Eric D. Forsman,[1] U.S. Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, Oregon 97331[1]

Robert G. Anthony, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331

and

Cynthia J. Zabel, U.S. Forest Service, Pacific Southwest Research Station, Arcata, California 95521

Distribution and Abundance of Red Tree Voles in Oregon Based on Occurrence in Pellets of Northern Spotted Owls

Abstract

Red tree voles are one of the least understood small mammals in the Pacific Northwest, because they live in the forest canopy and are difficult to sample using conventional trapping methods. We examined the distribution and relative abundance of tree voles in different regions of Oregon based on their occurrence in diets of northern spotted owls. We identified the skeletal remains of 2,954 red tree voles in regurgitated pellets collected from 1,118 different spotted owl territories. Tree voles were found in the diet at 486 territories. They were most common in the diet in the central and south coastal regions, where average owl diets included 13% and 18% tree voles. They were absent from owl diets on the east slope of the Cascades and in most of the area east of Grants Pass and south of the Rogue River. Our data were sparse from the northern Coast Ranges and northern Cascades, but suggested comparatively low numbers of voles in those regions. The proportion of tree voles in the diet was negatively correlated with elevation in the Cascades, where tree voles were common in the diet at elevations < 975 m, and rare in the diet at elevations > 1,220 m. The highest elevations at which tree voles were detected in owl diets were 1,324 m in the Cascades and 1,390 m in the Klamath Mountains. On average, we estimated that nesting pairs of spotted owls captured 54 tree voles per year in western Oregon, but there was large variation among and within regions. Although our data indicate that tree voles are widespread in Oregon, and fairly common in some regions, it is likely that tree vole populations have declined in areas where logging, fire, and human development have produced landscapes dominated by young forests.

Introduction

The red tree vole (*Arborimus longicaudus*) is one of the most unusual microtine rodents in the world. It occurs only in coniferous forests in western Oregon and northwestern California, is primarily arboreal, has a relatively low reproductive rate, and feeds primarily, if not entirely, on the needles and twigs of coniferous trees (Clifton 1960, Maser 1965, Maser et al. 1981, Johnson and George 1991, Hayes 1996, Verts and Carraway 1998) (Figure 1). A closely related species, the Sonoma tree vole (*A. pomo*), occurs in the coastal mountains of California, south to Sonoma County (Johnson and George 1991, Murray 1995). The dividing line between the ranges of the red tree vole and Sonoma tree vole is thought to correspond roughly with the Klamath River in northern California, but is poorly documented (Murray 1995).

Although many researchers have examined the life history, distribution and species-level genetics of tree voles (Howell 1926; Clifton 1960; Hamilton 1962; Maser 1965; Corn and Bury 1986, 1991; Gillesberg and Carey 1991; Johnson and George 1991; Murray 1995; Meiselman and Doyle 1996; Gomez and Anthony 1998, Bellinger et al. 2005), there is considerable uncertainty regarding the current distribution of tree voles and their relative abundance in different regions or forest types. This lack of knowledge is largely due to the fact that tree voles are primarily arboreal and are rarely captured in studies of small mammals (Corn and Bury 1986, 1991; Gilbert and Allwine 1991; Gomez and Anthony 1998). As a result, much of what is known about their distribution and abundance has been learned by the labor-intensive method of climbing trees to examine nests and capture individual animals by hand (Jewett 1920, Howell 1926, Clifton 1960, Maser 1965, Maser et al. 1981).

Because tree voles are so difficult to study using conventional methods, we decided to investigate their distribution and abundance by examining their relative frequency in diets of northern spotted owls

