Annotated Bibliography of the Red Tree Vole (*Arborimus longicaudus*), Sonoma Tree Vole (*A. pomo*), and White-Footed Vole (*A. albipes*)
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Cover: Captive tree vole by Eric Forsman
Abstract


This annotated bibliography contains all citations that we could find on tree voles (*Arborimus longicaudus, A. pomo*) and white-footed voles (*A. albipes*), including many unpublished sources in museum archives, court proceedings, and agency documents. Some documents not readily available in published form or museum archives are available upon request from the compilers.

Keywords: Red tree vole, Sonoma tree vole, white-footed vole, *Arborimus longicaudus, Arborimus pomo, Arborimus albipes*, Arvicolinae, Muridae.
Introduction

Because of their unique adaptations for living in the forest canopy and feeding on needles and twigs of conifers, red tree voles (*Arborimus longicaudus*) and Sonoma tree voles (*A. pomo*) have long intrigued mammalogists. While conducting studies of tree voles, we have come across a wealth of information on these enigmatic mammals, much of which is unpublished or buried in obscure sources that are not easily obtainable. Because much of this information was difficult to find, we synthesized it into a single bibliography with annotations describing the type of information presented in each source. We have also included information that we found on the closely related white-footed vole (*A. albipes*), which occupies a geographic range similar to the tree vole’s, and which is also at least partially arboreal. Our hope is that this bibliography will be of use to others who are interested in these unique animals.

We included many unpublished references, including field notes and specimen catalogs that we found in museums or other locations where they were difficult to locate. We found those obscure sources to be extremely helpful in tracing the history of research and management of *Arborimus* voles, and we think that future researchers will find those sources useful as well. We have also included many published papers on the evolutionary history of arvicoline voles because those papers helped us understand the evolutionary history of tree voles and white-footed voles, even if those species were not specifically mentioned in the published works. We also included a few papers on old-growth forests and conifer needle chemistry because we found them useful for understanding the unique relationship between tree voles and the structural and chemical attributes of the trees in which they live.

Because of the long and contentious debate over whether or not to protect tree voles on federal lands in Oregon and California, there is much gray literature on tree voles that has been produced in federal management reports and court cases. The many documents related to court cases are particularly interesting because they illustrate the difficulty of finding middle ground in the debate over management of forests in which tree voles and many other species of obscure plants and animals occur. We included as many of these management documents and court documents as we could find, although we undoubtedly overlooked some of them.

Although we tried to include a short annotation for every citation in the bibliography, we made no attempt to describe all of the details that were presented in each source. Our main objective was to provide a complete list of data sources, with a brief account of what was in each citation. To help readers find references by author or subject area, there is a subject index and author index at the end of the bibliography. A few of the unpublished references in the bibliography are in our
possession and are not available from other sources; These references are available upon request from the compilers. We also included an appendix in which we list citations and numbers of tree voles and white-footed voles captured in trapping studies in western Oregon and northwestern California. The latter appendix can be used to quickly peruse the results from a large number of trapping studies, without reading every citation.

Tree voles and white-footed voles belong to the subfamily Arvicolinae (voles, lemmings, and muskrats) in the family Muridae (Musser and Carleton 1993). Other subfamilies of murid rodents that occur within the range of the tree voles include the Murinae (old world rats and mice) and Sigmodontinae (new world rats and mice; Verts and Carraway 1998). Generic and specific taxonomy of tree voles and white-footed voles has changed over time. Based on the type specimen of the red tree vole, which was collected near Coos Bay, Oregon in 1890, True (1890) named the species *Phenacomys longicaudus*. Taylor (1915) proposed that *Phenacomys longicaudus* and *Phenacomys albipes* be assigned to a new subgenus (*Arborimus*). Based on a single specimen from Tillamook, Oregon, Howell (1921) concluded that there was another species of tree vole in northwest Oregon, which he called *P. silvicola*. Howell suggested that *P. silvicola* might co-occur with *P. longicaudus*. Miller (1924) referred to this new species as the dusky tree vole and shortened the name to *P. silvicola*. In a subsequent monograph on *Phenacomys* voles, Howell (1926) continued to maintain that there were two species of tree voles in northwest Oregon, which he referred to as the “Red Tree Mouse” and “Forest Tree Mouse.” Contrary to Taylor (1915), Howell (1926) concluded that placement of *P. longicaudus* and *P. albipes* in the subgenus *Arborimus* was based on such minor morphological differences that it was unwarranted. This was the last word on taxonomy of tree voles for many years, until Johnson (1968) conducted the first blood protein electrophoresis studies of tree voles and concluded that *P. silvicola* should be relegated to a subspecies (*P. l. silvicola*). In a later paper, Johnson (1973) proposed that *Arborimus* should be elevated to full generic rank and that all named forms of tree voles should be included in a single species (*A. longicaudus*: red tree vole). Johnson and Maser (1982) subsequently determined that the genus of the white-footed vole should also be changed from *Phenacomys* to *Arborimus*. Based on captive breeding studies, karyotypic analyses, and morphometric comparisons, Johnson and George (1991) proposed that tree voles in California should be placed in a separate species (*A. pomo*), which was later given the common name Sonoma tree vole. Murray (1995) subsequently concluded that the dividing line between *A. pomo* and *A. longicaudus* was the Klamath River in northern California. In this bibliography, we will use the Klamath River as the dividing line between *A. pomo* and *A. longicaudus*, regardless
of specific names used in the original papers. Recent genetic and morphological studies have detected genetic differences in tree voles in northern and southern Oregon but have also found so much overlap that those differences are useless for taxonomic differentiation (Miller et al. 2006). Because there is uncertainty regarding the subspecific taxonomy of tree voles, we refer to all tree voles from Oregon as *Arborimus longicaudus*, without regard to subspecific taxonomy.


   There is only one brief reference to *Phenacomys* in this paper, but it is a useful reference for anyone interested in the evolution of the Arvicolinae.


   This is an excellent summary of the distribution, morphology, ontogeny, reproduction, ecology, behavior, and genetics of the Sonoma tree vole. We found one minor error; the authors incorrectly cited Forsman et al. (1984) by stating that tree voles made up 50 percent of the diet of northern spotted owls (*Strix occidentalis caurina*) in Oregon. Forsman et al. (1984: 43) actually reported that the percentage of red tree voles in spotted owl diets in Oregon was highly variable among regions, ranging from 0 to 49 percent.


   In this case in which the plaintiffs challenged a Bureau of Land management timber sale, Judge Aiken dismissed the case and allowed the Rickard Creek timber sale to proceed. The judge ruled that the Bureau of Land Management did not violate the Federal Land Policy and Land Management Act by classifying Rickard Creek as a “non-high priority” tree vole site.


   Alexander reported crane fly larvae from a Sonoma tree vole nest at Stewarts Point, Sonoma County, California. The species was identified as *Limonia nubeculosa sciophila* after the larvae hatched in captivity.

The authors found red tree vole remains in ringtail (*Bassariscus astutus*) scat in southwest Oregon.


Andrews located 87 potential trees with red tree vole nests during line transect surveys on McDonald Forest in Benton County, Oregon, in 1994–1995. Of these, five trees had tree vole nest material located on the ground and seven were documented to be tree vole nests when they were climbed. The status of the other trees with potential nests was not verified, as the trees were not climbed.


In this general species account, Anthony discussed the tree vole and the white-footed vole. He said that tree voles were rare in museums and that little was known of their life history. He reported that average nest height was 9 m but did not acknowledge that this could have been biased by the fact that most early naturalists could not climb big trees. He repeated previous unsubstantiated speculation that male tree voles might be almost entirely terrestrial.


The authors used museum special traps and rat traps to sample small mammals in riparian forest habitats in the Cascades near Blue River and McKenzie Bridge, Lane County, Oregon. They sampled five old-growth stands, five mature stands, and two young stands. In 10,800 trap-nights, they captured nine white-footed voles but did not capture any tree voles. They concluded that additional information was needed to describe specific habitat associations of white-footed voles.

This paper contained nothing specific about tree voles; however, anyone interested in the diet and feeding behavior of tree voles might find it useful because it is a good reference on needle structure in Douglas-fir (*Pseudotsuga menziesii*), especially with regard to the development of resin ducts. Compared to needles of old-growth trees, needles of young Douglas-fir saplings were longer, had smaller vascular cylinders, larger resin ducts, and fewer hypodermal cells. These results suggest that tree age could play a role in the nutritional value or digestibility of Douglas-fir needles for tree voles, but this has not been investigated.


Ash and Schmelzer described a Portland Audubon Society field trip on 30 July 2005, during which researchers climbed to a nest and captured a red tree vole in the Oregon Coast Ranges a few kilometers west of Monroe, Benton County.


