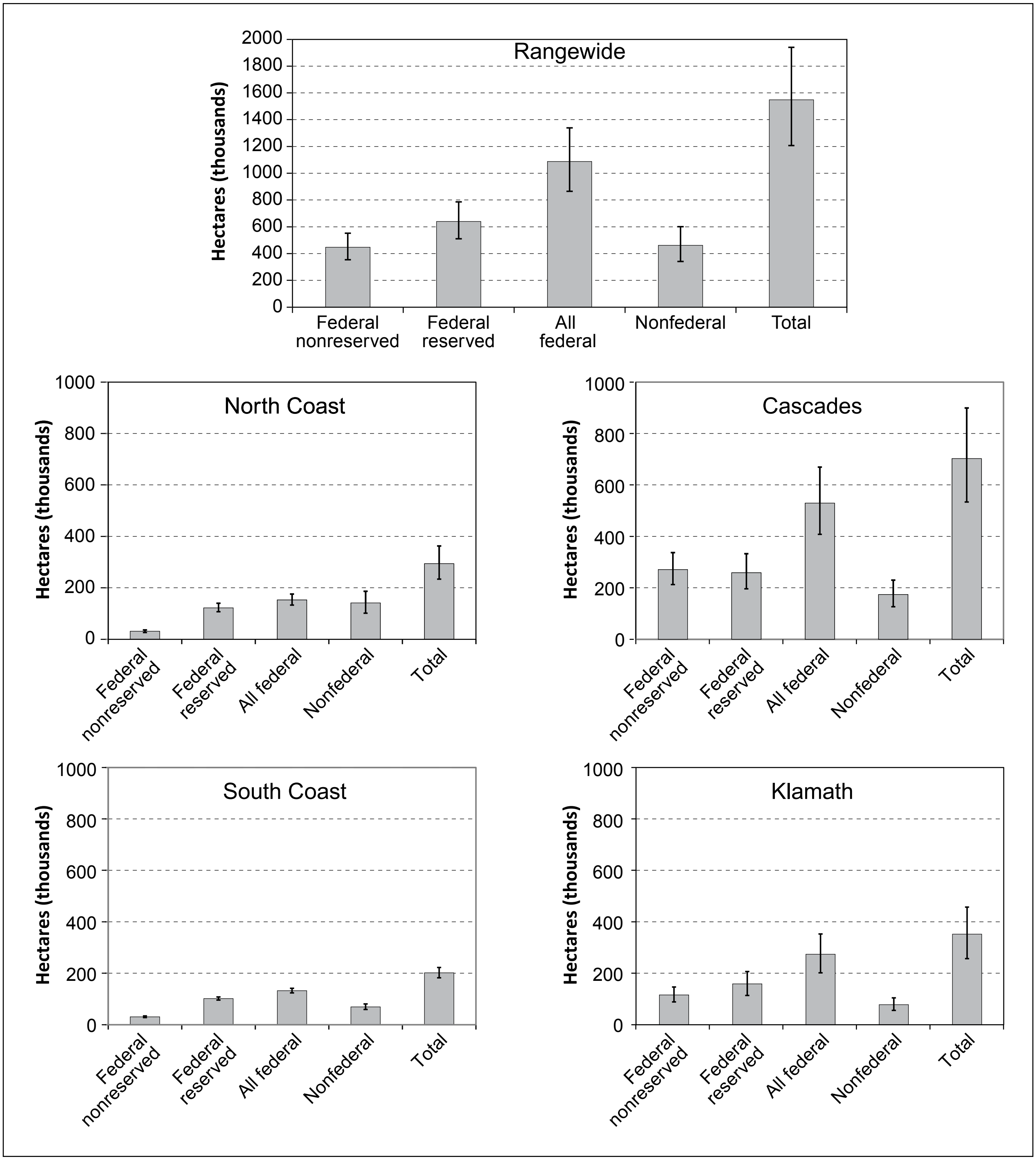

Figure 3-7—Area estimates (means and 95-percent confidence intervals) of potential red tree vole habitat (suitable and highly suitable habitat classes) for the range and by modeling region.

The highest suitability classes included the oldest and most structurally complex forests. These results were not unexpected and the fact that other researchers have found that the probability of red tree vole nest occurrence was positively associated with late-successional and old-growth forest conditions.

Overall, stand structure appeared to have the greatest influence on our models, especially in the coastal zones. To help land managers interpret what our habitat classes represent on the ground, we provided mean stand attributes summarized by habitat classes (table 3-4). The marginal class of habitat included young forests with an average age of 75 years. The highest suitability classes included the oldest and most structurally complex forests (table 3-4). These results were not unexpected, given the results in chapter 1, and the fact that other researchers have found that the probability of red tree vole nest occurrence was positively associated with late-successional and old-growth forest conditions (Dunk and Hawley 2009).

Finally, the map variables that went into producing the tree vole habitat model were all designed for use at large spatial scales (Ohmann and Gregory 2002). Thus, it is unreasonable to expect that the habitat map would perfectly match every patch of red tree vole habitat across the range of the species. However, as light detection and ranging data (LiDAR) (Dubayah and Drake 2000) become increasingly available in the future, we expect that it will be possible to develop increasingly accurate maps of tree vole habitat.

Table 3-4—Mean ($\bar{x}$ ± SE) and median (in parentheses) forest stand characteristics for modeled red tree vole habitat classes based on forest inventory plot data

Habitat class	Density of large conifers per ha[a]	Diameter diversity index	Percentage of conifer cover	Stand age
				Years
Unsuitable	6.8 ± 0.4 (0)	3.7 ± 0.1 (3.2)	51.9 ± 0.9 (58)	58.6 ± 1.9 (46)
Marginal	13.3 ± 1.1 (3)	4.9± 0.1 (5.2)	66.8 ± 1.1 72)	75.3 ± 4.6 (56)
Suitable	24.3 ± 1.5 (19)	6.0 ± 0.1 (6.0)	71.5 ± 1.0 (76)	91.8 ± 6.5 (66)
Highly suitable	34.2 ± 1.6 (30)	6.6 ± 0.1 (6.5)	69.8 ± 1.0 (73)	95.4 ± 5.7 (82)

[a] Conifers ≥75 cm diameter-at-breast-height (dbh).

Management Implications

Maps produced in our analysis provide context for analyzing the status and trends of red tree vole habitat. The habitat modeling and mapping process can be easily repeated using future Landsat imagery, allowing managers to continue to monitor habitat as it changes. Secondly, and perhaps more importantly, our habitat maps can be used to inform future management decisions on how to design projects to avoid or minimize impacts and where to focus conservation efforts for restoration and maintenance of future habitat. However, our habitat maps are meant to be used at the landscape scale (watershed scale or larger), and are not designed to identify any particular stand of habitat on the ground. They are well-suited for illustrating current concentrations of potential habitat on the landscape, and connectivity among these areas. These maps are similar in quality and accuracy to maps developed for monitoring habitat for northern spotted owls (Davis et al. 2011, Lint 2005) and marbled murrelets (Huff et al.2006, Raphael et al. 2011). When the NWFP Effectiveness Monitoring Program was developed, it included a potential module for "survey and manage species" that included the red tree vole (Mulder et al. 1999). Based on our models, we can now begin to monitor habitat for this arboreal species, providing land managers and regulatory agencies with useful maps and stand structure information for improving forest management and conservation of the species.

Models like ours will help managers address other species of concern, especially in cases where habitat suitability maps can be used to estimate species population dynamics and interactions. For example, the NWFP Effectiveness Monitoring Program has sponsored a series of rangewide demographic meta-analyses to monitor population trends of northern spotted owls (Anthony et al. 2006, Dugger et al. 2016, Forsman et al. 2011). A nascent feature of the spotted owl meta-analyses has been to incorporate covariates to model habitat and climate factors that may influence demography. Climate has been considered a surrogate for modeling population dynamics of some species of spotted owl prey, but links between diets of spotted owls and prey population dynamics are not well documented. Habitat suitability models for northern spotted owl prey such as red tree voles, northern flying squirrels (*Glaucomys sabrinus*), and wood rats (*Neotoma fuscipes*, *N. cinerea*), could be incorporated into predictive models for spotted owl diets which in turn may have utility in developing covariates for analyses of the demographic performance of spotted owls. These methods would provide natural resource managers with a powerful tool to better address the needs of species of concern and address broader issues of ecosystem management.

Chapter 4: Long-Term Trends in Habitat and Geographic Distribution of Tree Voles in Oregon, 1914−2006

Introduction

In previous chapters, we used field data, specimen records, and habitat models to describe the distribution and habitat of red tree voles (*Arborimus longicaudus*) and Sonoma tree voles (*A. pomo*). In this chapter, we use maps from 1914, 1936, and 2006 to describe how the distribution and extent of potential red tree vole habitat has changed in western Oregon during the last century. Our objective was to develop a better understanding of the history of habitat change and its potential effect on the distribution of tree voles and to help managers and policy makers understand why the red tree vole was listed as a species of special management concern in the Northwest Forest Plan (USDA and USDI 1994) and why the U.S. Fish and Wildlife Service concluded that the red tree vole warranted listing under the Endangered Species Act (USFWS 2011). This retrospective analysis is an important first step in understanding the extent of changes that have transformed the landscape of the Pacific Northwest during the last century.

Methods

The oldest forest map that we used to assess potential vole habitat was compiled in 1911−1913 and published by the Oregon State Board of Forestry.

The oldest forest map that we used to assess potential vole habitat was compiled in 1911−1913 and published by the Oregon State Board of Forestry (1914). This map was prepared under the direction of Francis Elliott, the State Forester of Oregon, and showed the location of lands covered with merchantable timber, young forests, harvested areas, areas covered with brush, recently burned areas, and land used primarily for agriculture and grazing. The 1914 map was based on examination of county records, followed by field reconnaissance and mapping surveys conducted by township. The minimum mapping unit was not specified in the instructions to surveyors; however, the minimum mapping unit polygon size in the digitized version of this map was 15 ha (http://www.oregon.gov/DAS/CIO/GEO/pages/alphalist.aspx#f).

We used a subset of the "merchantable timber" classification from the 1914 map to represent potential tree vole habitat in 1914. The instructions given to surveyors for mapping merchantable timber stated that, "Land bearing merchantable timber will, in the main, consist of areas covered with virgin timber" (fig. 4-1), which included both old- and "second-growth" forests (Elliott 1912: 65–66). Areas in which less than a third of the merchantable timber had been removed by fire or partial harvest were also classified as merchantable timber. The mapping instructions further stated that, "In determining whether or not a stand is merchantable,

Figure 4-1—A “virgin” forest of old-growth Douglas-fir in western Oregon, circa 1910 Photograph from Elliot (1912: 10).

Figure 4-2—Old-growth Douglas-fir near the Columbia River, circa 1930. Photograph from Andrews and Cowlin (1940: 3).

the size of the timber should be the only criterion. Even though the timber on a tract will be inaccessible for years to come, it should be considered merchantable if it has attained sawlog or piling size.” At that time, Douglas-fir piling dimensions had butt-end diameters of 33 to 43 cm, stripped clean of bark (Cline and Knapp 1912). The minimum diameter for merchantable logs was 41 cm beneath the bark (Cline and Knapp 1912). We further restricted the merchantable timber class in the 1914 map to exclude forest types not used by tree voles, including ponderosa pine, lodgepole pine, mixed pine, coast redwoods, and high-elevation subalpine forests of Pacific silver fir, mountain hemlock, subalpine fir, and

Englemann spruce. These forest cover types were not specifically identified in the 1914 map, but were excluded by masking areas that were identified as those forest types in a mapping exercise conducted in 1930s (Andrews and Cowlin 1940).