[1]Author to whom correspondence should be addressed. E-mail: eforsman@fs.fed.us

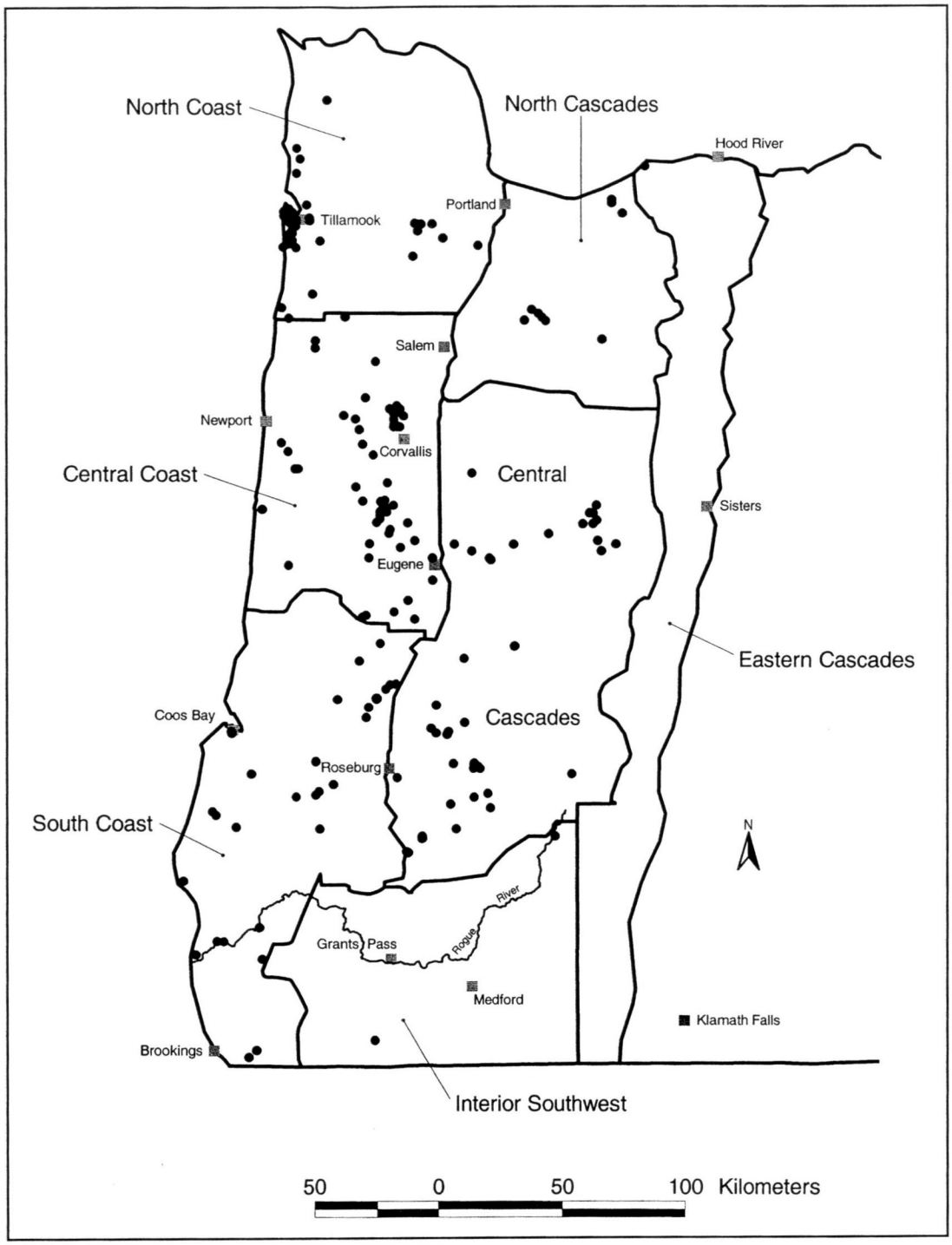

Figure 1. Historic locations of red tree voles in Oregon. Locations include data from Verts and Carraway (1998), Manning and Maguire (1999), and 54 records where tree voles were captured and released in 2000-2002, after collecting tissue samples for genetic analysis (E. Forsman data on file at USDA Forest Service PNW Research Lab, Corvallis, Oregon).

(*Strix occidentalis caurina*) in Oregon. Spotted owls are a major predator on tree voles, and it is easy to identify remains of red tree voles in the regurgitated pellets of the owls (Forsman et al. 1984). Although prey selection by owls is almost certainly not random, we felt that an examination of the diet of spotted owls would further elucidate the distribution of the tree vole and might also provide insights regarding local and regional variation in abundance of tree voles.