This report was a synthesis based on one study in Washington and two studies in Oregon (Corn and Bury 1991, Gilbert and Allwine 1991). Pitfall traps were used to sample small mammals. In total, 8,661 small mammals were captured in the three study areas. Based on a log-linear analysis of stand age vs. geographic province, the authors reported that red tree voles were closely associated with old-growth forests. In support of this conclusion, they cited two other studies in which there was some evidence for an association between tree voles and old-growth forest (Bury 1986, Corn et al. 1988). The authors concluded that “Although the data are minimal, existing information indicates that red tree voles are largely restricted to old-growth forests; younger forests apparently do not provide suitable habitat for this species.” This rather strong statement suggests either that the authors were unaware that many tree voles had been captured in young forests by specimen collectors, or that the authors considered the earlier
collections biased because many specimen collectors focused their sampling efforts in young forests. The authors also suggested that extensive loss or fragmentation of old-growth forests could eliminate tree voles from forested landscapes.


In this literature review, the authors concluded that tree voles were the most arboreal mammal in North America, were closely associated with large trees in Douglas-fir forests, and were most abundant in late-successional forests where canopies of large trees were interconnected.


Vernon Bailey described three days of searching for tree voles with Alfred Shelton at Spencer Butte in Lane County, Oregon, in 1914. After considerable effort, they finally captured a single vole, as described in the following narrative: “With a pair of climbing irons we took turns in climbing the trees. The next morning the third tree fell to my turn. It was about 2 feet in diameter at the bottom and the nest about 80 feet up on the first green branches. It was a hard climb but the large flat nest at once showed fresh signs and I dug in with great care. Not until I had dug out the last of the nest did the occupant leave the house and run out on one of the branches a few feet below. It was only about 20 feet from me so with a fine shot pistol I shot at one edge of it and brought it to the ground. The stomach and intestines are filled with bright green semi-fluid material, evidently the inner pulp of spruce [Douglas-fir] leaves. The feces are small and excreted in bundles of green pellets.” He concluded by stating, “The treetop mouse is not a rare species but probably the most inaccessible of our small mammals.” This field trip was later described in a full length article in the Oregon Historical Quarterly (Jobanek 1988).

Bailey described several of the early records of red tree voles in Oregon and recounts his trip to collect tree voles on Spencer Butte, Lane County, Oregon, in 1914. Bailey said that he often set traps in hopes of catching tree mice, without success. In 1907, William Bebb showed him several tree vole specimens that were collected by loggers. Bebb never published this information, but we found two of his specimens in the collection at the Bean Life Science Museum at Brigham Young University, both collected in 1905 near Marmot in Clackamas County, Oregon. Bailey also reported that Alfred Shelton collected two juvenile tree voles in 1914 at Spencer Butte, Lane County, Oregon. He described the day in 1914 when he and Shelton returned to Spencer Butte and captured an adult vole by climbing several trees until they chased a vole out of a nest and shot it with a collecting pistol. He described nests with green cuttings on top and says that trees had from one to five nests. Most nests were greater than 24 m above ground. He wrote, “The feces were deposited around the outside of the nest and helped to build up its solid walls and render it weatherproof.” He says that nests were built of “…fine midribs of a great number of spruce [Douglas-fir] needles, the sides of which had served as food.” This is one time when Bailey apparently got it wrong. When feeding on Douglas-fir needles, tree voles remove the resin ducts from the edges of the needle and consume the central part of the needle. Thus, we assume he must not have looked closely at the discarded remains.


Bailey was one of the first to discuss tree vole distribution in a spatial context. He stated that tree voles only occur in areas of extensive forest or areas of recently isolated forest. He pointed out that tree voles sometimes build their nests on top of old hawk or squirrel nests. He reported that Harry Wilder located several tree vole nests in burrows under logs or woodpiles near Douglas-fir trees that had low-hanging branches that were easily accessed from the ground. Bailey tried unsuccessfully to capture tree voles with snap-traps on logs or low branches. He reported that Harry Wilder and Irvine Clay thought that the main breeding season for tree voles was early spring to late summer but that tree voles breed throughout the year. He postulated that slow development of the young was an adaptation for living in an arboreal environment. He also reported that tree voles
did not consume water in captivity except when fed desiccated needles. He speculated that American marten (*Martes americana*) and fisher (*M. [= Pekania] pennanti*) were potential predators of tree voles.


In this obituary, Bailey described his friend William Bebb, dental surgeon, ardent naturalist, and specimen collector. In 1907, Bailey and Clint Merriam visited Bebb at his home in Pasadena, California, where they were stunned to find several red tree vole skins of good quality. They were curious how Bebb had collected these specimens because they had never seen a live tree vole and were only aware of the one mangled type specimen that was found dead in the road near Coos Bay, Oregon, in 1890. Bebb told them that he collected tree voles from Douglas-fir trees that were felled by loggers near Marmot, Clackamas County, Oregon.


In this short letter to Eric Forsman, Doug Bake confirmed a date (21 July 2003) when he could meet and discuss his career as a logger and tree vole collector in the north Coast Ranges of Oregon. Doug said that he started collecting tree voles after another logger (Peter Walker) told him that museum collectors were eager to obtain specimens. Doug eventually collected 98 red tree voles, most of which are in the Slater Museum of Natural History at the University of Puget Sound. We found that on some of those specimens, his name was incorrectly spelled “D. Bates.” For more details on Doug Bake’s collecting efforts see Forsman and Swingle (2010).


The authors reported that requirements to “survey and manage” wildlife species on federal forest lands were resulting in a reduction in harvest. They cited an example in which predisturbance surveys for red tree voles resulted in portions of the proposed harvest area being protected from logging. When managers were faced with numerous tree vole nest structures in a sale area, they had to weigh the potential cost of climbing nest trees to determine tree vole activity status and reconfiguring the proposed sale unit versus simply dropping the sale and moving to another area. In addition,
the need to protect numerous tree vole nest areas within a harvest unit sometimes made timber sales operationally unfeasible, meaning that trees could not be logged without damaging protected areas.


   In table 4, Baker lists the red tree vole and white-footed vole as only occurring in lowland conifer forests of the Pacific coast.


   Based on model simulations of forest growth, the authors suggested that red tree voles may benefit from thinning in young forests because thinning produces trees with larger crowns. They provided no data on the actual response of tree vole populations to thinning.


   In this newspaper article, Barnard reported that the 9th U.S. Circuit Court of Appeals ruled that the Bureau of Land Management failed to conduct a public review before dropping the red tree vole from the list of species that require formal surveys in proposed timber sales.


   Based on fossil evidence, the authors suggested that *Phenacomys* and *Clethrionomys [= Myodes]* that occupied closed canopy forests decreased during warm periods of the past, and that *Phenacomys* became progressively rarer during the last glacial-interglacial transition as the climate became warmer.


   Barrows collected 375 prey items from four pairs of northern spotted owls in three widely scattered locations in northwestern California. The sample included 64 Sonoma tree voles (17.1 percent of total prey items). He did not
say how diets differed among areas, which included two locations in Marin County that were outside the range of the tree vole (Point Reyes and San Geronimo), and one location within the range in Mendocino County.


Barrows reported that diets of northern spotted owls in northwestern California in 1977–1983 included 9 to 50 percent tree voles.


Behle reported that he collected an adult female tree vole that was run over by a car near Coyote Peak on Bald Hills Road, Humboldt County, California.


The authors reviewed the career of Charles Repenning, a paleontologist who was a leader in the effort to reconstruct the evolutionary history of arvicoline rodents. Repenning was a mentor to many, whose long and productive career was cut short by a burglar who shot him in his home. Repenning and many of his colleagues used the shape of the lower first molar as the primary structural feature for assessing evolutionary lineages of arvicolines. Based on a sample of six fossil individuals that included two lower M1 molars, Repenning (1987) proposed the new species *Phenacomys brachyodus*. Repenning et al. (1987) suggested that *Phenacomys* was derived from an unknown form of *Cromeromys*. Repenning (1998, 2001) suggested that *Phenacomys* were immigrants to North America from Asia via the Bering Land Bridge during the Pleistocene ice ages.

The authors used genetic base pairs to compare taxonomic relationships among red tree voles, dusky tree voles, Sonoma tree voles, white-footed voles, and heather voles (*Phenacomys intermedius*). There were clear taxonomic differences in all pairings except for the red tree vole and its putative subspecies, the dusky tree vole. The authors concluded that red tree voles and white-footed voles were closely related, supporting their inclusion in the same genus (*Arborimus*). The authors also suggested that their results indicated a Pleistocene radiation of the *Arborimus* clade, concordant with pulses of diversification observed in other murid rodents. The authors concluded that the elevation to full generic rank of *Arborimus* from *Phenacomys* was open to debate, as their data did not clearly support a decision one way or the other.

28. **Benson, S.B. 1930–1956.** Unpublished field notes. On file with: University of California, Berkeley, Museum of Vertebrate Zoology. Seth Benson’s voluminous notes described numerous field trips during which he and his wife Emma, along with students and colleagues, collected a total of 49 Sonoma tree voles in Humboldt and Sonoma Counties, California. Benson and his graduate students kept many of these voles in captivity for periods of 2 to 30 days. He and Emma located 6 to 8 clouded salamanders (*Aneides ferreus*) in a single Sonoma tree vole nest. Like many naturalists who studied tree voles in California, Benson traveled to the Wilder Ranch near Carlotta, Humboldt County, where Harry Wilder showed him tree vole nests and freely dispensed his knowledge of tree vole life history. Wilder told Benson that tree voles had become scarce around his ranch because the forest behind the ranch had been logged and the population had been reduced by collectors.