Our second map of potential habitat was based on a forest map compiled by the U.S. Forest Service Pacific Northwest Forest and Range Experiment Station in 1936 (Andrews and Cowlin 1940). This map was based on aerial photos, county records, and field reconnaissance, and had slightly better spatial resolution than the 1914 map. Surveyors were told to map forest patches ≥16 ha, but were given liberty to map patches as small as 8 ha, if it did not slow progress (Andrews and Cowlin 1940). The digitized geographic information systems (GIS) version of this map (Harrington 2003) had a few polygons that were smaller than 8 ha, but for our purposes, we only used polygons that were ≥15 ha to approximate the minimum mapping unit of the 1914 map. From the 1936 map, we identified potential tree vole habitat as areas mapped as old-growth (fig. 4-2) or large second-growth Douglas-fir, Sitka spruce, or western hemlock (table 4-1; Andrews and Cowlin 1934).

Our third habitat map was the 2006 map of potential tree vole habitat described in chapter 3. This map, which had a spatial resolution of 1 ha, included forested stands that averaged >80 years of age and primarily consisted of Douglas-fir trees that were >51 cm diameter-at-breast-height (dbh). To make this map comparable to the hand-drawn maps from 1914 and 1936, we used GIS filtering and smoothing techniques to remove small isolated pixels of habitat and produce a habitat map with a minimum mapping unit of 15 ha.

Table 4-1—Forest classifications used to map potential red tree vole habitat based on the digitized version of the 1936 forest habitat map of western Oregon (Andrews and Cowlin 1936)

Forest type	Definition
Old-growth Douglas-fir	Forest with 60 percent by volume of Douglas-fir where the major part of the volume was in trees >102 cm diameter-at-breast-height (dbh). Also included what was termed “small old growth” where the major part of the volume was in slower growing trees 51–102 cm dbh, mainly occurring in the Cascade Mountains.
Large “second-growth” Douglas-fir	Forest with 60 percent by volume of Douglas-fir where the majority of the volume was in trees 51–102 cm dbh. Mostly stands that were between 90–160 years old.
Large Sitka spruce or western hemlock	Forest with 50 percent by volume of Sitka spruce or western hemlock in which most of the volume was in Sitka spruce >61 cm dbh or western hemlock >51 cm dbh. Rarely in pure stands; usually in mixture with Douglas-fir, western redcedar, or true fir.

We used the 1914, 1936, and 2006 forest cover maps to manually delineate in GIS the potential geographic distribution of red tree voles in Oregon at each time step.

We used the 1914, 1936, and 2006 forest cover maps to manually delineate in GIS the potential geographic distribution of red tree voles in Oregon at each time step. We summarized changes in potential habitat and red tree vole distribution for the entire range in Oregon and also by the geographic subregions defined in chapter 1 (fig. 1-1). Means are reported along with $\bar{x}$ ± 95 percent confidence intervals.

Results

Change in Potential Habitat

We estimated that the total amount of potential tree vole habitat present in Oregon in 1914 was 3.3 million ha or 62 percent of the 5.3 million ha of forested area capable of developing into potential tree vole habitat (fig. 4-3). At that time, much of the potential habitat was distributed in a relatively contiguous "mosaic" that covered most of the western Cascades and much of the Klamath Mountains (fig. 4-3). The mean size of potential tree vole habitat patches in 1914 was 12 900 ± 9800 ha.

By 1936, the estimated amount of potential tree vole habitat had declined to 2.8 million ha, or 53 percent of the forested area capable of developing into potential tree vole habitat (fig. 4-3). The decline was due primarily to harvest and to the 1933 Tillamook Burn, which incinerated slightly over 99 000 ha (10 percent) of forest land in the North Coast Subregion (Morris 1934, 1936). As a result of habitat fragmentation from timber harvest and fire, the mean size of potential habitat patches declined to 4900 ± 3800 ha, a reduction of more than 62 percent in a span of 22 years. Despite the considerable reduction in mean patch size of potential vole habitat, however, there were still many areas where habitat occurred as large contiguous mosaics.

By 2006, we estimated that 22 percent (1.2 million ha) of the area capable of developing into potential tree vole habitat in western Oregon was still covered by potential habitat (fig. 4-3). This amounted to a 65-percent overall reduction in the area of potential tree vole habitat between 1914 and 2006 (fig. 4-4). The 1.2 million ha of potential vole habitat that was present in 2006 included 819 000 ha that was classified as potential habitat in 1914 plus 342 000 ha that had developed into potential habitat since 1914. The latter areas mostly consisted of mature forests that had regenerated on areas burned in large wildfires between 1840 and 1940. The loss of potential vole habitat was accompanied by a 98 percent reduction in the average size of the remaining patches of potential habitat, from 12 900 ± 9800 ha in 1914 to 240 ± 50 ha in 2006. In other words, the areas of potential vole habitat changed from the dominant forest type on the landscape in 1914 to a highly fragmented network of smaller patches within a mosaic of predominantly young forests by 2006 (fig. 4-3).

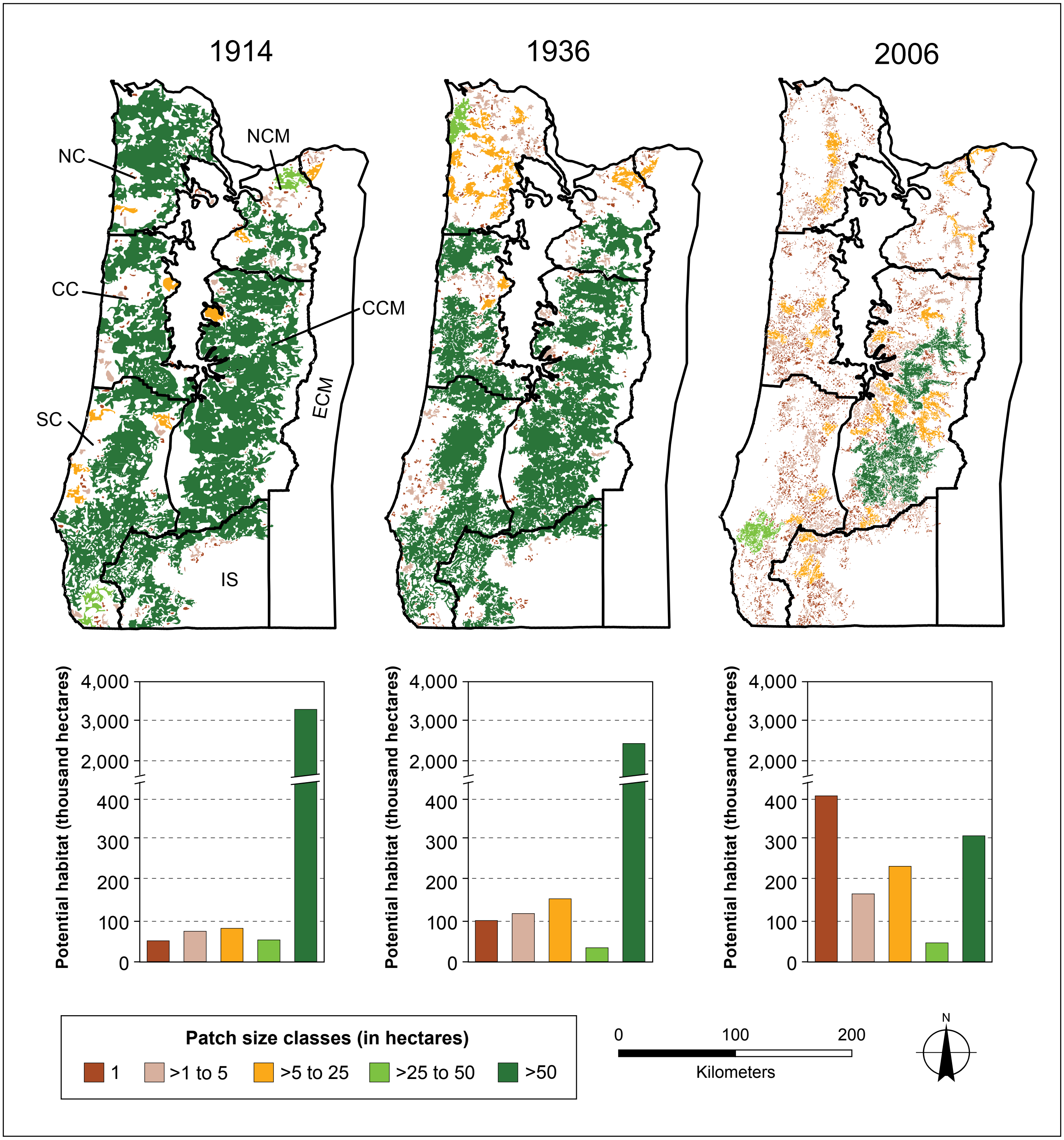

Figure 4-3—Estimated distribution of potential red tree vole habitat in Oregon in 1914, 1936, and 2006. Subregions were North Coast (NC), Central Coast (CC), South Coast (SC), Interior Southwest (IS), Central Cascades (CCM), North Cascades (NCM), and East Cascades (ECM).

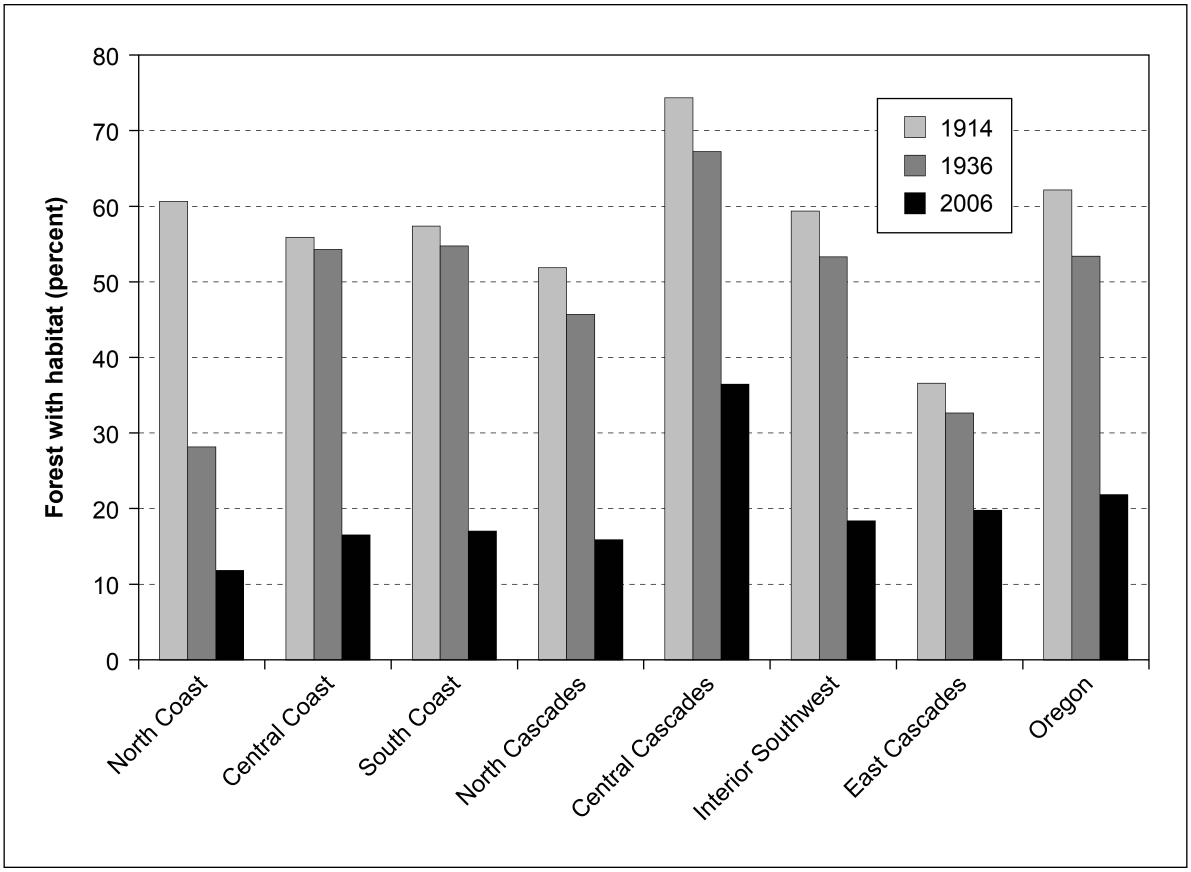

Figure 4-4—Estimated percentage of habitat capable lands in western Oregon covered by potential habitat for red tree voles in 1914, 1936, and 2006. "Habitat capable lands" refers to lands capable of producing habitat for red tree voles.