Study Area

The study area included most of western Oregon plus scattered locations on the east slope of the Cascade Range (Figure 2). Most pellets were collected from the Coast Ranges, Klamath Mountains, and western Cascades, where researchers were conducting demographic studies of spotted owls (Forsman et al. 1996). For our analysis we subdivided the study area into seven geographic regions corresponding with major mountain ranges or subdivisions of major mountain ranges (Figures 1, 2).

With the exception of the Willamette, Umpqua and Rogue River Valleys, the study area was characterized by mountainous terrain covered by coniferous forests (Franklin and Dryness 1988). Forests of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) predominated in the western Cascades and Coast Ranges, with a narrow zone of sitka spruce (*Picea sitchensis*) and western hemlock along the coastal headlands. Forests in the Klamath Mountains of SW Oregon were predominantly mixed conifer forests of Douglas-fir, grand fir (*Abies grandis*), incense cedar (*Libocedrus decurrens*), and pines (*Pinus* spp.), or mixed evergreen forests of Douglas-fir and tanoak (*Lithocarpus densiflorus*) (Franklin and Dyrness 1988). On the eastern slopes of the Cascades Range, vegetation was predominantly mixed associations of grand fir, Douglas-fir, incense cedar, and ponderosa pine (*Pinus ponderosa*), with ponderosa pine predominating at lower elevations and grand fir predominating at higher elevations.

Methods

Pellets were collected from below owl roosts, air dried, and placed in labeled containers with the date and location of collection. Most pellets were collected during March-August, the period when owls were nesting and raising young. Thus, our analysis primarily reflects predation during that period. No attempt was made to sample owl territories randomly. Observers simply collected pellets whenever they found them below owl roosts.

We used individual owl territories as the sample unit for analyses. Data from each territory were lumped into a single sample, regardless of which years pellets were collected. Composition of the diet was estimated separately for each territory and then averaged across territories to estimate the average diet in each region. We used the entire data set for assessment of tree vole distribution, but means, standard errors, and coefficients of variation were based only on data from owl territories with ≥ 10 prey items in the sample. The only exception was the North Cascades Region, where the sample of owl territories with n ≥ 10 prey (N = 4) was so small that we used estimates from all 23 territories sampled, regardless of the number of prey in each sample.

All analyses were based on the number or biomass of tree voles in each sample, expressed as a percentage of the total prey numbers or biomass. We estimated the number of prey in each sample of pellets by counting skulls, mandibles, bones of the appendicular skeleton, or pieces of exoskeleton, whichever gave the highest count. To avoid double-counting large mammals or birds we combined data from multiple pellets or pellet fragments collected in the same roost area on the same day. Vertebrate prey were identified with the aid of dichotomous keys (Maser and Storm 1970, Verts and Carraway 1984) and a reference collection of skeletons. We differentiated between red tree voles and the closely related white-footed vole (*Arborimus albipes*) and heather vole (*Phenacomys intermedius*) based on anatomical differences described in Maser and Storm (1970). To assess the accuracy of our identification of tree vole remains we submitted skulls or jaws of 19 tree voles to a genetics laboratory for confirmation of species based on genetic sequencing of the cytochrome b region of mitochondrial DNA. That analysis indicated that all 19 voles were correctly identified (M. Renee Bellinger, USDI Biological Resources Division, Forest and Range Experiment Station, personal communication).