29. **Benson, S.B.; Borell, A.E. 1931.** Notes on the life history of the red tree mouse *Phenacomys longicaudus*. Journal of Mammalogy. 12: 226–233. Although the title states that this paper is about the red tree vole, it was actually based on observations of Sonoma tree voles in California, which had not been designated as a separate species at the time of publication. The authors described nests, young, diet, and behavior of tree voles based on observations of voles in the wild and kept 27 tree voles in captivity. They captured Sonoma tree voles by climbing trees near Carlotta, Kneeland, Bridgeville, and the Van Duzen River in Humboldt County, and near...
Monte Rio, Camp Meeker, Occidental, and Bohemian Grove in Sonoma County. They searched for, but did not locate tree voles in Marin and Santa Cruz Counties.

They noted that tree vole nests were placed on firm supports that were close to a food source of green needles. Some tree vole nests were built on top of old bird or squirrel nests. Most nests were on branches close to the trunk, but some were as much as 9 m out on limbs. Most nests were in Douglas-fir or grand fir (Abies grandis), but a few were in redwoods (Sequoia sempervirens). The authors did not say what the voles that nested in redwoods were feeding on, but they did say that nests in redwoods were always located near Douglas-fir trees. The authors reported that captive tree voles ate rolled oats, fresh apples, fresh carrots, fresh squirrel meat, dried pears, dried apples, raisins, Cedrus deodara, and Abies venusta, even when supplied with fresh Douglas-fir and grand fir. This is interesting because we and others (e.g., Clifton 1960) found that captive tree voles generally refused exotic foods except for occasional individuals that would eat apple.

The authors reported that reproduction occurred throughout the year, but they did not discuss seasonal variation in reproduction. They observed a one-month-old captive eating fir needles while still suckling. They corrected Howell (1926) and agreed with Taylor (1915) by stating that tree voles ate the midrib of Douglas-fir needles after removing the lateral edges of the needle, which contained the resin ducts. They described the feeding behavior of a captive tree vole as “almost machine-like.” The vole would rapidly pass a needle through its incisors from right to left and immediately flip the needle around to chew along the opposite side of the needle. Not all needles had the resin ducts removed in the same manner. In some cases, only part of the resin duct was removed. They also observed captives eating young needles without removing the resin ducts. They pointed out that resin ducts of Douglas-fir were easy to identify because one side was smooth and the other side had unique scallop-shaped marks that were left by the vole’s incisors.

Unlike most other collectors who have captured tree voles by climbing nest trees, Benson and Borell captured about the same number of females and males. They reported that males and females usually did not inhabit the same nests except for one nest in which they found an adult male with a subadult female. They also found one tree with three occupied nests.
They reported that tree voles were easily kept in captivity as long as they were provided with fresh food. They also reported keeping six tree voles in a bathtub filled with sawdust for 4 days. The six voles slept in the same nest in the tub. After removing four voles from the bathtub, the two remaining voles lived together for 1 month. They did not report if these voles were related or not, and they did not discuss the long-term survival of these normally solitary voles kept in such unusual conditions. The captive voles drank considerable water, and the authors noticed that voles kept in warm rooms drank more water than those kept in cool rooms.

They reported that some tree voles were infected by the small mite, *Atricholaelaps californicus*. They also found an arboreal salamander (*Aneides lugubris*) in a nest at Bohemian Grove, Monte Rio, and what they thought was a black salamander (*A. flavipunctatus*) in an abandoned tree vole nest near Occidental, Sonoma County. We are not aware of any other reports of black salamanders in tree vole nests.


The authors found that there were more broken crowns and cavities in old-growth stands of Douglas-fir than in young or mature forests. While not particularly surprising, these findings are germane to the ecology of tree voles because we and others have found that many tree vole nests are located in cavities or broken tops of old trees.

31. **Biswell, B.L. 1994.** Intertree movement and spatial distribution of nest trees occupied by individual red tree voles: implications for conservation [Poster]. In: 75th anniversary meeting of the Society of Mammalogists, Washington, DC (Available upon request from the compilers).

Biswell studied the movement patterns of nine adult and four subadult red tree voles that were radio-collared in western Oregon in 1992–1993. Adults were followed for 35 to 106 days, and analysis of nest site usage was based on four to five daytime locations per week to assure independence between observations. Individual voles used two to seven nest trees each, and the greatest straight-line distance between two nests that were occupied consecutively by the same individual was 76 m. When moving to
a new tree, adult voles reoccupied previously constructed nest structures at least 68 percent of the time. Of the 39 nest trees located via telemetry, 36 percent contained more than a single nest, and one tree contained seven nest structures. Subadults were followed for 23 to 40 days during which time two dispersed from their natal nest trees. One subadult was located in five different trees and reached a maximum straight line distance from its natal nest of 340 m. Biswell concluded that dispersing subadults were successful in crossing small forest roads, small streams, and 30-m-wide canopy gaps while traveling between nest sites, which required movement on the ground.


This abstract from the 2002 annual meeting of the Society for Northwestern Vertebrate Biology included a more complete analysis of the data described by Biswell and Forsman (1999). Biswell studied red tree vole nest abundance in five watersheds containing various levels of old forest and tested for differences in abundance across watersheds and between serial stages. He conducted approximately 46.7 km of line transect surveys in 96 randomly selected stands in the Coast Ranges and interior valley foothills in western Oregon. Average densities of recently occupied or occupied vole nest trees in four watersheds were 0.2 to 3.3 nest trees/hectare. Densities of occupied or recently occupied nest trees varied substantially within and among forest age-classes, and a few “hot spots” strongly influenced overall density estimates in four of the watersheds. Biswell concluded that “…cautious management is needed to ensure sufficient numbers of sites to maintain appropriate levels of biological function and species interactions within this region.”


This was the third of four versions of the survey protocol for red tree voles on federal forest lands (see also Biswell et al. [2000], Huff et al. 2012, USDA FS and USDI BLM 1996). It included a literature review and a revision of the previous protocol.

This was the second of four versions of the survey protocol for red tree voles on federal forest lands (see also Biswell et al. 2002, Huff et al. 2012; USDA FS and USDI BLM 1996). The first part of the protocol included a literature review on taxonomy, distribution, biology, home range, dispersal, abundance, habitat, and nests of red tree voles. The second half described the survey protocol. This protocol was designed primarily to determine if tree voles were present in areas proposed for harvest.


In 2000, contractors were hired to conduct surveys of red tree voles north of the Klamath River on the Klamath National Forest, Siskiyou County, California. They surveyed 47 km of transect in 77 mature forest plots and detected potential tree vole nests in 173 trees. They climbed to all potential nests and found that 18 (10.4 percent) were red tree vole nests. Based on a distance sampling analysis, the authors estimated that the effective sampling distance (mean ± SE) for all 173 potential nest structures was 21.0 ± 0.6 m. They did not provide a separate estimate for red tree vole nests.


In this abstract from the 1999 annual meetings of the Society for Northwestern Vertebrate Biology and the California North Coast Chapter of the Wildlife Society, Biswell and Forsman stated they conducted 157 line transect surveys, totaling 47.5 km, in 96 randomly selected stands distributed between five watersheds in western Oregon. Stands ranged from young regenerating forests on clearcuts to late-successional forest.
Watersheds were about 5,000 ha and contained from 5 to 55 percent late-successional forest. Surveyors detected 703 nest structures of which 84 (12 percent) were tree vole nests. The other 619 nests (88 percent) were built by other arboreal rodents or birds. While tree vole nests were detected in all age classes surveyed, the number of nests increased with stand age and with the amount of late-successional forest occurring within the watershed. The authors concluded that the specialized habitat requirements and low dispersal capabilities of tree voles could lead to extirpation of the species in heavily managed landscapes dominated by young forests.


The goals of this study were to expand upon what was known of red tree vole distribution and abundance in different vegetation communities and to determine the geographic boundary between the red tree vole and Sonoma tree vole. The results were briefly described in abstracts at two different meetings (Biswell 2002, Biswell and Forsman 1999).


This paper mentions a red tree vole that was captured in a live-trap near Cottage Grove, Lane County, Oregon. See Borrecco (1973) for details. Hooven’s initials were actually E.F.


Blois used amplified fragment length polymorphisms (ALFP) and mitochondrial DNA (mtDNA) analyses to address diversity and population structure in the Sonoma tree vole. The mtDNA analysis indicated that there was a north and south clade of the Sonoma tree vole, but the AFLP analysis indicated that all samples belonged to a single panmictic
population. Blois concluded that, for *A. pomo*, “...the combined AFLP and mtDNA data support the recognition of two separate Management Units, but only a single Evolutionarily Significant Unit within the species.” She also reported capturing three tree voles at the Humboldt State University Schatz Demonstration Tree Farm, 1.6 km north of Maple Creek, Humboldt County.

40. **Blois, J.L.; Arbogast, B.S. 2006.** Conservation genetics of the Sonoma tree vole (*Arborimus pomo*) based on mitochondrial and amplified fragment length polymorphism markers. *Journal of Mammalogy.* 87: 950–960. This was the published version of Blois’ thesis. The mtDNA analysis indicated that there was a north and south clade of the Sonoma tree vole, but the AFLP analysis indicated a single panmictic Sonoma tree vole population. Based on the mtDNA results, the authors concluded that tree voles north of the Klamath River in California should be included in the red tree vole clade identified by Miller et al. (2006) and Murray (1995).