Estimated Effect on the Geographic Distribution of Tree Voles

Based on the distribution of potential habitat and historical records of red tree voles, we estimated that the rangewide geographic distribution of red tree voles in 1914 included 5.3 million ha in Oregon, mostly west of the crest of the Cascade Mountains, but with a small extension east of the crest in the Hood River basin (fig. 4-3). The Applegate River and the upper reaches of the Rogue River largely defined the edge of the range in southern Oregon. We estimated that the geographic distribution of the vole covered 4.1 million ha by 2006, a 23-percent reduction since 1914 (fig. 4-5). We attributed this reduction to habitat loss and probable extirpation of tree voles in portions of the historical geographic range. The largest estimated range contractions were 80 percent in the North Coast Subregion and 73 percent in the North Cascades Subregion, which experienced large decreases in habitat. (fig. 4-5).

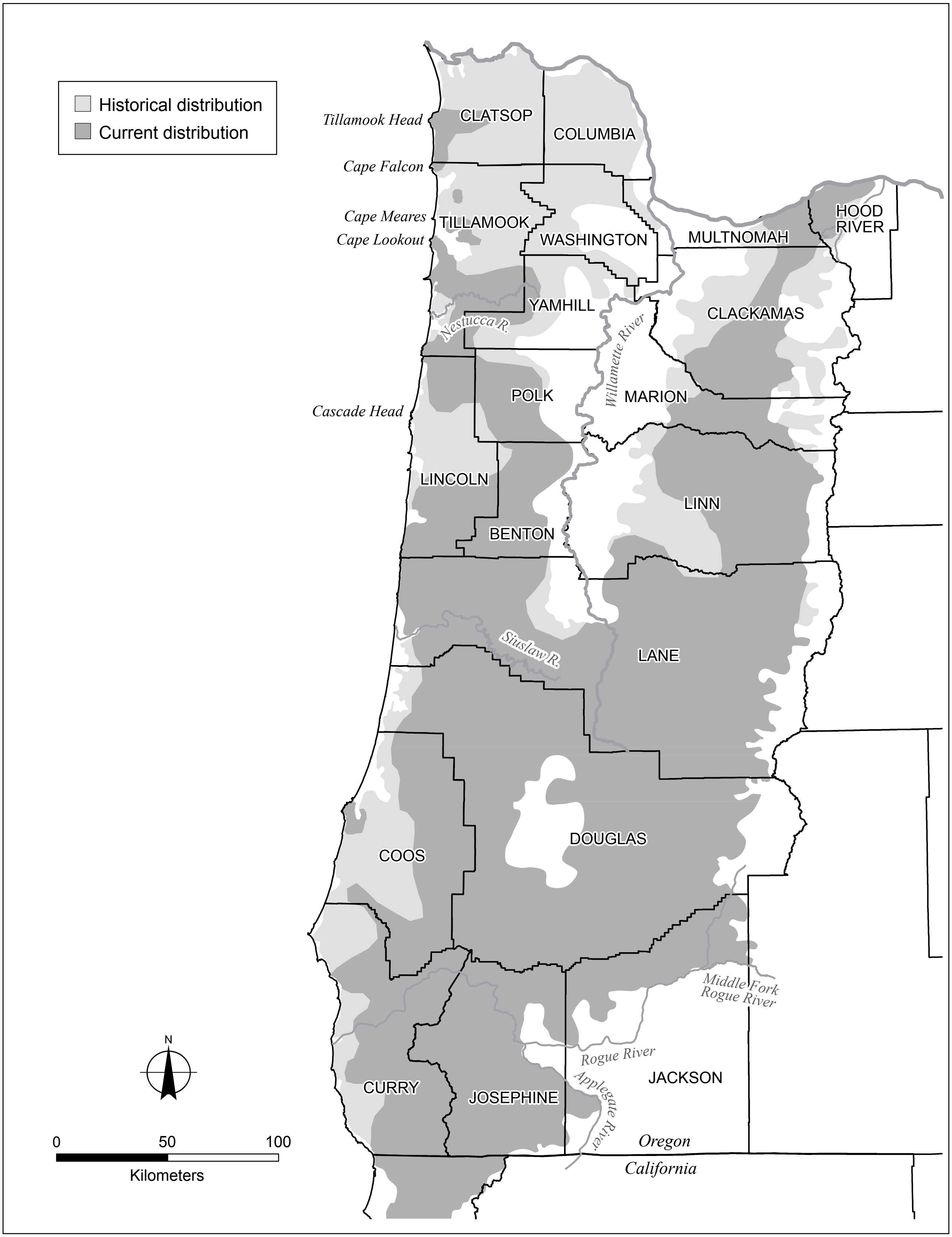

Figure 4-5—Historical (1914) and current (2006) estimates of red tree vole distribution based on species locations and modeled habitat maps.

Discussion

Based on our estimates of the amount of potential red tree vole habitat, as modeled in chapter 3, and the amount of potential habitat estimated from the 1914 and 1936 geographic distribution maps, we concluded that red tree voles probably had a much larger range in the early 19^{th} century than in 2006 (fig. 4-5). Despite a series of very large wildfires that occurred between 1840 and 1902, much of the Coast Ranges and western Cascades were still covered by extensive areas of contiguous old forest in 1914 (fig. 4-3). At that time, industrial timber harvesting was in its early stages in western Oregon but the rate of harvesting was steadily increasing and there were already large areas adjacent to the Columbia River that had been clearcut (fig. 1-6).

Evidence of forest decline in Oregon was observed as early as 1909, when Kellogg (1909) estimated that old forests had already declined by 12 percent and were being cut at a rate that was three times faster than the rate of replacement. A little over a decade later, Greeley (1925) reported that forests in western Oregon were considerably more diminished and fragmented than in the previous century. Shortly thereafter, Peavy (1929: 17) predicted that old forests on private lands in Oregon would be "…approaching exhaustion in twenty-five years, and considerable inroads will have been made in national forest stumpage." For the time of Peavy's prediction, we estimated that 48 percent of potential tree vole habitat in Oregon was on private lands. Despite the obvious economic implications of these trends, potential impacts on wildlife were not mentioned until Merriam (1938: 104) noted that forest depletion could lead to "…destruction of, or injury to, scenic features and wild life habitats."

By 1936, the amount of old forest cover had declined by about 14 percent and larger patches were shrinking and being subdivided by wildfires and a steadily increasing footprint of clearcut harvest.

By 1936, the amount of old forest cover had declined by about 14 percent and larger patches were shrinking and being subdivided by wildfires and a steadily increasing footprint of clearcut harvest. However, there were still, extensive stands of old-growth Douglas fir covering the foothills and lower slopes of the Cascades for almost the entire length of the state of Oregon (Andrews and Cowlin 1940). In most of the Coast Ranges of Oregon, large areas of old Douglas-fir forests were still intermixed with extensive areas of young forest, but much of the old forest in the North Coast Subregion had been removed by timber harvest or by the 1933 Tillamook Burn (fig. 1-6) (Andrews and Cowlin 1940). Harvest rates of Douglas-fir forests continued to exceed growth rates. In their summary findings Andrews and Cowlin (1940: 1) wrote, "The major forest problem in the Douglas-fir region is the necessity for instituting a system of managing old-growth forests for continuous production. This means that clearcutting over vast areas, which has resulted in large areas of nonstocked harvested land, must be halted." They advised a shift to single tree or a small group-selection forest management (Andrews and Cowlin 1940). Around that same time there was a brief shift from clearcuts to selective cutting on federal lands

(Kirkland and Brandstrom 1936), but this shift was largely abandoned by 1950 in favor of the old paradigm of harvesting with clearcuts (Curtis 1998, Munger 1950).

By 1952, timber harvesting had peaked on private lands in western Oregon (Wall 1972) and old forests on private timberlands were becoming increasingly rare. Meanwhile, the rate of harvest of old forests on public forests was beginning to increase markedly (Wall 1972), and fragmentation of the remaining areas of old forest was becoming a matter of concern (Huff et al. 1992, USDA and USDI 2000). Peavy's predictions in 1929 proved to be remarkably prescient.

Although the amount of potential tree vole habitat has been greatly reduced during the last century, tree voles in Oregon currently receive considerable protection because of restrictions on harvest of old forests on reserved federal forest lands. As long as those restrictions remain in effect, it is likely that red tree voles will continue to occupy extensive areas of old forest on federal lands in western Oregon.

Management Implications

Although the amount of potential tree vole habitat has been greatly reduced during the last century, tree voles in Oregon currently receive considerable protection because of restrictions on harvest of old forests on reserved federal forest lands (USDA and USDI 1994). As long as those restrictions remain in effect, it is likely that red tree voles will continue to occupy extensive areas of old forest on federal lands in western Oregon.

The situation on nonfederal lands is far less certain because most tree vole habitat on private and state lands has already been harvested or burned at least once, and there is no mandate to retain or produce extensive areas of old forest on nonfederal lands. Where there is little federal land, the persistence of the species will depend primarily on forest practices on private and state lands. The Oregon Forest Practices Act does not require state or private landowners to protect red tree voles or their nests, even if it is known that tree voles are present (http://www.oregon.gov/ODF/privateforests/pages/fpaguidance.aspx). There is also no requirement that state or private landowners survey areas prior to harvest to determine if red tree voles are present. Given this situation, it is reasonable to assume that red tree voles in Oregon will eventually become rare or absent on most state and private forest lands, which has already occurred in the northern Coast Ranges. However, there are a few examples that make us hopeful that at least some landowners will try to reverse this trend. For example, the Oregon State University School of Forestry has continued to protect some areas of mature forest on the McDonald-Dunn Research Forest near Corvallis, Oregon, and tree voles continue to occupy some of those old forests and some adjacent young forests (see chapter 1). There are also other examples in which municipal watersheds owned by the cities of Corvallis and Portland are being managed on longer rotations and are still inhabited by red tree voles. These examples demonstrate that it is possible to retain tree voles in managed landscapes, albeit not without some cost in terms of reduced timber production. In addition, managers should not lose sight of the fact that management that is designed to provide habitat for tree voles will likely provide habitat for many other species as well, especially species that thrive in forests with high canopy closure, large trees, and trees with cavities and other structural features that provide support for arboreal nests or den sites.

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Summary

Tree voles (*Arborimus longicaudus; A. pomo*) are unique arboreal arvicoline rodents that inhabit coniferous forests in western Oregon and northwestern California. In 1995–2013, field surveys conducted by the U.S. Forest Service and U.S. Bureau of Land Management produced a large amount of data on the distribution and relative abundance of tree voles and their nests. We used those data, plus data from museum specimens, owl pellets, and our own surveys to describe the current and historical range of tree voles in Oregon and California. We also compared the minimum density of tree vole nests in different forest age-classes. Our results indicate that tree voles still occur in much of their historical range, but have become uncommon or rare in some parts of their range where timber harvesting, large wildfires, or both have resulted in the almost complete conversion of old forests to young forests (<80 years old). In Oregon, red tree voles (*A. longicaudus*) primarily inhabited areas below 1000 m elevation, with occasional detections of voles or their nests up to 1159 m in the northern Cascades, 1475 m in the central Cascades, and 1585 m in the Klamath Mountains. We hypothesized that tree voles are restricted to lower elevations because their arboreal nests do not provide adequate protection from cold winter temperatures and because foraging at high elevations in winter may be hindered by snow- and ice-covered limbs. It is also possible that high-elevation conifer species do not provide adequate food for tree voles. All of these hypotheses are untested. Although most sources of data that we used were not selected randomly, we argue that the many thousands of forest stands and owl territories sampled were representative of conditions within the range of the red tree vole and accurately portrayed regional differences in the distribution and relative abundance of red tree voles. We were less confident that our results were representative of conditions within the range of the Sonoma tree vole because so much of the range was on private lands that had never been surveyed for tree voles.