We estimated the total biomass of prey in each sample by multiplying the estimated mean mass of each species by the number of individuals

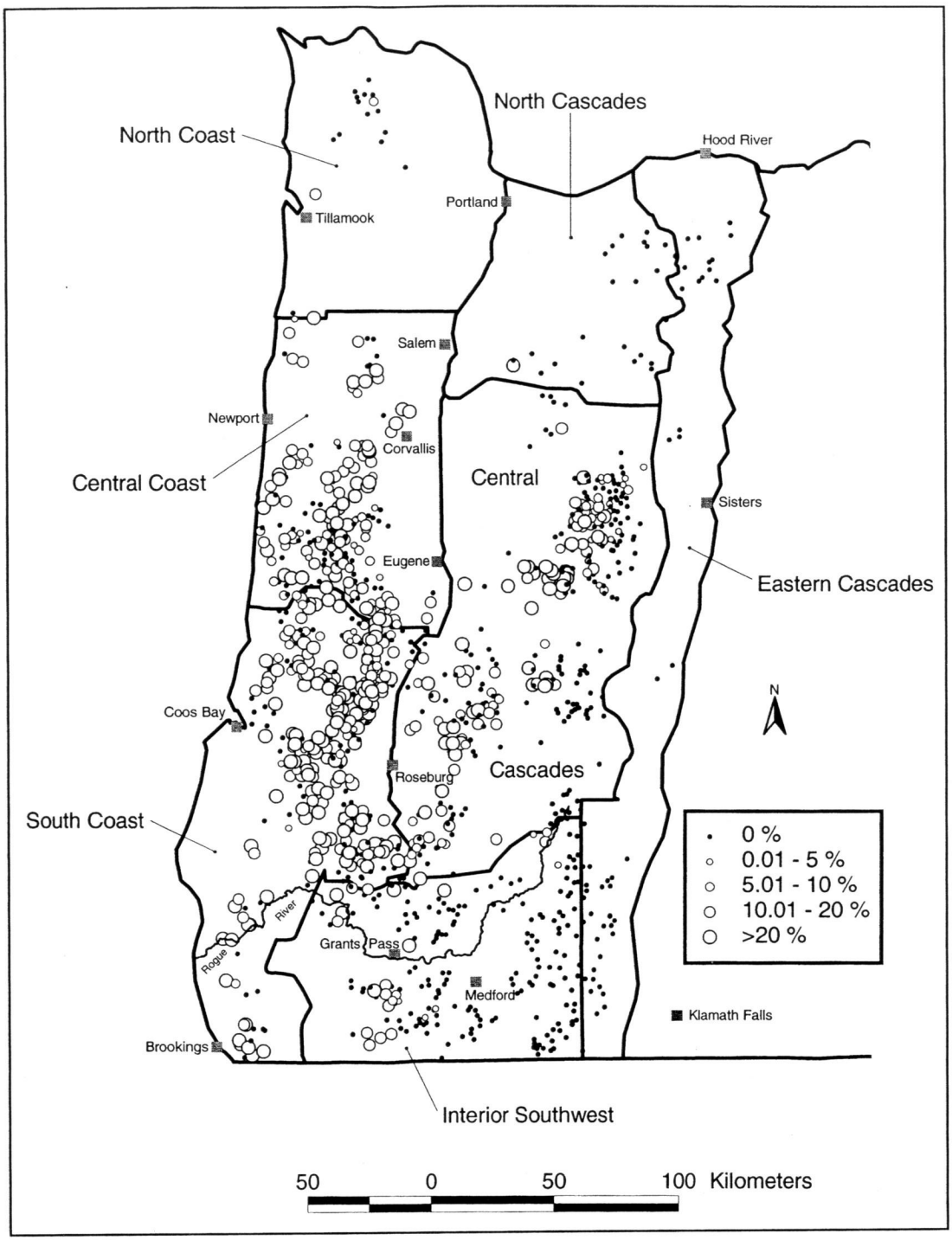

Figure 2. Locations of 1,118 territories in which diets of northern spotted owls were sampled in one or more years during 1970-2003. The size of the circle representing each owl territory indicates the percentage of prey numbers that were red tree voles.

of each species in the sample and summing the products. Percent biomass in each prey category was then estimated by dividing the biomass of each species by the total biomass in the sample. Estimates of mean mass of birds and mammals were obtained from Dunning (1993) and Verts and Carraway (1998).