The authors compared small mammal fossil remains located in a cave north of Redding, Shasta County, California. They reported that the taxa located in the cave currently exist in northern California, but the relative abundance changed over time. The fossil samples indicated that the white-footed vole was persistently present during late Pleistocene but only intermittently present during the Holocene. The cave was east of the current distribution of the white-footed vole in California.

42. **Bochkov, A.V. 2011.** Mites of the subgenus *Microtimyobia* (Acariformes: Myobiidae: *Radfordia*) with their host-parasite relationships with the cricetid rodents (Cricetidae). *Zootaxa.* 2954: 1–86.

In this literature review, Bochkov revised the myobid mites associated with voles. This included two mites associated with tree voles, *Radfordia (Graphiurobia) arborimus* (Fain and Whitaker 1975) and *R. (Microtimyobia) arborimus* (Fain and Lukoschus 1977).


On pages 142–144, Booth gave a brief description of white-footed voles and tree voles. He said that the tree vole was one of the most peculiar voles in the world owing to its arboreal nature and its diet of conifer needles. He
stated that the putative subspecies of the red tree mouse, the dusky tree mouse, lives mainly in Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) trees rather than Douglas-fir.


In 1971, Borrecco captured a single red tree vole in a Sherman live-trap at Carlson Creek, 25.8 km south of Cottage Grove (T23S, R04W, Section 13, E1/2) in Lane County, Oregon. Vegetation on the study plot was a stand of young Douglas-fir growing on a 19-ha area that was clearcut and burned in 1959 and then planted in 1960, 1964, and 1970.


Brock collected two adult and three juvenile Sonoma tree voles near Capetown and Petrolia, Humboldt County and Freestone, Sonoma County, California.


Brown’s report included a chapter by Forsman et al. on pages 259–267 in which the authors say that tree voles comprised 13 percent of spotted owl prey in temperate coniferous forests and 5 percent of spotted owl prey in mixed-conifer forests in western Oregon.


Brown provides no new data on tree voles, but on page 171 in appendix 8, he suggested that tree vole home ranges include at least one tree.


Brown said that he found a “colony” of dusky tree voles on Oregon State University’s McDonald Forest, 13 km north of Corvallis, Benton County, Oregon, in 1963. He captured an adult male in one nest and four half-
grown juveniles in another nest, both about 9 m above ground. Apparently he did not see the adult female. On 15 May 1963, he captured one adult female and two newborns that weighed 2.56 and 2.60 g, respectively, in a nest about 0.4 km south of the first area. The female was kept alive for 15 days and then killed. She had three embryos in her uterus with crown-rump length averaging 4.5 mm. Brown concluded that this indicated that tree voles experienced “…postpartum ovulation and pregnancy upon occasion.” Brown claimed that his specimens were sent to the University of Wyoming, but the specimens are not at that institution. Like Vernon Bailey, he said that nests and sleeping chambers were lined with midribs of Douglas-fir needles, but it is obvious that he did not look closely at the nest material, or he would have realized they were the edges of the needles. He also described a tree vole nest that was occupied by two deer mice (Peromyscus maniculatus).

Brylski described the distribution, habitat, and reproduction of the white-footed vole. He emphasized that there was little information on the basic life history and predators of this species in California.

In this species account, the authors described the distribution, habitat, nests, and taxonomy of the Sonoma tree vole. The information is somewhat dated.

This field guide provides brief descriptions of the habitats and life-histories of the heather vole, white-footed vole, and red tree vole.

52. Burton, K. 2005. Personal communication in email to Eric Forsman (Available upon request from the compilers).
On 11 July 2005, wildlife biologist Ken Burton saw a Steller’s jay (Cyanocitta stelleri) trying to kill a Sonoma tree vole by pecking it. The jay flew off as Burton drove up, leaving the tree vole alive but stunned on the Bald Hills Road east of Arcata, Humboldt County, California.

The small mammal data used in this analysis was the same information described in Corn and Bury (1986, 1988) and Corn et al. (1988). These data were collected in 1983 at H.J. Andrews Experimental Forest, Oregon, and Wind River Experimental Forest, Washington. Pitfall traps were opened in May 1983 and monitored for 180 days. The authors compared traps with short drift fences to traps without fences. They concluded that drift fences did not improve capture rates of small mammals. In 38,880 trap-nights, they captured 2,029 mammals, including 17 red tree voles at H.J. Andrews. The tally of numbers in this report is slightly different than in their other papers (2,029 vs. 2,104; Corn and Bury 1986, 1988). We suspect this may have been because they did not include mammals captured on an experimental grid. The capture rate of tree voles was 0.044 tree voles per 100 trap-nights. They concluded that tree voles were “…extremely difficult to trap by any method.”


The authors concluded that *Phenacomys* was the only genus in the tribe *Phenacomynini*. *Microtus* was noted as the closest living relative to *Phenacomys*. Because these authors apparently did not recognize the genus *Arborimus* as distinct from *Phenacomys*, we assume they would also have included *Arborimus* in the same tribe.


Based on information in Hamilton (1962), the authors suggested that the red tree vole may have lactational embryonic diapause or lactational delayed implantation.


In his section on chisel-toothed mammals on pages 517–519, Cahalane made several unsupported or incorrect statements about tree voles. He
said that tree voles may live on the ground, with the male more likely to do so, but he provided no data to support this, and he ignored the evidence that ground nesting by tree voles was actually extremely rare. Like Bailey (1915), Howell (1926) and Brown (1964), he incorrectly stated that tree voles ate the edges of Douglas-fir needles and discarded the central part of the needle. And then he topped it off by saying that tree voles occurred from eastern Canada to east-central California.


The California Academy of Sciences library has field notes for William Hamilton, III (1961), Chester Lamb (1921), Joseph Mailliard (1920–1936), and Harry Wilder (1911), all of whom worked on Sonoma tree voles. We examined Mailliard’s notes (see reference 258) but did not have time to examine the others, so we do not know if they pertain to tree voles or not.

58. **California Fish and Game. 1986.** Mammalian species of special concern in California, red tree vole. Sacramento, CA: California Department of Fish and Game. 2 p.

This species account included information on the distribution, population status, habitat, and nests of the Sonoma tree vole. The anonymous author(s) suggested that what was most needed was information on population status and distribution. They also suggested that where tree voles are present, clearcutting should be replaced with selective logging.

59. **California Fish and Game. 1986.** Mammalian species of special concern in California, white-footed vole. Sacramento, CA: California Department of Fish and Game. 2 p.

This general species account included information on the distribution, population status, habitat, taxonomy, and management of the white-footed vole. The author(s) emphasized that there were only 12 specimen records of white-footed voles from California and that virtually nothing was known about the status of the species.


Camp described the 1913 Museum of Vertebrate Zoology North Coast Counties Expedition, during which 17 adult and 12 juvenile Sonoma tree voles were collected in Mendocino and Humboldt Counties, California.
This expedition resulted in three published papers on Sonoma tree voles (Taylor 1915a, 1915b, 1961).


Camp took these pictures of the “Phenacomys grove” and “Phenacomys colony in grand firs” near Mendocino City, California, during the 1913 North Coast Counties Expedition. The expedition members collected Sonoma tree voles at this site after some local boys showed them how to capture tree voles by climbing nest trees.


In this short synthesis of previous and ongoing studies, Carey presented a table in which he displayed tree vole capture data from pitfall studies conducted by Corn and Bury (1986, 1988, 1991). Based on Corn and Bury’s data, he concluded that tree voles were more abundant in old-growth than in mature and young forests. He stated that “…I have observed red tree vole colonies in some young stands. But my experience indicates that the vole is not widespread in young and mature forests; ongoing research shows vole nests can be very abundant in old-growth forests.” He did not define what he meant by a “colony” and presented no data to support the notion that tree voles are a colonial species. He also suggested that tree voles were weak dispersers, incapable of dispersing through clearcuts, clearings, or areas of blow-down.


In this literature review, Carey stated that “Red tree voles are rare in closed sapling-pole-sawtimber and large sawtimber stands, but relatively abundant in old growth in the Cascades and Coast Ranges of Oregon.” He did not cite any evidence for this statement. He suggested that tree voles rarely traveled on the ground but provided no data regarding the frequency of terrestrial movements. In discussing limiting factors, he suggested that old-growth forests are ideal habitat for tree voles because (1) old forests are more stable than young forests, (2) primary production of needles
is higher in old forests, and (3) old-growth canopies have higher water-holding capacity and intercept fog that voles use as a source of free water by licking the needles. In table 4, he classified forests of small sawtimber and large sawtimber as population sinks, but provided no data to support this hypothesis.

64. **Carey, A.B. 1996.** Interactions of northwest forest canopies and arboreal mammals. *Northwest Science* 70. (Special Issue): 72–78.