Throughout most of their range in western Oregon and northwestern California, red tree voles fed primarily on the needles and twig bark of Douglas-fir (86 percent of 421 nests examined) and rarely grand fir (<1 percent). The main exception was in the comparatively narrow zone of Sitka spruce and western hemlock along the coast of northwestern Oregon, where red tree voles fed primarily on western hemlock, Sitka spruce, or both (98 percent of 54 nests examined). Sonoma tree voles fed primarily on Douglas-fir, but some individuals also fed on grand fir, and we found several nests in which Sonoma tree voles fed on introduced Monterey pine. Although tree voles occasionally built nests in coast redwood and western redcedar, they did not feed on redwood or redcedar, both of which were apparently unpalatable.

We used climate data, red tree vole nest locations, and Landsat maps of forest

structure and tree species composition to produce distribution models and habitat maps for the range of the red tree vole. Our models indicated that the most important biotic variables explaining the distribution of red tree voles were density of large conifers, diameter-diversity index, percentage of conifer cover, and combined basal area of conifer forage species (all positive relations). The abiotic variables that ranked highest were potential summer fog, maximum summer temperature, and average annual precipitation. Based on habitat maps produced from our models, we estimated that in 2007 there were approximately 1.6 million ha of red tree vole habitat, of which 70 percent was located on federally managed lands.

Although tree voles occasionally built nests in coast redwood and western redcedar, they did not feed on redwood or redcedar, both of which were apparently unpalatable.

Comparison of a generalized version of our 2006 habitat map from Oregon with historical forest maps from 1914 and 1936 indicated that the amount of tree vole habitat in Oregon declined by 65 percent between 1914 and 2006. This decline was most dramatic (80 percent) in the northern Coast Ranges where most lands were owned by private timber companies or the state of Oregon. Commensurate with this decline was a dramatic reduction in the average patch size of potential tree vole habitat, from 12 900 ha in 1914 to 240 ha in 2006. The majority of habitat loss was due to clear-cut harvesting of old forests and conversion to intensively managed young stands. However, large wildfires also removed large amounts of habitat, especially in the northern Coast Ranges and northern Cascade Range. Subsequent salvage and conversion of the burned areas to intensively managed young forests has maintained much of that area in unsuitable habitat conditions for tree voles.

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Based on maps of known tree vole locations, modeled habitat, and historical forest cover maps we estimated that the geographic distribution of the red tree vole in Oregon declined from approximately 5.3 million ha in 1914 to 4.1 million ha in 2006, a 23 percent reduction. We attributed this decline to habitat loss. The largest estimated range contractions were in the northern Coast Ranges and northern Cascade Range where most old forests on state and private lands had been converted to young forests. We suggest that isolation from extant tree vole populations may preclude eventual re-colonization of harvested or burned areas in northwestern Oregon.

Our analysis of the combined data from all sources suggests that tree voles are still present throughout much of their historical range, but have become rare or absent in some areas that have been converted to young, intensively managed forests. In western Oregon and northwestern California, red tree voles will likely continue to thrive in the extensive areas of old forest on federal lands that are currently protected by the Northwest Forest Plan (USDA and USDI 1994). Where federal lands are lacking, however, there is a high likelihood that tree voles will gradually disappear unless landowners actively manage for at least some old forests. This is especially true in the northern Coast Ranges of Oregon where there is little federal forest land. In California, Sonoma tree voles occur primarily on private and state lands, where landowners are required to follow state forestry regulations, but are not specifically required to protect tree voles or their habitat. Thus, the persistence of Sonoma tree voles in many areas is uncertain. However, the continued persistence of Sonoma tree voles in small tracts of forest as far south as Freestone and Bodega in Sonoma County, California, suggests that Sonoma tree voles may persist in highly fragmented forest landscapes, as long as some areas of tree vole habitat are retained. One mitigation measure that might reduce declines on private lands would be to encourage landowners to manage forests to retain some of the structural attributes that provide good nest structures for tree voles.

Ultimately, the persistence of both species of tree voles will depend on the willingness of humans to protect old forests, which provide stable, high-quality habitat for tree voles, and support source populations for recolonization of adjacent areas that have been harvested or burned.

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Tree Species Mentioned in This Report

Common name	Scientific name and authorities
Bigleaf maple	*Acer macrophyllum* Pursh
Bishop pine	*Pinus muricata* D. Don
California laurel	*Umbellularia californica* (Hook. & Arn.) Nutt.
Canyon live oak	*Quercus chrysolepis* Liebm.
Coast redwood	*Sequoia sempervirens* (Lamb. ex D. Don) Endl.
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
Englemann spruce	*Picea engelmannii* Parry ex Engelm.
Grand fir	*Abies grandis* (Douglas ex D. Don) Lindl.
Incense-cedar	*Calocedrus decurrens* Torr.) Florin
Jeffrey pine	*Pinus jeffreyi* Balf.
Lodgepole pine	*Pinus. contorta* Douglas ex Loudon
Monterey pine	*Pinus radiata* D. Don
Mountain hemlock	*Tsuga mertensiana* (Bong.) Carrière
Noble fir	*Abies procera* Rehder
Oak	*Quercus* spp.
Oregon white oak	*Quercus garryana* Douglas ex Hook.
Pacific madrone	*Arbutus menziesii* Pursh
Pacific silver fir	*Abies amabilis* (Douglas ex Loudon) Douglas ex Forbes
Ponderosa pine	*Pinus ponderosa* Lawson & C. Lawson
Shasta red fir	*Abies magnifica* A. Murray bis var. *shastensis* Lemmon
Sitka spruce	*Picea sitchensis* (Bong.) Carrière
Subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.
Sugar pine	*Pinus lambertiana* Douglas
Tanoak	*Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh
True fir	*Abies* spp.
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
Western redcedar	*Thuja plicata* Donn ex D. Don
Western white pine	*Pinus monticola* Douglas ex D. Don
White fir	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.
Whitbark pine	*Pinus albicaulis* Engelm
Yellow-cedar	*Cupressis nootkatensis* D. Don

English Equivalents

When you know:	Multiply by:	To find:
Centimeters (cm)	0.395	Inches
Meters (m)	3.281	Feet
Kilometers (km)	0.621	Miles
Hectares (ha)	2.471	Acres
Square meters (m^2)	0.0002471	Acres
Square kilometers (km^2)	0.386	Square miles

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Appendix 1

Field notes used to document the historical and current distribution of red tree voles and Sonoma tree voles.

Author	Year	Location of notes
McLellan, J. Ellis	1894	Smithsonian Institution Manuscript Collection (USNM)
Camp, Charles L.	1913	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Shelton, Alfred C.	1913	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Stone, George	1913	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Taylor, Walter P.	1913	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Bailey, Vernon O.	1914	Smithsonian Institution Manuscript Collection (USNM)
Shelton, Alfred C.	1914	University of Oregon Natural and Cultural History Museum (UOMNH)
Mailliard, Joseph	1921–1926	California Academy of Sciences (CAS)
Benson, Seth B.	1930–1956	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Lamb, Charles T.	1932	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Watson, H. C.	1932	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Behle, William H.	1933	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Hooper, Emmett T.	1936	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Johnson, David H.	1936	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Davis, William B.	1936–1937	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Fisher, Harvey I.	1942	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Miller, Alden H.	1942	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Russell, Ward C.	1942	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Storer, Robert W.	1944	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Jollie, Malcom	1945	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Koford, Mary	1949	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Pearson, Oliver P.	1949	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Brock, Elbert M.	1954–1956	University of California–Berkeley Museum of Vertebrate Zoology (MVZ)
Johnson, Murray L.	1957–1985	University of Washington Burke Museum of Natural History(UWBM)
Hamilton, William J., III	1956−1959	University of Puget Sound Slater Museum of Natural History (PSM)
Roberts, Don	1956−1959	University of Puget Sound Slater Museum of Natural History (PSM)
Maser, Chris	1967–1974	University of Washington Burke Museum of Natural History (UWBM
Vrieze, John M.	1979	Humboldt State University Vertebrate Museum (HSU)
Gannon, William T.	1981	Humboldt State University Vertebrate Museum (HSU)
Webb, Mike G.	1981	Humboldt State University Vertebrate Museum (HSU)
Murray, Michael A.	1993	Humboldt State University Vertebrate Museum (HSU)
Hayes, John P.	1995	Forestry Sciences Laboratory, Corvallis, Oregon

Appendix 2

Number of specimens of red tree voles (ARLO) and Sonoma tree voles (ARPO) in archived collections as of 2012. Of the 35 museums with tree voles, we visited 25 (indicated by asterisks) to examine specimens.

Institution	ARLO	ARPO
Academy of Natural Sciences of Drexel University (ANSP)	0	1
American Museum of Natural History (AMNH)*	21	12
Brigham Young University Bean Life Science Museum (BYU)	2	0
California Academy of Sciences (CAS)*	0	31[a]
California State University Long Beach (CSULB)*	0	2
Carnegie Museum of Natural History (CM)*	0	11
Cornell University Museum of Vertebrates (CUMV)	0	1
Corvallis Forestry Sciences Laboratory, Oregon (CFSL)*	38	0
Harvard University Museum of Comparative Zoology (MCZ)*	0	7
Humboldt State University Vertebrate Museum (HSU)*	12	76
Indiana State University Department of Life Sciences (ISUVC)	1	0
Kansas University Natural History Museum (KU)*	26	8
Michigan State University Science and Culture Museum (MSUM)	1	1
Museum of Texas Tech University (TTU)	3	0
Natural History Museum of Los Angeles County (LACM)*	3	14
Oregon State University Fisheries and Wildlife Collection (OSUFW)*	99[a]	1
Redwood Forestry Sciences Laboratory, California (RWSL)	1	1
Royal Ontario Museum (ROM)*	6	2
San Diego Natural History Museum (SDNHM)*	23	4
Smithsonian National Museum of Natural History (USNM)*	44	22
Texas A & M Biodiversity Research and Teaching Collections (BRTC)	0	4
The Field Museum of Natural History (FMNH)*	3	0
University of Alaska Museum of the North (UAM)*	38	0
University of California–Davis Museum of Wildlife and Fisheries (UCDAVIS)*	0	6
University of California–Los Angeles Dickey Collection (UCLA)*	1	35[a]
University of California–Berkeley Museum of Vertebrate Zoology (MVZ)*	5	140[a]
University of Florida Museum of Natural History (UF)	0	3
University of Michigan Museum of Zoology (UMMZ)*	9	5
University of Montana Zoological Museum (UMZM)*	0	2
University of New Mexico Museum of Southwestern Biology (MSB)	4	4
University of Oregon Museum of Natural and Cultural History (UOMNH)*	2[a]	0
University of Puget Sound Slater Museum of Natural History (PSM)*	309	324[a]
University of Washington Burke Museum of Natural History (UWBM)*	43	35[a]
University of Wisconsin Zoological Museum (UWZM)*	9	1
Washington State University Charles R. Conner Museum (CRCM)*	15	2
Totals	718	755

[a] In addition to the specimens found in museums, we confirmed 17 specimens that were lost or discarded as follows: CAS (7 ARPO), MVZ (1 ARPO), PSM (1 ARPO), OSUFW (5 ARLO), UCLA (1 ARPO), UOMNH (1 ARLO), and UWBM (1 ARPO).