We used linear correlation to determine if the abundance of tree voles in the diet was correlated with elevation at the nest site or primary roost area used by the owls. This analysis was conducted with an arcsine-transformation of the proportional diet data to improve the fit to a bivariate normal distribution (Zar 1999). Elevations were determined with an altimeter, or by plotting the location on a USGS topographic map, or by overlaying the UTM coordinates of nest trees on a 33-m resolution digital elevation map.

We estimated the number of tree voles captured per year by individual spotted owls based on the assumption that a spotted owl of average mass (610g) consumes 12% of its body mass (73.2 g) of food per day, or 26,718 g per year (Forsman et al. 2004). Then, the number of tree voles consumed per year by an individual owl is equal to 26,718 multiplied by the proportional biomass of tree voles in the diet, divided by the mean mass of a tree vole (26 g). The critical assumption in this estimate is the amount of food consumed per day. Other estimates were available (Weathers et al. 2001), but we felt that our estimate of 12% of body mass consumed per day was reasonable considering other data from spotted owls (Forsman 1980) and from other owls (Graber 1962). To estimate the number of tree voles captured per year per owl territory we multiplied the number of voles captured per owl by 2 for non-nesting pairs and 2.6 for nesting pairs with 2 young. The latter estimate was based on the assumption that nesting pairs fed their young for approximately 4 mo (Forsman et al. 1984), and that the average biomass consumed per day was the same for juveniles and adults. Statistical analyses were conducted with Program SPSS (Version 11.5, SPSS Inc. Chicago, IL). The significance level for rejection of null hypotheses was set at $P = 0.05$.

Results

Distribution and Relative Abundance

We identified a total of 24,497 prey items from 1,118 owl territories. Of the total prey, 2,954 (12.1%) were tree voles, which occurred in the diet at 486 (43%) of the 1,118 territories (Figure 2). Diet samples were ≥ 10 at 547 territories (Table 1). Tree voles were most common in the diet in the South Coast and Central Coast Regions and in the Central Cascades (Table 1). They were relatively uncommon in the diet in the North Coast and North Cascades Regions, but our samples in those areas were small (Table1, Figure2). In the Interior Southwest Region, tree voles were relatively common in owl diets in areas west of Grants Pass, but were rare or absent from the diet in the area east of Grants Pass and south of the Rogue River (Figure 2). Because most of our samples from the North Cascades Region were small and were from territories at elevations >760 m, we did not feel that our sample adequately represented that area, particularly at lower elevations. No tree voles were found in owl pellets from the east slope of the Cascades, which was an expected result, as there are no previous records of tree voles in that region (Verts and Carraway 1998).

TABLE 1. Abundance of red tree voles in diets of spotted owls in Oregon, subdivided by geographic regions, 1970–2003. Means indicate percent of total prey in the diet that were red tree voles. *N* indicates number of owl territories sampled.

	Mean ± SE (%)	C.V.	Range (%)	*N*
North Coast	4.8 ± 2.7	168.8	0-22	9
Central Coast	12.7 ± 1.1	86.0	0-45	90
South Coast	18.2 ± 0.9	69.7	0-67	180
Interior Southwest	2.6 ± 0.7	242.2	0-30	75
Central Cascades	7.7 ± 0.8	132.8	0-48	154
North Cascades[1]	1.9 ± 1.5	374.0	0-33	23
Eastern Cascades	0.0	-	-	35

[1] All estimates were based on samples from owl territories with ≥ 10 prey except for the North Cascades Region. In the latter region the number of territories with ≥ 10 prey was so small (N = 4) that we used all territories regardless of the number of prey in each sample.

In those regions where they occurred, the proportion of tree voles in the diet was highly variable among owl territories (Table 1). Variation among territories was particularly high in the North Coast, Interior Southwest, and North Cascades Regions (Table 1).

TABLE 2. Abundance of red tree voles in diets of spotted owls in Oregon, subdivided by elevation bands in which owl nests were located, 1970–2003. Means indicate percent of total prey in the diet that were red tree voles. *N* indicates number of owl territories sampled in each elevation band.