Carey concluded this literature review with the oft-repeated observation that the red tree vole is the most arboreal mammal in the Pacific Northwest. He stated that tree voles have the narrowest niche of Pacific Northwest arboreal mammals, require free water in the form of fog or rain droplets, and are most abundant in old growth. He speculated that the interconnected limbs of old-growth trees facilitate access to other voles and serve as escape routes from predators.


Carey provided a general overview of the ecology and habitat relationships of red tree voles. He suggested that old-growth forest is optimum habitat for tree voles and that tree voles are declining as a result of logging.


Most of this report is dedicated to sampling methods for northern flying squirrels (*Glaucomys sabrinus*). In two paragraphs that refer to tree voles, the authors state that tree voles are hard to study because they can only be consistently captured by climbing trees. They suggest that searching for nests in felled trees may be a more effective method for sampling tree voles than ground-based transects.


In this book section, the authors agreed with Hall (1981) who argued that the scientific name of the red tree vole should be *Phenacomys longicaudus*. This was in contrast to Johnson (1973) and Johnson and Maser (1982), who proposed the use of *Arborimus longicaudus*. 

Carleton and Musser reversed their 1984 position and classified the red tree vole and Sonoma tree vole as *Arborimus longicaudus* and *A. pomo*, respectively.


This bibliography included many citations for red tree voles and white-footed voles, all of which we include in the current bibliography.


The authors compared the relative performance of nonspatial and hierarchical Bayesian spatial models for predicting the probability of occurrence of red tree voles and two other species. The best spatial model for red tree voles included quadratic terms for percentage slope, tree basal area, maximum tree diameter at breast height (dbh), and standard deviation of conifer dbh. The best nonspatial models were the same except that the maximum tree dbh was a linear function.


This press release described a legal challenge to the Rickard Creek Timber Sale on the Salem District of the Bureau of Land Management. The plaintiffs argued that the sale would harm tree voles that were present within the sale area, which included 37 ha of potential clearcut and 8 ha of thinning in old forest.

72. Center for Biological Diversity; Oregon Chapter of the Sierra Club; Audubon Society of Portland; Cascadia Wildlands Project; Oregon Wild. 2007. Petition to list the dusky tree vole (*Arborimus longicaudus silvicola*) as threatened or endangered under the Endangered Species Act.

The petitioners argued that U.S. Fish and Wildlife Service should do one of three things: (1) list the dusky tree vole as a threatened or endangered subspecies, (2) list the north coast population of the red tree vole as a threatened or endangered distinct population segment, or (3) list the red tree vole as threatened or endangered throughout its range.


In this paper on phylogenetic relationships of the Arvicolinae, the authors speculated that the red tree vole evolved from *Phenacomys deeringensis*, an extinct species that occurred in Alaska.


The authors used genetic distances and dental morphology to compare the phylogeny of arvicolids as inferred from the fossil record. In a phenogram analysis, the red tree vole was isolated from three other congers in North America, the Sonoma tree vole, white-footed vole, and heather vole. Hinton (1926) considered *Phenacomys* (= *Arborimus*) as a primitive genus and Repenning’s (1983) paleontological data suggested that *Phenacomys* was isolated from other voles about 4 million years ago.


The authors used the white-footed vole as one of the outgroups in their phylogenetic analysis. They estimated that *Phenacomys* and *Arborimus* diverged approximately 2.45 million years ago.

The authors used line-transect surveys to sample nests of Sonoma tree voles in different forest age classes in Humboldt County, California, in 2001–2005. Because 33 percent of nests were found in unharvested or partially harvested old-growth stands, the authors suggested that forest managers should retain mature Douglas-fir trees in harvest areas. However, they did not provide specifics regarding the distribution or density of leave trees.


On page 90, the authors provided a brief description of the biology and distribution of red tree voles and white-footed voles.


From 1957 through 1960, Percy Clifton sold the American Museum of Natural History many specimens including 21 red tree voles, 12 Sonoma tree voles, and 3 white-footed voles. We found 36 letters between Clifton and the museum curators (George G. Goodwin and Richard G. Van Gelder) in the museum archives. Goodwin offered Clifton $10 per tree vole after receiving Clifton’s initial inquiry. Clifton responded that he thought $10 per tree vole was too low because of the effort required to collect them (a mild understatement!). In his counter-offer, Goodwin refused to budge on the price per tree vole, but agreed to pay for other small mammals, up to $100 for all. Upon receiving the specimens, Goodwin sent a letter to Clifton complimenting him on the quality of the skins and skulls. After receiving the initial shipment, Goodwin apparently decided he had enough tree voles because he sent Clifton a letter telling him that he would only pay $5 per tree vole in the future, and that what he really needed was more white-footed voles. In his final letter, Clifton wrote Goodwin that he had collected three white-footed voles near Tillamook, Oregon, after several hundred trap-nights.

We found five letters at the University of Wisconsin Zoological Museum that documented specimen transactions between Percy Clifton and museum curators (W. Reeder and Jon Ghiselin) in 1958–1960. Percy sold them nine red tree voles and one Sonoma tree vole. Some comments from Reeder and Ghiselin indicated that they were not happy because some of the specimens were captive-bred, the skulls and skeletons were not cleaned, and data were “scant.”


In this thesis, Clifton produced an amazing amount of quantitative data on the reproductive biology, natal development, and behavior of tree voles. Although it was produced in 1960, this thesis was apparently unknown to all mammalogists who worked on tree voles during the next four decades, because it was never cited until Clifton brought it to the attention of Jerry Mires at the Roseburg District of the Bureau of Land Management in 2001. By that time, Clifton had recently retired from his job as a medical doctor and was living near Sutherlin, Oregon.

In his introduction, Clifton stated that tree voles were not colonial in the traditional sense, but were usually found in proximity to each other. He captured about 33 adult tree voles and several young tree voles from a study area near the town of Gaston in the Chehalem Mountains of Oregon in 1956–1959. He kept the voles in captivity in wire cages constructed of ½-inch hardware cloth. His captive voles produced 25 litters in captivity, including three litters from females that were pregnant when captured, and 22 litters from females that were bred in captivity. Clifton also collected tree voles from several other locations, including Roseburg, Douglas County, Oregon, Cottage Grove, Lane County, Oregon, and Albion, Mendocino County, California. Based on his observations of captive voles, he estimated that the average gestation period of red tree voles was 28 days, 14 hours \((n = 6)\), and that the average gestation of hybrid crosses between red tree voles and Sonoma tree voles was 26 days, 21 hours \((n = 3)\). Some of his wild-caught adult voles lived over 2 years in captivity.

Clifton searched for voles primarily in young forests of Douglas-fir. He captured voles by grabbing them as they fled the nest or by having an assistant grab the voles when they jumped from the nest. He stated that even if a vole escaped on the first capture attempt, he could usually return
the next day and capture it from the same nest. He fed voles needles on capture but gradually weaned many of them onto a diet of rolled oats and apple as did Benson and Borell (1931). He provided measurements of 33 dusky tree voles and described how their rusty brown pelage differed from the red pelage of red tree voles. He said that compared to dusky tree voles, red tree voles were more inclined to jump from the nest, were swifter runners, and built larger nests. He also said that dusky tree voles had smaller litters (usually two) than red tree voles (usually two or more). He compared cranial characteristics between the subspecies.

Clifton captured 16 of his adult specimens 6.4 km east of Gaston, Yamhill County, Oregon, on the northern end of Ribbon Ridge about 3.2 km north of the Laurelwood Academy. He described the habitat as young stands of dense Douglas-fir that were 12 to 24 m tall, with dense canopies and little undergrowth. He captured another 12 adult specimens approximately 6.4 km north of Newburg, directly below the gravel road that runs along the top of Ribbon Ridge, about 9.7 km southeast of Bald Peak State Park. He suggested that tree voles were at one time present the full length of the ridge, but at the time of his study, voles were only present in a few remnant stands of young trees that had not been clearcut. He suggested that many tree voles were killed during logging operations, but he provided no direct evidence except that he could find no tree voles or nests in the few remaining trees in areas that had been logged.

He suggested that tree voles preferred dense forests because they provided protection from predators and had interconnecting branches that allowed the voles to travel from tree to tree instead of descending to the ground. Regarding the young forests in which he collected most of his voles he says, “They are easily found in second- or third-growth trees, but they may be present in old-growth. This so-called third-growth is characterized by dense, small, fir trees on which the limbs often come to the ground.”

Regarding predators, Clifton speculated that northern flying squirrels may prey upon tree voles. He described tree vole nests torn apart by unknown predators and said that he found tree vole skulls below hawk and owl nests. He also reported the top of a tree vole nest torn off and flattened by a raccoon (*Procyon lotor*) that he saw sitting on the nest.

He provided a detailed description of how tree voles removed resin ducts from needles of Douglas-fir and how they ate twig bark. He said that a male vole always passed the needle from left to right through its mouth
when removing the resin ducts. He also used a microscope to determine that voles discarded the vascular bundle or midrib of western hemlock needles after eating the outer edges. He said that voles collected in Douglas-fir near Gaston would eat either Douglas-fir or western hemlock and seemed to have no preference for one or the other.