Appendix 3

Number of red tree voles and Sonoma tree voles documented during field or laboratory studies, but not represented by specimens in museums. These records were based on field notes and data forms of collectors as well as our own observations and included voles that escaped during capture attempts, voles that escaped from captivity and voles that were captured and discarded or released.

Type of observation[a]	Red tree vole	Sonoma tree vole
Vole seen at nest but not captured	45	14
Escaped from captivity	3	4
Specimen discarded	4	42
Captured but not located in any museums	55	57
Live-trapped on the ground and released	2	0
Live-trapped at nest and released*	3	0
Captured at nest and released*	101	2
Captured at nest and radio-collared*	40	0
Total	253	119

[a] Observation categories indicated by asterisks were exclusively from our studies. Other categories were mostly documented from field notes of other observers.

Appendix 4

The following figures show model response curves for predictor variables used in development of the rangewide habitat map for the red tree vole. The mean response of the 10 replicates is shown in red and $\bar{x}$ ± 1 SD in blue.

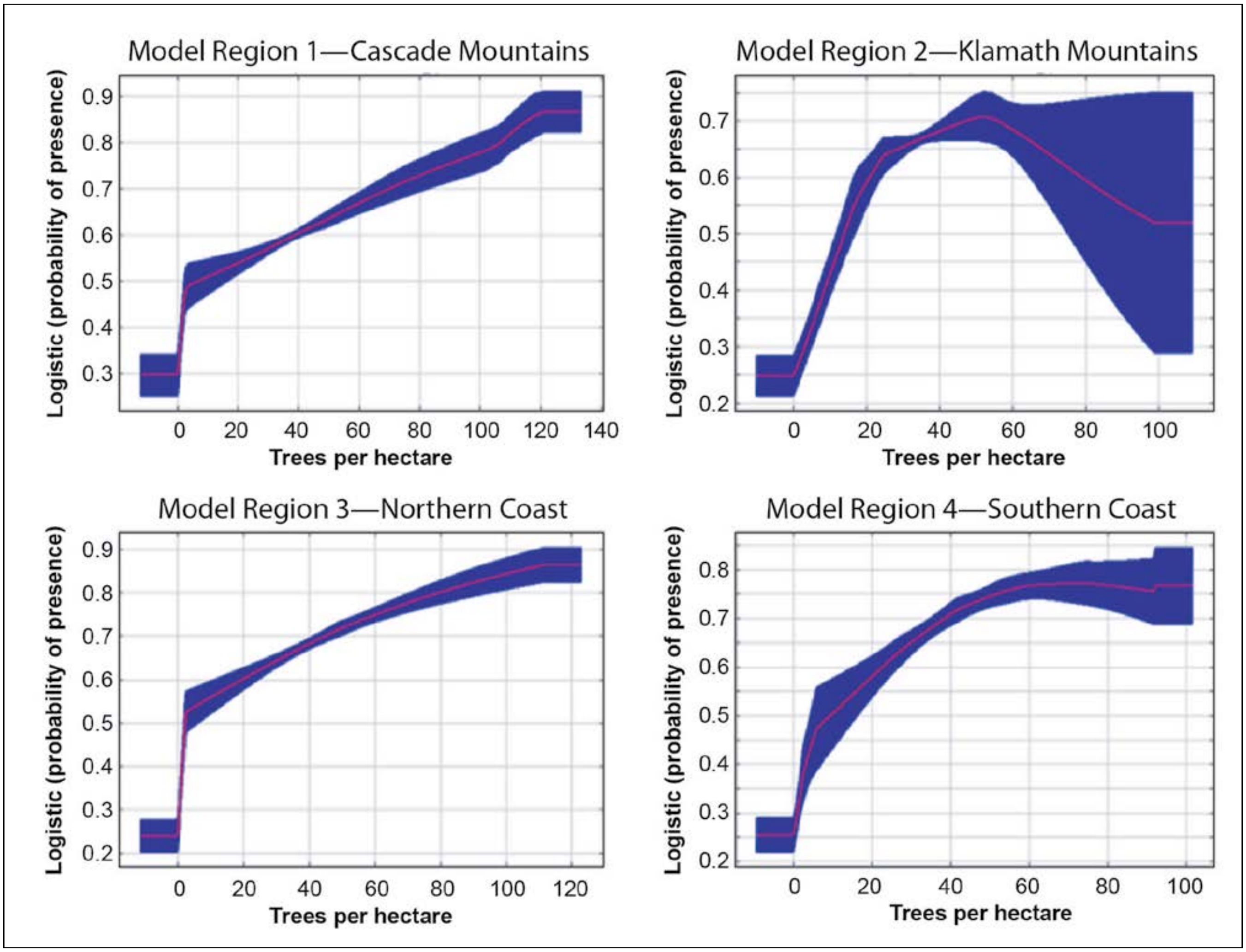

Figure A4-1—Density per ha of large (≥75 cm dbh) conifers.

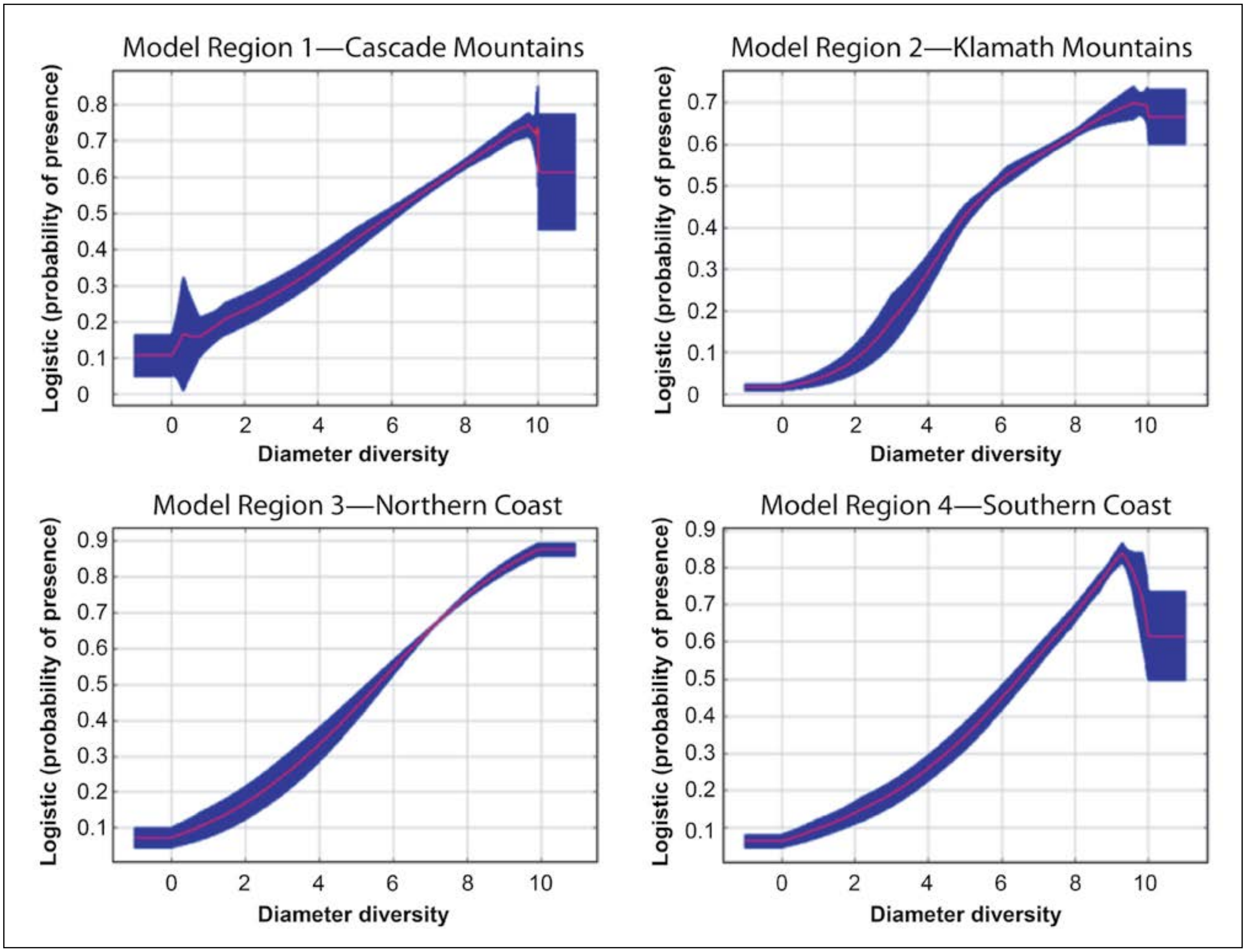

Figure A4-2—Diameter diversity index.

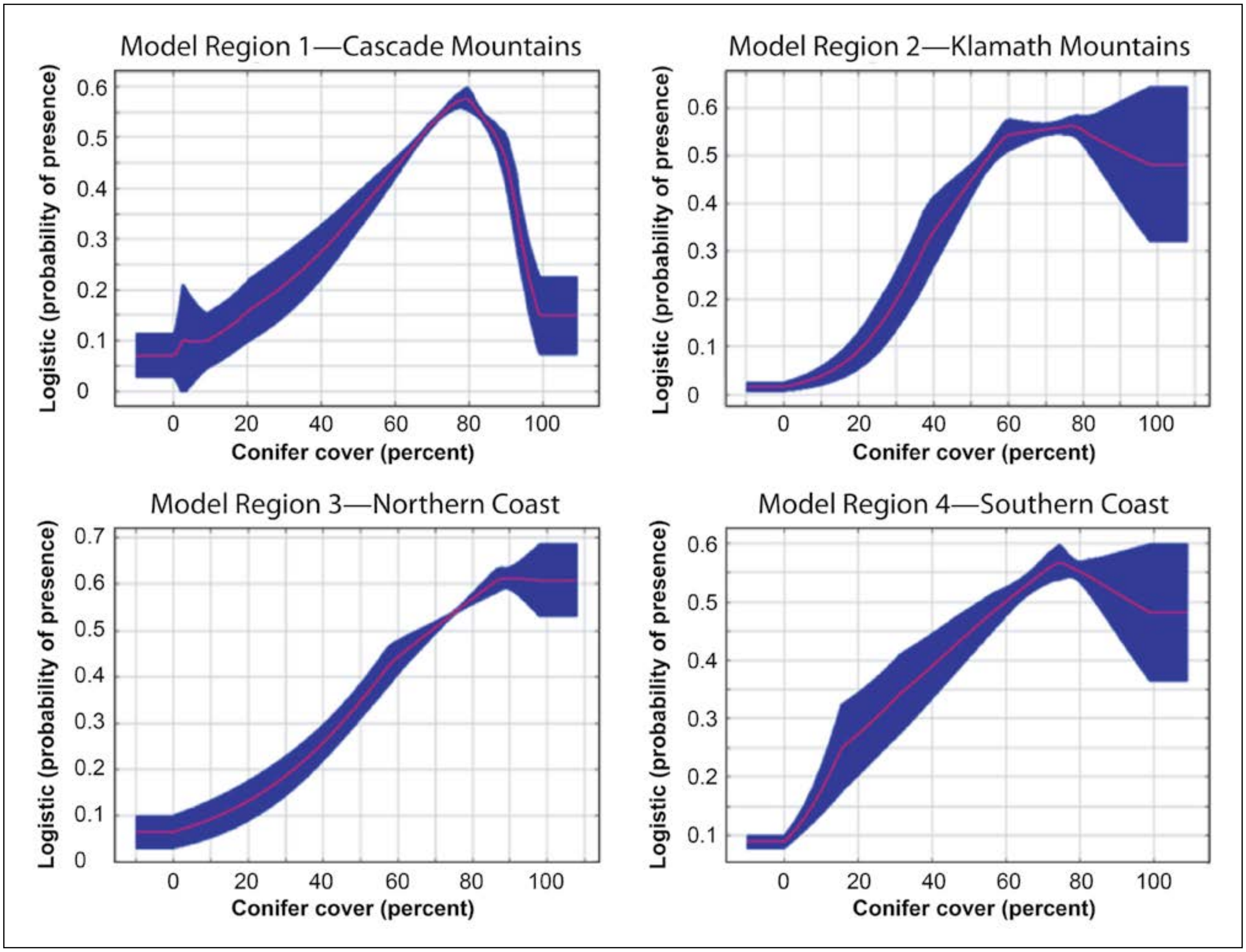

Figure A4-3—Percentage of conifer cover.