Elevation	Central Coast		South Coast		Interior Southwest		Central Cascades	
in meters	*N*	Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE
<366	75	11.8 ± 1.2	107	17.1 ± 1.2	0		7	9.0 ± 3.2
366-487	12	18.2 ± 3.8	33	18.9 ± 1.7	0		8	10.0 ± 2.6
488-609	2	9.7 ± 1.4	29	19.9 ± 2.5	2	0.5 ± 0.5	18	18.2 ± 3.2
610-731	1	18.0	7	15.8 ± 4.9	10	7.1 ± 3.7	28	12.0 ± 2.3
732-853			3	31.5 ± 16.1	7	5.2 ± 3.3	17	6.7 ± 2.4
854-975			1	36.4	9	2.5 ± 1.3	25	5.8 ± 1.4
976-1,097					16	0.4 ± 0.3	20	3.8 ± 1.2
1,098-1,219					11	2.0 ± 1.5	13	3.0 ± 1.5
1,220-1,341					7	3.5 ± 2.8	7	0.2 ± 0.2
1,342-1,463					7	1.7 ± 1.7	6	0.0
>1,463					6	0.0	5	0.0

Abundance Relative to Elevation

Correlations between elevation and abundance of tree voles in the diet were weak or non-existent in the Central Coast Region ($r = 0.175$, $P = 0.098$), South Coast Region ($r = 0.157$, $P = 0.035$), and Interior Southwest Region ($r = -0.217$, $P = 0.061$). However, there was a strong negative relationship between the proportion of tree voles in the diet and elevation in the Central Cascades Region ($r = -0.421$, $P<0.001$). A plot of the data in different elevation bands in the Central Cascades suggested that tree voles were most abundant at elevations below 975 m, and were rare or absent at elevations > 1,200 m (Table 2). The highest elevations at which tree voles were found in the diet were 1,324 m in the Cascades and 1,390 m in the Klamath Mountains near Oregon Caves National Monument.

Numbers of Tree Voles Consumed By Spotted Owls

Based on our regional estimates of tree vole biomass in the diet, we estimated that nesting pairs of spotted owls in western Oregon captured > 50 tree voles per year on average (Table 3). Mean estimates of the number of voles captured per year were highly variable among and within regions (Table 3).

TABLE 3. Mean % biomass of red tree voles in spotted owl diets and estimates of the average number of red tree voles captured per year by spotted owls in western Oregon, 1970–2003.

			Mean no. captured per year per		
Geographic region	*N*	% Biomass (Mean ± SE)	Individual Owl	Non-nesting Pair	Pair with 2 Young
North Coast	9	1.0 ± 0.6	9.7 ± 5.9	19.4 ± 11.8	25.3 ± 15.3
Central Coast	90	3.7 ± 0.5	38.5 ± 4.9	77.0 ± 9.7	100.1 ± 12.7
South Coast	180	4.2 ± 0.3	43.2 ± 2.8	86.3 ± 5.6	112.2 ± 7.2
Interior Southwest	75	0.6 ± 0.2	6.0 ± 1.8	12.0 ± 3.5	15.6 ± 4.6
Central Cascades	150	2.2 ± 0.3	22.3 ± 2.9	44.5 ± 5.7	57.9 ± 7.4
North Cascades[1]	23	0.5 ± 0.4	5.1 ± 4.2	10.3 ± 8.6	13.4 ± 10.9
Mean	6	2.0 ± 0.7	15.0 ± 6.3	41.6 ± 13.7	54.1 ± 17.8

[1]All estimates were based on samples from owl territories with ≥10 prey except for the North Cascades region, in which we used all territories regardless of the number of prey in each sample (because of small sample size).

Discussion

Our analysis indicates that tree voles are widely distributed in western Oregon, and that their abundance varies greatly both within and among geographic regions (Tables 1, 2, 3). They appear to be most common in the South and Central Coast Regions and Central Cascades, with highest densities in the South Coast Region. Jewett (1920) also suggested that tree voles in Oregon were most common in the southwest coastal region. The high among-pair variation in diet within regions suggests high spatial variation in the abundance of tree voles. However, this is somewhat speculative, because there are other factors that could cause variation among pairs, such as individual variation in prey selection or temporal variation in sampling effort.