He conducted feeding trials with captive voles and estimated that when a vole was fed only needles, its daily intake was 22.9 g per day. Foods that were refused by his captive tree voles were white fir (Abies concolor), Pacific yew (Taxus brevifolia), Engelmann spruce (Picea engelmannii), lodgepole pine (Pinus contorta), fresh meat, carrots, lettuce, blackberries, wild rose fruits, hazelnuts, lichens, mushrooms, moss, canned fruit, and many others.

He said that stomachs of wild-caught tree voles contained only finely pulverized needles and little bits of twig bark. He found no lichens in vole stomachs, in contrast to the single stomach examined by Wight (1925). He observed that voles often tried to escape by crossing from tree to tree on interlocking limbs, and he suggested that they probably used the same limbs to forage in adjacent trees.

He said that he observed captive voles lapping up drops of water adhering to conifer needles. He also reported that voles that were fed fresh needles had wet fecal pellets, whereas voles that were fed dry needles had comparatively dry fecal pellets.

He stated that most tree vole nests near Gaston were built in or on deserted nests of squirrels, hawks, or birds, and that the majority of nests were against the trunk of the tree. He found no preference regarding slope aspect or which side of the bole the nest was located. He never found more than one occupied nest in the same tree.

He described numerous parasites, including mites, fleas, ticks, and tape-worms. He also mentioned, but did not describe, large numbers of arthropods found in nests. He observed a disease that killed many captive voles that had fluke-like parasites in their nasal passages. He also mentioned hemoflagellates and a contagious fungal infection.

He said that temperament varied considerably among individual voles. In most cases, tree voles placed in the same cage did not tolerate each other. Females briefly tolerated males in their cages when they were ready to breed but would attack and drive off males on most other occasions. On
one occasion, a female attacked and killed a male that was left with her for 2 to 3 hours. Males were also intolerant of each other. However, female siblings were sometimes kept together for long periods of time with no evidence of aggression.

Based on a female that had five litters in a year, Clifton suggested that six to seven litters per year may be possible. He described a female born in late February that mated on 27 May and produced young on 26 June, when she was about 4 months old. He suggested that the breeding season starts as early as the first of January and ends in August, with most tree voles producing no young in September through December. He found that the sex ratio at birth was about 50:50 and suggested that the preponderance of females captured by tree climbers was because female nests were more obvious. He found no evidence that males were more likely to flee the nest than were females.


In the 1960s, Carol Clothier produced a series of unique pen-and-ink drawings of red tree voles for Murray Johnson. We found the drawings among Murray’s archived papers at the Burke Museum. Clothier’s models for the drawings were captive tree voles collected by Chris Maser.


The authors used pitfall traps and Sherman live-traps to sample small mammals in the Oregon Coast Ranges in 1988–1992. In 50,256, trap-nights they captured one red tree vole and one white-footed vole. They did not say whether they caught the voles in pitfalls traps or live-traps.


In this species account, Collins described the taxonomy, distribution, life history, habitat, and conservation status of the white-footed vole in California and included management recommendations for the species.

The authors suggested that the Arvicolinae were monophyletic, first appeared in the late Miocene, and then rapidly diversified 3 to 5 million years ago. They used the heather vole as their *Phenacomys* sample and did not mention tree voles or white-footed voles.


Coriell compared the climbing behavior of tree voles and California voles (*Microtus californicus*). His sample of tree voles included 3 that he captured, 19 captive-bred and 3 wild-caught voles that he obtained from Murray Johnson. He concluded that tree voles were better adapted for climbing than were terrestrial voles. No data were presented on the actual mechanics of climbing.


This document describes the locations of the pitfall trapping grids in which Corn and Bury sampled small mammals in Oregon. From 1984 through 1985, they trapped 31 red tree voles and two white-footed voles in the central Coast Ranges, Oregon.


Corn and Bury reported that capture rates of tree voles in pitfall traps were highest in old-growth forests. These were the same data reported in Bury and Corn (1987) and Corn and Bury (1988), but with much more information on the locations of captured voles. Of 2,104 mammals captured, 18 (0.86 percent) were red tree voles. However, the authors only used 17 of the tree voles in their analysis of habitat associations, because one vole was captured in a test grid that was not part of the main study. All tree voles captured in old-growth were in mesic or wet sites. Elevations of tree vole capture locations ranged from 510 to 1,040 m. The total number of trap-nights was 38,880, and the number of tree voles captured per 100
trap-nights was 0.046. One tree vole was captured in a clearcut 200 to 300 m from the nearest forest edge and the authors speculated that it may have been a dispersing individual. They concluded that, “Although the sample size is small, our data support the contention that, *A. longicaudus* finds optimum habitat in wet and mesic old-growth forests.” Most of the voles were captured in the late spring and late autumn. Relatively few were captured during mid-summer. Of the 18 tree voles captured, 78 percent were males. The authors speculated that the disproportionate sex ratio of captured voles could have been due to (1) males using terrestrial nests more often than females, (2) males having larger home ranges, or (3) males dispersing farther than females. They did not consider the alternative hypothesis that males were spending more time on the ground than females because they were frequently traveling between trees to seek out females.


This paper was based on the same data described in Corn and Bury (1986) but included additional information on capture locations. Based on the proximity of captures of red tree voles and heather voles in the Cascade Range, the authors suggested some degree of spatial overlap between the two species. They suggested a scenario in which “…*A. longicaudus* originally occurred in old-growth forests along the river drainages at lower elevations, but its distribution probably was reduced by extensive logging of this habitat. The original primary habitats of *P. intermedius* were above timber line and high-elevation meadows, but this species is extending its range west along the higher ridges as they are clearcut. Occasionally, there is a small amount of overlap, but, in general, *P. intermedius* and *A. longicaudus* would have interdigitated parapatric distributions along the Cascade Range south from the Columbia River to the area between McKenzie Pass and Willamette Pass.”

The authors used pitfall traps to sample 48 sites in the Oregon Coast Ranges, including 3 clearcuts, 8 young stands (40 to 75 years), 10 mature stands (80 to 120 years) and 27 old-growth stands (150 to 525 years). They opened traps in October and sampled continuously for 50 days in 1984 and 30 days in 1985. They captured 3,047 mammals, including 13 (0.43 percent) red tree voles. All but one of the tree voles were captured in old-growth. In their discussion, they said that, “The 17 red tree voles we trapped in the Coast Ranges constitute a small sample, but since 1983, 46 red tree voles have been trapped in the Coast and Cascade Ranges of Oregon by old-growth researchers (this study; Corn and Bury 1986; Gilbert and Allwine 1991). Most ($n = 39$) were captured in old-growth stands and because the trapping effort was about evenly split between old-growth stands and younger stands, a significant excess of captures were in old-growth.” They also reported that Raphael (1988) captured an additional 19 Sonoma tree voles in pitfall traps in Douglas-fir forests in northwestern California. Although the difference in relative abundance among stand age-classes was not significant, most Sonoma tree voles captured by Raphael were in stands older than 100 years. They also stated that Meiselman and Doyle (1996) found that nests of Sonoma tree voles in northwestern California were more abundant in old-growth forests than in younger forests. Based on these collective observations, they concluded that “These results indicate that red tree voles are strongly associated with old-growth Douglas-fir forests.”


This paper was based on the same data as Bury and Corn (1987), Corn and Bury (1986), and Corn et al. (1988). They sampled 18 different stands on the H.J. Andrews Experimental Forest, including 8 old-growth stands (195 to 450 years), 3 mature stands (80 to 195 years), 4 young stand (30 to 80 years), and 3 recent clearcuts. They captured 17 red tree voles, including 12 in old-growth forest, 3 in mature forest, 1 in young forest, and 1 in a
clearcut. They stated that tree voles were associated with old-growth forest and speculated that, “…the extensive logging of low-elevation old-growth forests in Oregon has probably eliminated much of the habitat of red tree voles. The giant Douglas-fir trees, which seem to be preferred as nest sites, will not occur in managed forests.”


In this court case, the plaintiffs challenged the 2004 supplemental environmental impact statement (EIS; USDA FS and USDI BLM 2004) and the 2007 final EIS (FEIS; USDA FS and USDI BLM 2007) in which the Forest Service and Bureau of Land Management decided to remove the “survey and manage” requirements from the Northwest Forest Plan. The goal of the 2007 FEIS was to reduce cost, time, and effort required to conserve rare and little-known species. In the 2007 FEIS, the agencies concluded that survey and manage, “…has unexpectedly limited the Agency’s ability to accomplish the goals and objectives of the Northwest Forest Plan,” and that the best remedy would be to cease to implement the survey and manage requirements entirely. The court did not issue a final verdict and directed the parties to confer about appropriate case management.


In this settlement agreement, the plaintiffs and the defendants agreed that the 2001 Record of Decision and Standards and Guidelines for survey and manage species would remain in effect. This ruling meant that the U.S. Forest Service and Bureau of Land Management had to continue conducting predisturbance surveys for red tree voles. However, the court also
accepted a long list of exemptions for situations in which surveys were not required, including the exemptions agreed to in a previous settlement between Northwest Ecosystem Alliance v. Rey (see Pechman 2006).