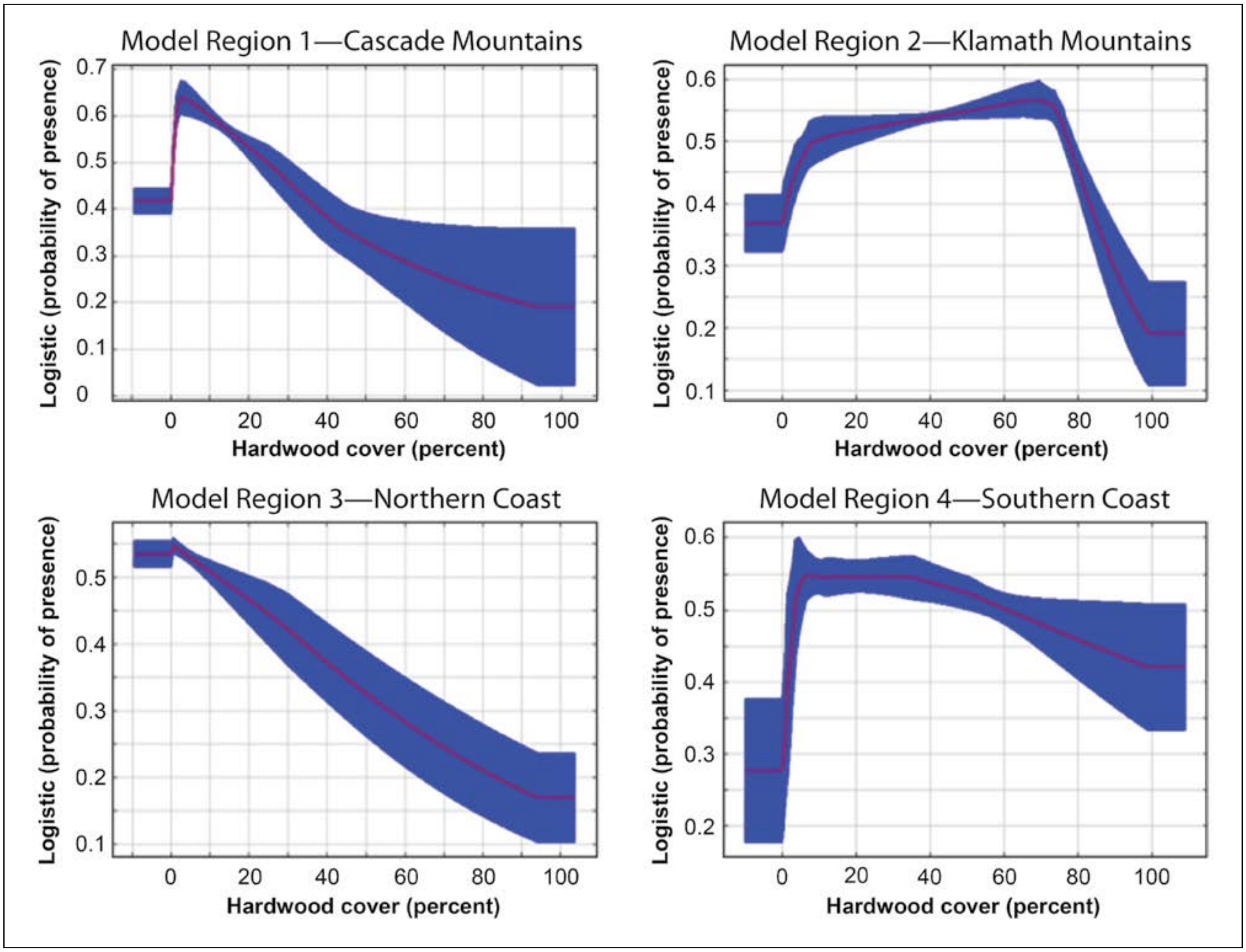

Figure A4-4—Percentage of hardwood cover.

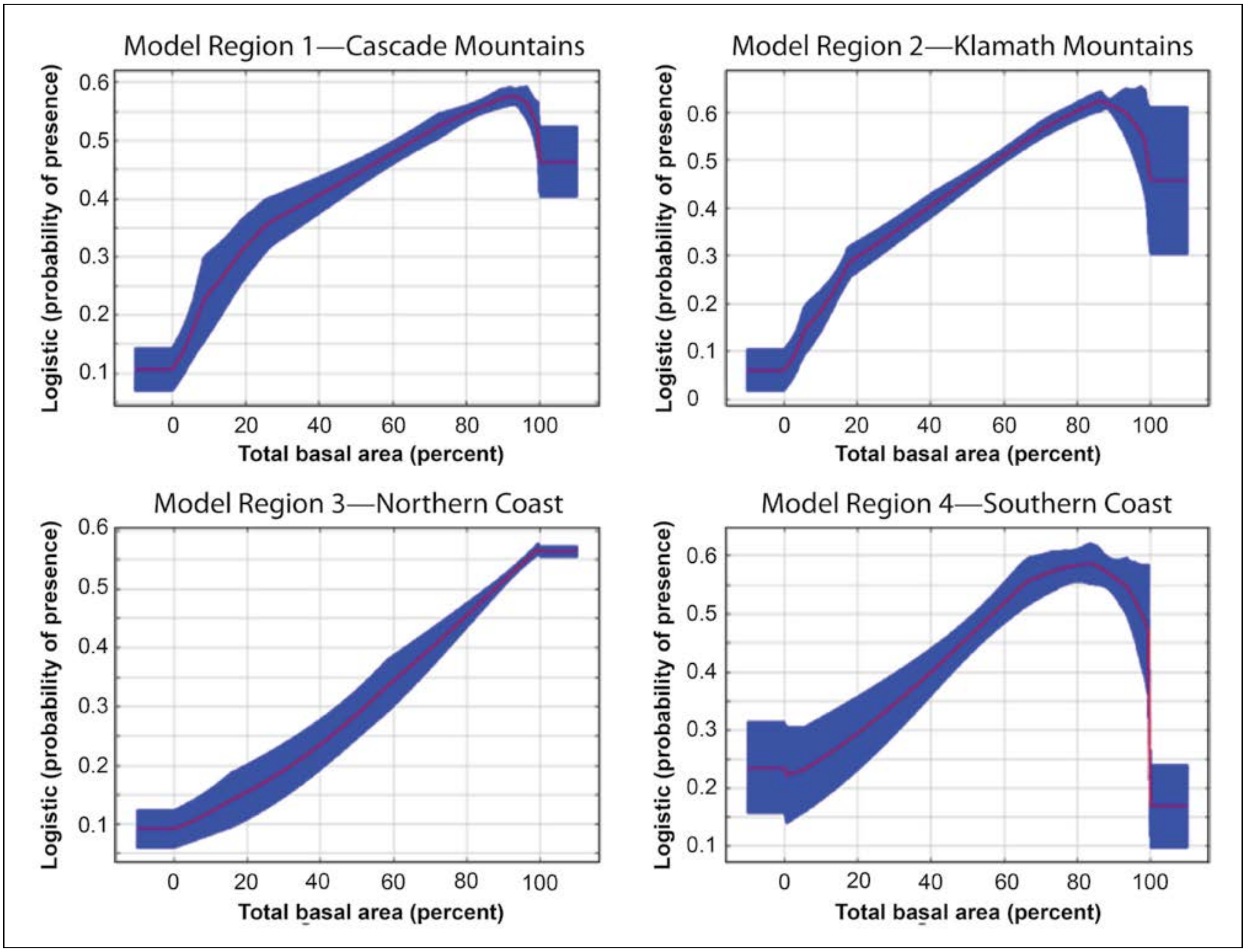

Figure A4-5—Percentage of total basal area of red tree vole food-source trees (Douglas-fir, grand fir, western hemlock, and Sitka spruce).

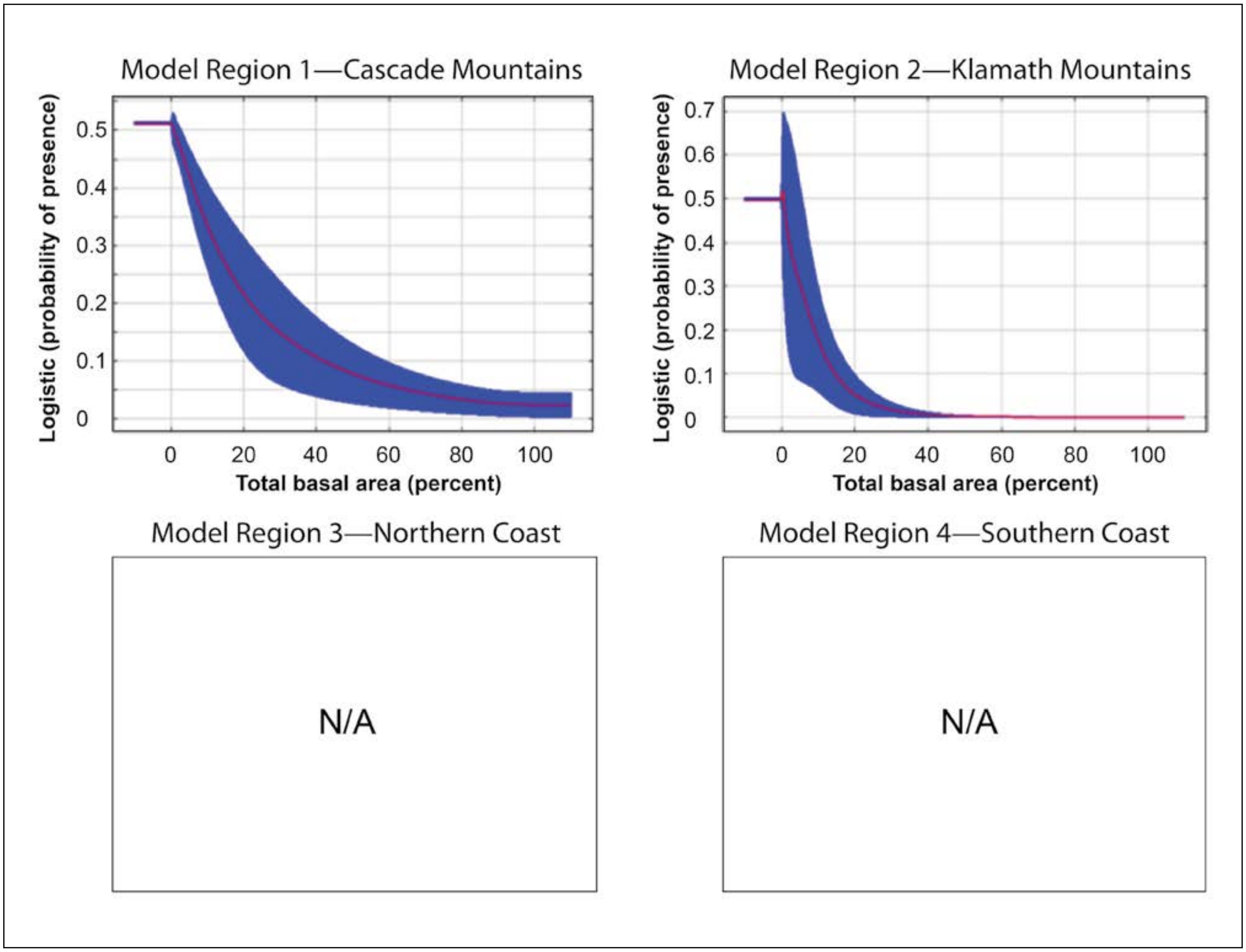

Figure A4-6—Percentage of total basal area of subalpine forest tree species (Pacific silver fir, subalpine fir, noble fir, Shasta red fir, Yellow-cedar, Engelmann spruce, whitebark pine, and mountain hemlock).