One concern with our data was that the diet might not reflect the relative abundance of tree voles in different regions if owls switched to other prey in regions where other types of prey were available that were easier to capture or that provided more biomass per unit effort. If this were a serious bias, we would have expected that tree voles would be less common in the diet in the South Coast Region, where the combined biomass of prey types that are supposedly preferred by northern spotted owls, such as woodrats (*Neotoma* spp.) and flying squirrels (*Glaucomys sabrinus*), was presumably higher than in the western Cascades and northern Coast Ranges (Carey et al. 1992). In fact, we observed just the opposite trend, which led us to believe that the regional patterns that we observed accurately reflected regional variation in abundance of tree voles.

Our results suggest that, in the Central Cascades, the abundance of tree voles declines with increasing elevation, and that tree voles are uncommon at elevations above 1,220 m (Table 2). Corn and Bury (1986) captured no tree voles in pitfall traps at elevations >1,036 m in the central Cascades of Oregon, and Huff et al. (1992) reported a maximum elevation record of 1,300 m in the Oregon Cascades. Few studies of tree voles have been conducted at high elevations in southwest Oregon, but our data and two specimen records (Verts and Carraway 1998) demonstrate that tree voles occur up to at least 1,390 m at Oregon Caves National Monument. In view of the number of studies that suggest that tree voles are rare above 1,300 m in the Cascades, we believe that a single record of a tree vole captured at 1,600 m in the Cascades (Manning and Maguire 1999) was exceptional, and does not indicate large numbers of voles at high elevations in the Cascades. Hamilton (1962) suggested that tree voles may be rare in high elevation true fir forests because their arboreal nests do not provide adequate insulation against cold winter temperatures. It is also possible that tree voles find it difficult to forage in high elevation forests during winter, when tree branches are frequently covered with snow and ice for extended periods.

Our sample of owl diets from the North Cascades Region was small and mostly included data from owls that occupied areas above 760 m elevation (16 of 23 pairs). In contrast, most historic records of tree voles in the north Cascades were from lower elevations along the Columbia River or in the western foothills of the Cascades (Verts and Carraway 1998). Thus, our sample was inadequate to address the distribution or abundance of tree voles in the north Cascades, except to say that they appear to be uncommon at elevations above 760 m. Similarly, our sample from the North Coast Region was too small to address distribution or abundance of tree voles adequately, but did indicate that tree voles still occur in some areas in Clatsop and Tillamook Counties.

Although spotted owls are clearly a major predator on tree voles, the population density of spotted owls is low compared to many other birds and mammals that feed on tree voles. These include Stellers jay's (*Cyanocitta stelleri*), saw-whet owls (*Aegolius acadicus*), long-eared owls (*Asio otus*), pygmy owls (*Glaucidium gnoma*), red-tailed hawks (*Buteo jamaicensis*), ringtails (*Bassariscus astutus*), and ermine (*Mustela frenata*) (Howell 1926; Maser 1965; Forsman and Maser 1970; Reynolds 1970; Maser et al. 1981; Alexander et al. 1995; Graham and Mires in press; James K. Swingle, Oregon State University, personal communication). The fact that tree voles persist in many areas, despite these many predators, suggests that tree vole populations are considerably larger than is indicated by the meager sample of specimens in museums.

Although our data indicate that tree voles are still relatively widespread in Oregon, and are fairly common in some regions, our study cannot be used to assess population trends of tree voles or to assess the response of tree vole populations

to different types of forest management. Our data came entirely from areas occupied by spotted owls, which tend to include extensive areas of old forest intermixed with younger forests. Thus, our data should not be used to infer the occurrence of tree voles in areas where old forests have been largely eliminated by harvest. Extensive areas of state, private, and federal land in western Oregon have been converted to intensively managed young forests during the last century, and some evidence suggests that tree voles are less common in such forests than in old forests (Aubry et al. 1991). The uncertainty regarding trends in tree vole populations can only be resolved with more field surveys to better document the distribution of the vole and with experimental studies to evaluate the influence of various types of habitat manipulation on tree voles.

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