This broad-ranging review of the biology of the northern spotted owl, included a section (appendix pages 3-14 to 3-15) in which the authors described the habitat associations and distribution of red tree voles. They relied primarily on data from pitfall trapping studies and ground-based survey transects to reach the conclusion that tree voles were most abundant in old-growth forest. However, they also included a personal communication from Eric Forsman, who suggested that pitfall traps might be a biased estimator of tree vole abundance in different forest types. They stated that searching of felled trees (Gillesberg and Carey 1991) may be the most cost-effective method to survey large areas but did not present any kind of cost-benefit comparison between that approach and other approaches. They also stated that tree voles were colonial but presented no evidence to document that assertion.


The authors presented a red tree vole distribution map for western Oregon. In the text, they described the range, habitat, reproduction, food habits, and ecology of tree voles. They incorrectly stated that the range of the Sonoma tree vole extended south to San Francisco Bay, when it actually ends near Freestone and Bodega in Sonoma County, well north of San Francisco Bay. Their range map also included areas where recent surveys suggest that tree voles do not occur, including most of Clatsop County and all of Columbia County, and most of western Multnomah County. They also stated that tree voles feed on true firs (Abies spp.), which is only partly true, as tree voles have only been documented to eat one species of true fir, grand fir. They concluded by saying that the distribution is discontinuous and that tree voles usually occur in old forest.
This species account described the range, habitat, reproduction, food habits, ecology, and conservation status of the white-footed vole in Oregon. They also presented a range map based on locations and habitat modeling.

Dalquest’s notes from 1943 through 1944 recorded that he, his wife Peggy, and Bob Storer collected nine Sonoma tree voles at Camp Meeker and Monte Rio in Sonoma County, California. Like many before him, he mistakenly concluded that discarded resin ducts were midribs of Douglas-fir needles. He noted postpartum mating after capturing an adult female that had one embryo and was nursing. He documented an occupied Sonoma tree vole nest that also contained two arboreal salamanders.

The authors cited Johnson (1973) to support their conclusion that the red tree vole is one of the most obligate folivorous mammals in North America. They compared ascorbate levels in eucalypts and conifers, including Douglas-fir and suggested that “…high ascorbate intakes by animals feeding on evergreen foliage may facilitate the metabolism or excretion of undesirable compounds (e.g., phenols, terpenes) that are also in the foliage.”

In his notes from 1936 to 1940, William Davis described the capture of seven Sonoma tree voles near Occidental, Sonoma County, California. Some of these voles were kept alive in captivity, but all died within 2 to 6 days.

Dearden used red tree vole specimens from the U.S. National Museum in his analysis of taxonomy and anatomy of voles in the genus Lagurus.

In this published version of his dissertation, Dearden examined the bacula of three red tree voles. The bacula that he examined were markedly different from the tree vole baculum pictured in Hamilton (1946: 370), and Dearden goes on at great length to describe the differences.


With regard to the foliose lichen *Lobaria* spp, Denison said that “Certain vertebrates, such as the rodent called the red tree vole, supplement their diet with this lichen, among other plants.” He did not say how he came to this conclusion or cite a reference that tree voles eat lichens. Wight (1925) is the only article that we are aware of to claim that the stomach of a tree vole contained lichen.


The authors compared capture and mortality rates among Sherman traps, custom-made steel-mesh traps, and pitfall traps. The traps were used around the Portland metropolitan area at Forest Park, Tryon Creek State Park, Powell Butte Nature Park, Oxbow Regional Park, and Tualatin River National Wildlife Refuge. In 65,600 trap-nights, they captured 2,710 small mammals, none of which were red tree voles or white-footed voles.


In 1981–1983, Doyle used Sherman live-traps to study small mammal abundance in different forest habitats on the H.J. Andrews Experimental Forest near Blue River, Lane County, Oregon (40,152 trap-nights). She also attempted to evaluate competitive interactions between small mammals by removing deer mice from some sampling grids (52,752 trap-nights). In 92,904 trap-nights, she captured one white-footed vole and no tree voles.


This was the published version of the habitat association section of Doyle’s dissertation. She used Sherman live-traps to sample small mammals on the


This paper was based on the random-grid strategic survey conducted by the U.S. Forest Service and Bureau of Land Management Survey and Manage Program (Rittenhouse et al. 2002). The authors modeled red tree vole habitat associations based on presence or absence of tree vole nests in a stratified random sample of Forest Inventory and Analysis and Current Vegetation Survey plots. Plots were stratified into four groups based on forest age and land use allocations in the Northwest Forest Plan. The percentage of plots in each category was 60 percent in reserve/late-successional old growth (LSOG), 20 percent in reserve/non-LSOG, 10 percent in nonreserve/LSOG, and 10 percent in nonreserve/non-LSOG. The best models included spatial coordinates, percentage slope, basal area of trees 45 to 90 cm diameter breast height (dbh), maximum tree dbh, and standard deviation of conifer dbh. The authors concluded that presence of red tree vole nests was strongly associated with old-growth/late-seral forest conditions. Of the 365 1-ha plots in the sample, 96 (26 percent) had one or more trees with a tree vole nest. The estimated rate of false negatives (nests present but undetected during ground surveys) was 6 percent.


In table 2, Eisenberg rated the red tree vole as highly arboreal and highly herbivorous. He concluded with, “The surprising thing to me is that in the Holarctic temperate zone, more species of rodents have not evolved to arboreal, folivorous niches utilizing conifers in the manner that Arborimus longicaudus has in the northwest coast of North America.”


The authors described a new species of mite (Radfordia arborimus) found on a red tree vole collected by Chris Maser.
California, Berkeley, Museum of Vertebrate Zoology.
In his field notes for 8 September 1942, Fisher said that he caught a male
tree vole in a snap-trap set in a brush pile beneath a Douglas-fir that had an
apparent tree vole nest.

*Peromyscus leucopus*. Evolution. 32: 45–55.
The authors found that birth weight in the white-footed mouse (*Pero-
myscus leucopus*) declined with larger litter size. They pointed out that
Hamilton (1962) found that birth weights also declined with litter size in
the Sonoma tree vole.

110. Fontaine, J.B. 2007. Influences of high severity fire and postfire logging
on avian and small mammal communities of Siskiyou Mountains, Oregon,
In 2004–2005, Fontaine used Sherman live-traps to sample small mam-
mals in the Siskiyou Mountains after the Biscuit Fire, which occurred
in 2002. In 8,900 trap-nights he captured one tree vole in an unburned
mature stand (0.01 tree vole captures per 100 trap-nights).

111. Forsman, E.D. 1975. A preliminary investigation of the spotted owl in
Forsman described diets of northern spotted owls in different regions of
western Oregon based on a sample of 2,647 prey items found in regurgi-
tated pellets collected from 42 pairs of owls. He found that red tree voles
comprised 30.6 percent of the diet in the Coast Ranges, 12.5 percent of the
diet in the western Cascades, 12.7 percent of the diet at Oregon Caves, and
8.5 percent of the diet in the eastern Siskiyou Mountains. He concluded
that spotted owls were an important predator on tree voles.

112. Forsman, E.D. 1980a. Habitat utilization by spotted owls in the west-
Ph.D. dissertation.
Forsman summarized annual and seasonal variation in diets of northern
spotted owls on the H.J. Andrews Experimental Forest in Lane County,
Oregon. Of 753 prey identified in owl pellets, 97 (12.9 percent) were red
tree voles. Northern flying squirrels and tree voles were the most common
prey items in the diet during winter, when other sources of food were less
available. Based on tree voles in pellets, Forsman estimated that a nesting pair of spotted owls on the H.J. Andrews study area would consume 184 tree voles per year.


Forsman identified 256 prey items in pellets of three radio-marked pairs of northern spotted owls in 1980. Of the 256 prey items, 24 (9.4 percent) were red tree voles.


Of the 23,847 prey items identified in northern spotted owl pellets, 54 percent were arboreal mammals, including red tree voles. In addition, the authors found five white-footed voles in spotted owl pellets. The authors suggested that forest management practices that were beneficial to arboreal and scansorial mammals would also be beneficial to spotted owls.


Of 23,847 prey items identified in pellets of northern spotted owls collected from 1970 through 2001, 2,954 (12.3 percent) were red tree voles, and 5 (0.02 percent) were white-footed voles.


The authors identified 24,497 prey items from 1,118 northern spotted owl territories in western Oregon. Of these, 2,954 (12.3 percent) were red tree voles. The analysis indicated that tree voles were widely distributed in western Oregon but were most common in the south and central Coast Range and central Cascades. Tree voles were uncommon in diets of owls that occupied areas above 1200 m in the central Cascades.


The authors reported that a sample of 817 prey items from northern spotted owl pellets in the western Cascades of Oregon contained 13 percent red tree voles. A collection of 654 prey items from spotted owl pellets in mixed-conifer forest contained 5 percent tree voles.


The authors described prey remains identified in 36 pellets from northern saw-whet owls (Aegolius acadicus) in a 30- to 50-year-old stand of Douglas-fir 4.0 km north of Bellfountain, Benton County, Oregon. Of 42 prey identified, 3 (7 percent) were tree voles.


The authors described the diets of northern spotted owls in western Oregon based on 4,527 prey items. They reported that the mean percentage of red tree voles in the diet varied from 5 to 49 percent in different regions of western Oregon.