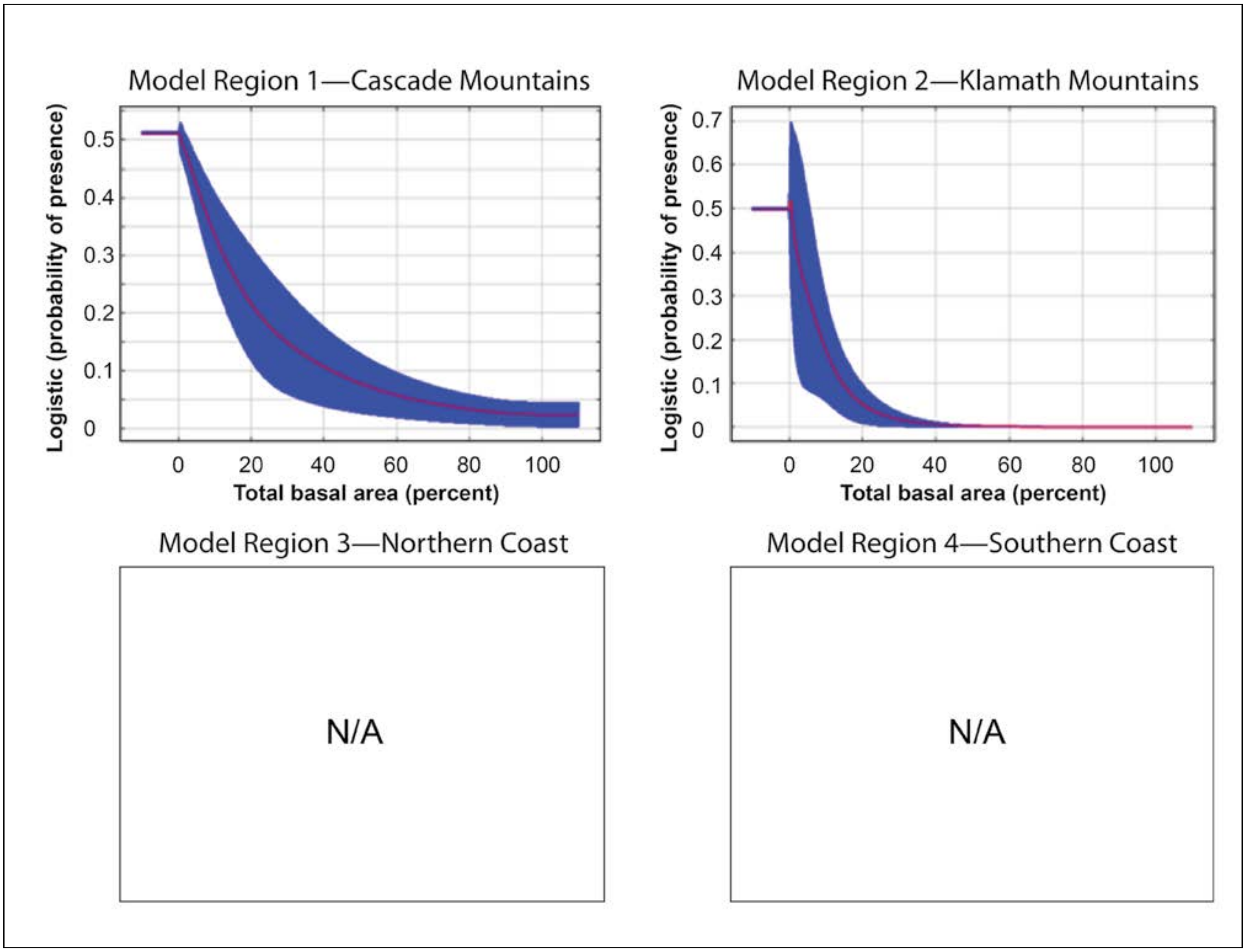

Figure A4-7—Percentage of total basal area in white fir.

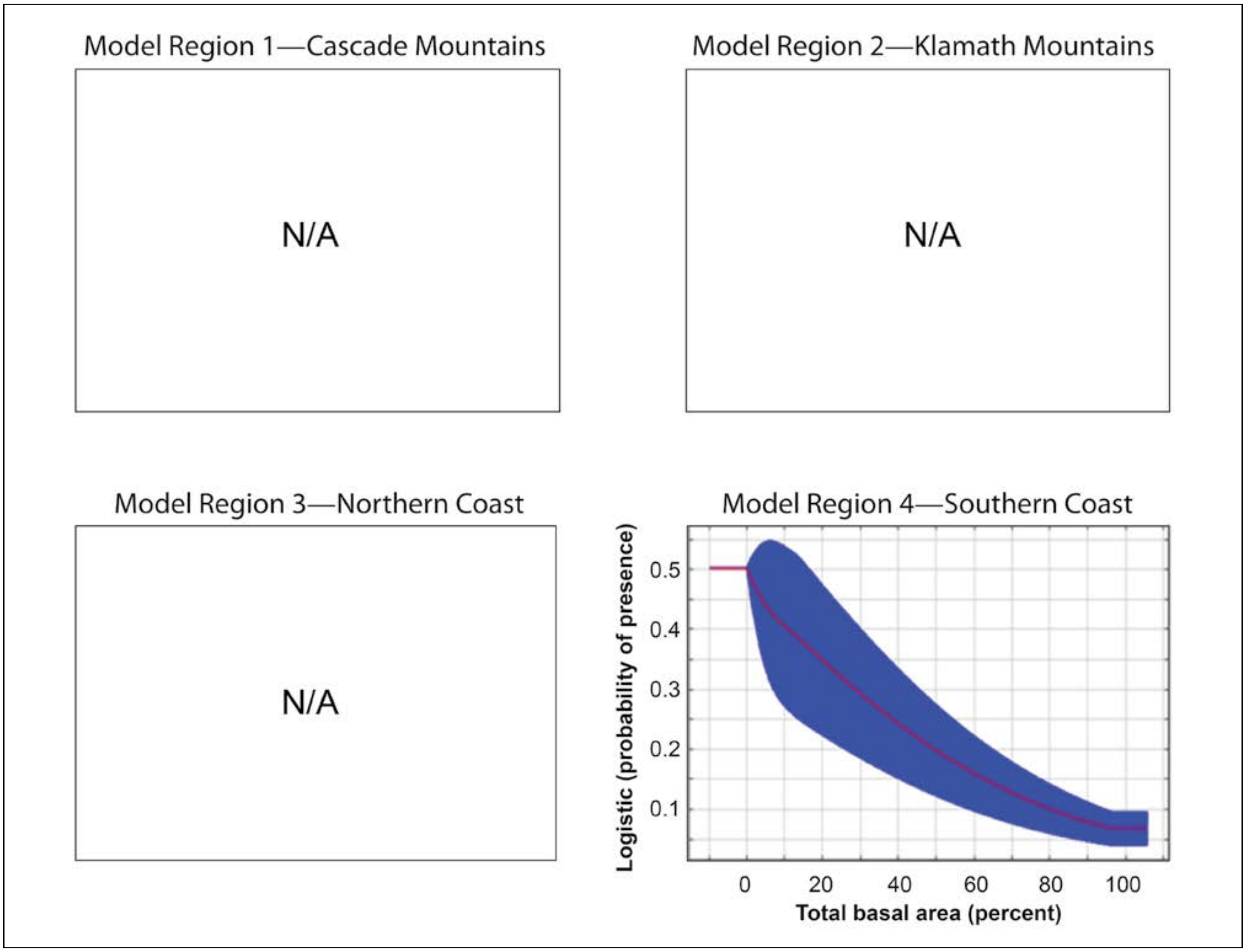

Figure A4-8—Percentage of total basal area in coast redwood.

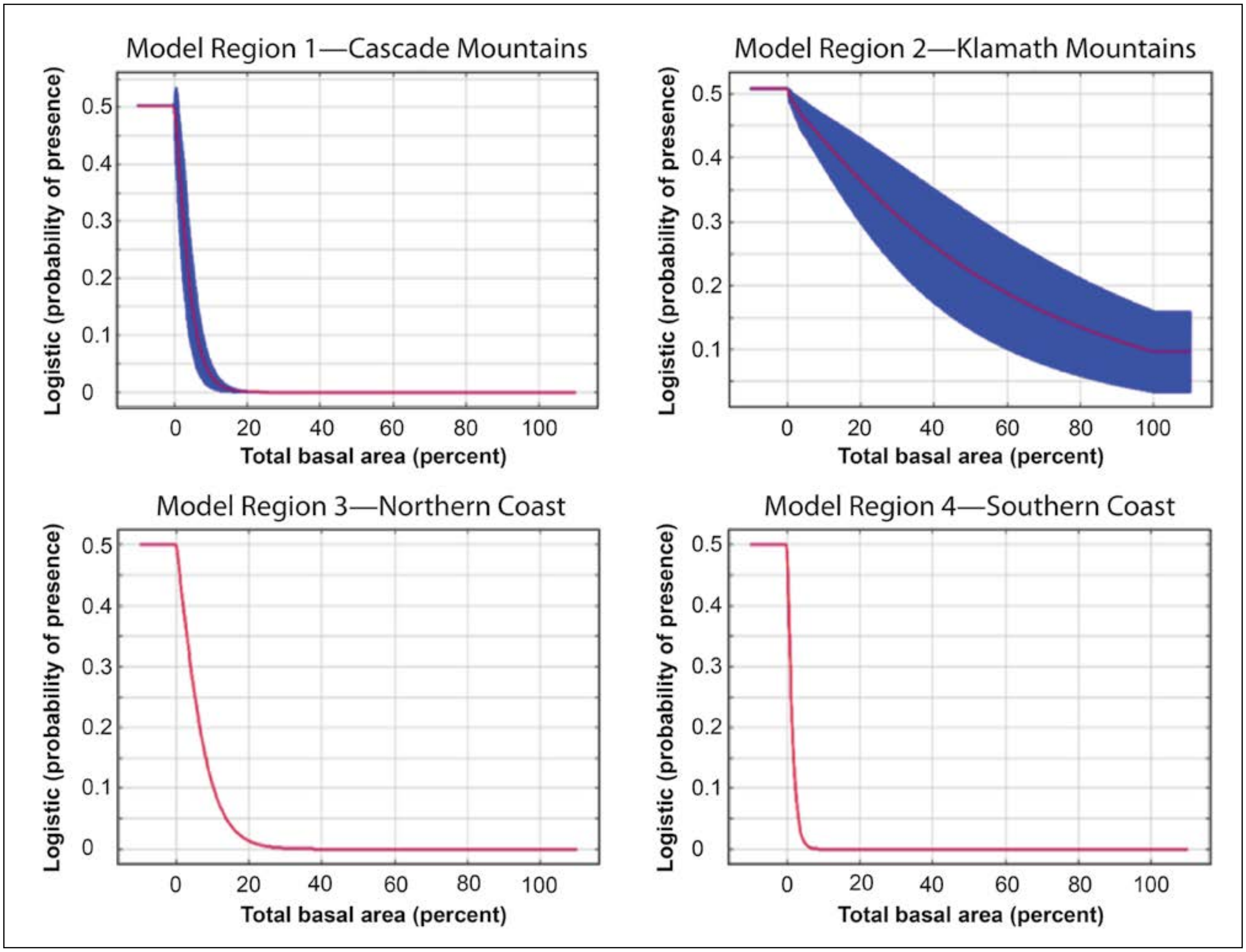

Figure A4-9—Percentage of total basal area in pine forest tree species (lodgepole pine, Jeffrey pine, and ponderosa pine).

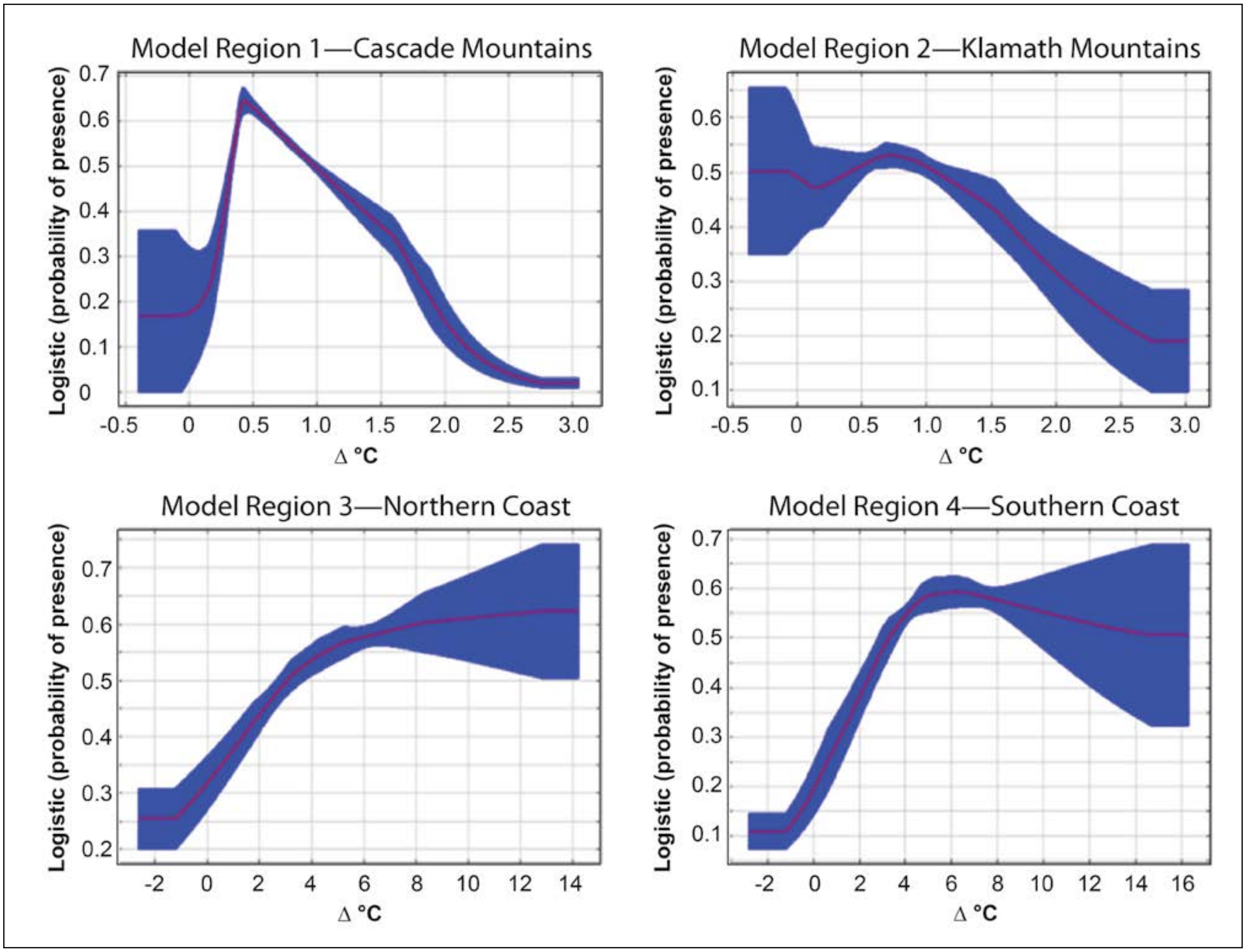

Figure A4-10—Summer fog was modeled as the difference between average summer dew point and average summer minimum temperature in the months of July and August, 2000–2005 (http://www.prism.oregonstate.edu/).

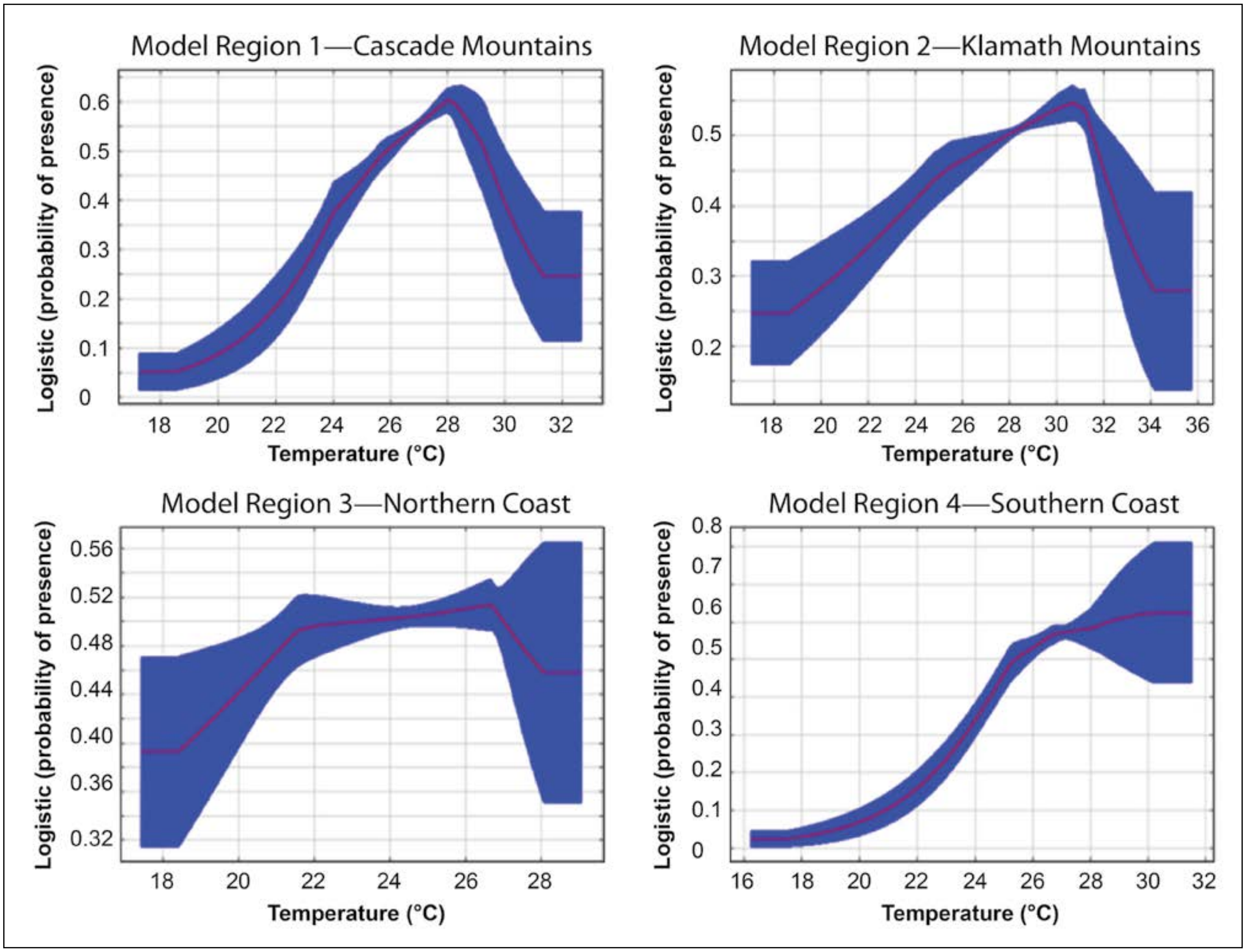

Figure A4-11—Mean maximum temperature in the month of August, 1971–2000 (http://www.prism.oregonstate.edu/).

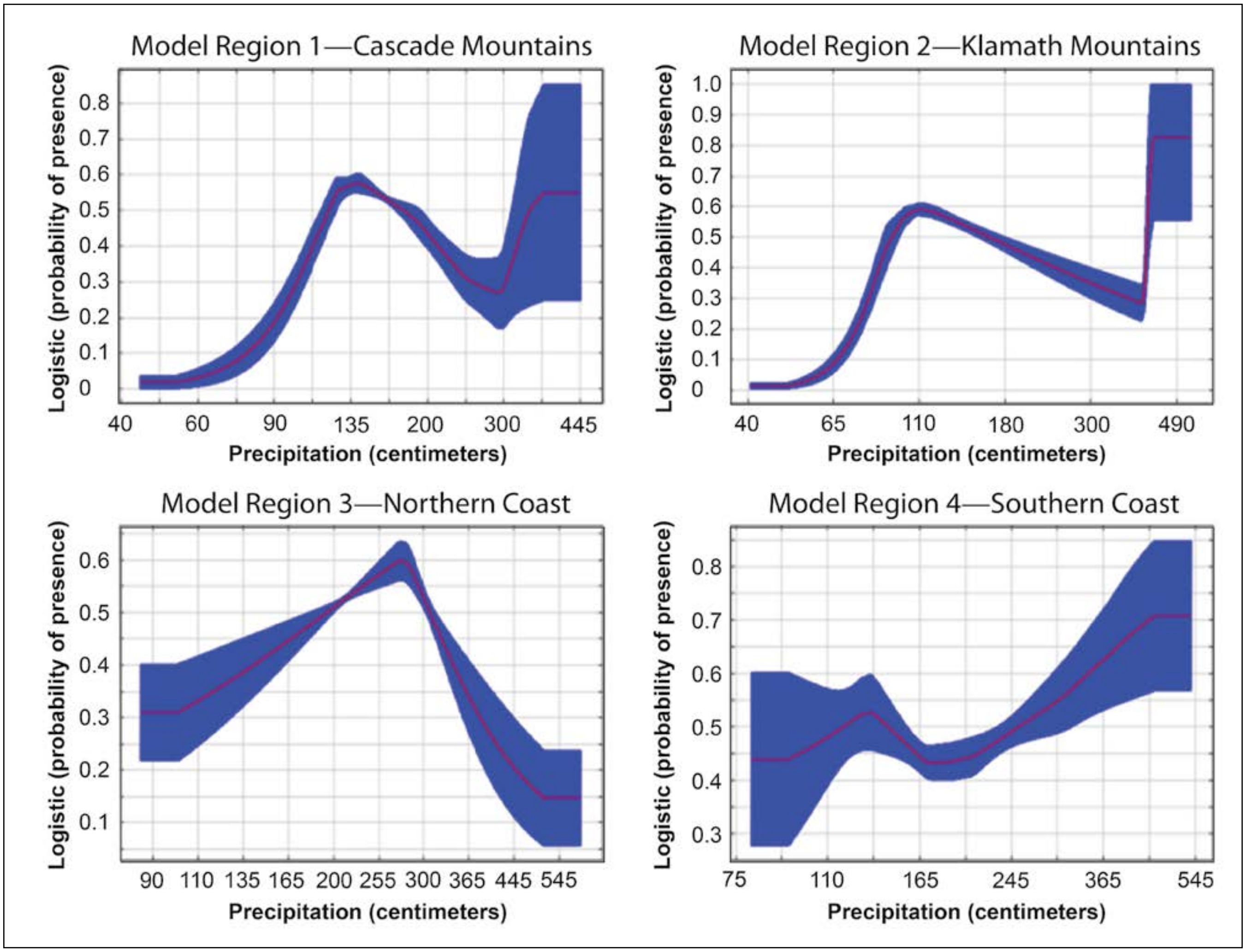

Figure A4-12—Mean annual precipitation (logarithmic scale) in 1971–2000 (http://www.prism.oregonstate.edu/).

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