In 2011, the authors searched for tree vole nests while driving or walking along 176 km of logging roads on the Weyerhaeuser Millicoma Tree Farm in Coos and Douglas County, Oregon. Of 132 potential nests detected, 52 percent were climbed to see if they were built by tree voles. Only three occupied nests were found, all in young stands that were 30 to 36 years old. This survey revealed that tree voles were uncommon in the young forests that dominated the tree farm, but were still present in a few areas.


Of 21,721 small mammals identified in pellets of northern spotted owls, 15,455 were arboreal or scansorial, 6,199 were primarily terrestrial, and
were bats. Of 2,953 tree voles in the sample, only 2 (0.07 percent) had healed fractures. The authors concluded that tree voles were so small and light that they rarely broke bones when they fell or jumped from trees. However, the authors did not consider that tree voles may be unable to climb or feed after breaking legs, so the frequency of injuries from falls may be underestimated based on the frequency of healed fractures in owl pellets.


Forsman and Price measured water consumption by red tree voles in a laboratory setting where the voles were fed a natural diet of well-hydrated conifer needles. Under these conditions, the voles drank little free water and sometimes went for weeks or months without drinking any water. The authors concluded that tree voles obtained nearly all their water from their food. Although observations of tree voles licking water from needles in laboratory conditions have led many authors to suggest that tree voles require free water in the form of dew or rain in order to survive (Benson and Borell 1931; Carey 1991, 1996, 1999; Clifton 1960; Maser 1966; Taylor 1915), there is actually no evidence that tree voles in the wild need significant amounts of water other than what they obtain from their food. Tree voles and other species of voles that drink copious amounts of water in laboratory settings may be responding to conditions in which they are maintained in unnatural conditions with low humidity and food that is low in water content.


These notes described an interview conducted on 13 December 2004 with Percy Clifton at his residence on Calapooya Creek east of Sutherlin, Douglas County, Oregon. The notes describe how Percy first became interested in tree voles and eventually ended up completing a master’s thesis on tree voles at Walla Walla College in Washington (Clifton 1960). Clifton grew up near Gaston, Washington County, Oregon, where as a child he liked climbing trees to capture northern flying squirrels and tree voles. In a biology class at Walla Walla College, professor Ernest Booth
showed the students a picture of a tree vole and said that it was an interesting species that they would likely never see. After class, Clifton approached Booth and told him that not only had he seen tree voles, but he had captured them and kept them as pets. Booth was skeptical until Percy went home on break and returned to school with a tree vole. This eventually led Booth to accept Percy as a graduate student. For his master’s project, Percy captured tree voles at various locations in Oregon and California and raised them in captivity. His wide-ranging thesis is probably the most detailed paper ever written on the reproductive biology and behavior of tree voles. After graduating from college, Clifton made a living for a few years collecting specimens in Mexico for Raymond Hall at the University of Kansas. He then went back to school and became a medical doctor. He retired in 1999 and settled on Calapooya Creek. As described earlier (see Clifton 1960), his thesis was never published in a professional journal, and remained largely unknown until Percy brought it to the attention of Jerry Mires in 2001.


The authors interviewed retired biology professor Kenneth (Ken) Walker and his wife Charlotte at their home in Monmouth, Oregon, on 4 April 2005. Ken was the son of Alex Walker, who was one of the earliest naturalists to collect tree voles in Oregon. During 1916–1967, Alex, his wife Rosaline, his brother Peter, and other family members collected 30 tree voles on the north coast of Oregon, primarily around Tillamook. Ken said that to collect tree voles, his father would climb to the nest and his mother would stand below with a shotgun to shoot tree voles if they could not be captured by hand. As a kid, Ken said he also climbed trees to capture tree voles. Ken said that he remembered climbing for tree voles at Oceanside and Short Beach on Cape Meares and at Cape Lookout, west of Tillamook. Alex also collected tree voles with his brother Peter near Cape Lookout (see Walker 1930). Ken said that Peter’s son Robert collected six red tree voles while logging around Tillamook in 1960.

The authors found that tree voles were rare in the northern Coast Ranges of Oregon and suggested that patches of old forest may serve as refugia for tree voles in areas where most forests have been logged and converted to young forest.


In this 2 March 2006 interview at his home near Winters, California, Bill Hamilton recounted the years when he and Don Roberts captured or raised in captivity over 258 Sonoma tree voles and 1 red tree vole. Most of the voles they captured were collected from sites near Jenner and the lower Russian River, in Sonoma County, California. Most of their specimens were eventually donated to the Slater Museum of Natural History at the University of Puget Sound.


The authors described the first confirmed arboreal nests of white-footed voles. They suggested that use of arboreal nests by white-footed voles may be a seasonal response to the presence of the leaves of red alder (*Alnus rubra*) during spring and summer.


The authors described four species of amphibians that occurred in tree vole nests, including clouded salamanders, arboreal salamanders, Pacific tree frogs (*Pseudacris regilla*), and a California giant salamander (*Dicamptodon ensatus*). They suggested that arboreal activity by amphibians may be a more common phenomenon than is generally known. They hypothesized that tree vole nests may attract arboreal amphibians because they are warm and damp inside, and often have high concentrations of invertebrates that are potential food for salamanders.

In this historical account, Forsman and Swingle described the life of Doug Bake, a logger who collected 98 tree voles in the region around Tillamook, Oregon. Most of the specimens that Doug collected were given to Alex Walker or Murray Johnson and ended up in the Slater Museum of Natural History at the University of Puget Sound.


The authors described past and current distribution of red tree voles and Sonoma tree voles based on data from owl pellets, specimen collections, and field surveys. They also modeled red tree vole habitat using presence-only data and described regional variation in diet of tree voles. In a concluding chapter, they used historical and recent forest habitat maps to describe long-term changes in tree vole habitat.


The authors used video cameras to record activity patterns and behavior at nests of three female red tree voles near Corvallis, Benton County, Oregon. All three voles were primarily nocturnal but occasionally foraged for brief periods during the day when they had large young in the nest. The median amount of time spent outside the nest per night was 27 minutes (range = 0 to 712 minutes), and most of this time was spent foraging. Nocturnal activity consisted primarily of long periods inside the nest interspersed with short periods of intensive foraging, during which voles ran out of the nest, harvested cuttings and hauled them back to the nest. Cuttings were stored inside the nest or on top of the nest. The mean ± SE number of foraging bouts per night was 3.4 ± 0.1 (range = 1 to 13), and the mean number of cuttings harvested per night was 20.4 ± 3.5 (range = 0 to 75). Mean length of cuttings was 13.7 ± 3.5 cm (range = 1 to 37). Females harvested more cuttings when they had large young in the nest, and there was no evidence that they ate anything but the needles and bark of the cuttings that they brought to their nests. Juveniles first began to explore outside the nest when they were 30 to 35 days old and dispersed when they were 47 to 54 days old. During the last 2 weeks, before they dispersed, juveniles spent
considerable time outside the nest at night, becoming increasingly adept climbers and gradually beginning to harvest their own food. Dispersal of siblings occurred on the same night, and in at least some cases, appeared to be precipitated by female aggression towards the young.


In 2003–2008, the authors conducted surveys to document the eastern and northern range limits of the range of red tree voles in the Columbia River Gorge and Hood River basin, Oregon. They concluded that the northern limits of the range of the vole included the forested bluffs and canyons bordering the Columbia River Gorge from a few kilometers east of Troutdale, east to within a few kilometers of Hood River. They also found tree vole nests in the headwaters of Lake Branch of Hood River on the east slope of the Cascades. This is the only region where tree voles occur on the east slope of the Cascades. Of 70 tree vole nests located, 74 percent were in forests dominated by mature or old-growth trees, and 26 percent were in forests that were 25 to 60 years old.


During winter of 2011–2012, the authors searched for tree vole nests while walking linear transects in 33 randomly selected plots on the Clatsop and Tillamook State Forests in the northern Coast Ranges of Oregon. Each plot was sampled with 500 m of transect. Potential nests detected while walking transects were climbed to determine if they were tree vole nests. Tree vole nests were detected in only one of 33 plots sampled. That plot was in 125-year-old forest on the western edge of the Tillamook State Forest.

The authors climbed trees and searched for tree vole nests in old forests in state parks in the northern Coast Ranges of Oregon. They found recently occupied tree vole nests at Oswald West and Ecola State Parks. These were the first confirmed nests at these locations. All nests were in Sitka spruce or western hemlock trees.


This was primarily a paper on the eastern heather vole (*Phenacomys ungava*), but Foster concluded that red tree voles, dusky tree voles, and white-footed voles were clearly distinct when compared to heather voles.


The authors pointed out that large, old-growth Douglas-fir trees were individualistic and commonly had deep crowns with irregularly arranged, large, coarse branch systems. They suggested that this structure may provide ideal habitat for specialized vertebrates, such as the red tree vole, northern spotted owl, and northern flying squirrel, as well as nitrogen-fixing lichens. They cited Meslow et al. (1981) in support of the hypothesis that red tree voles find optimum habitat for foraging and nesting in old-growth forests of Douglas-fir and western hemlock. They concluded that old-growth trees provide nest sites, food, and cover for tree voles, and they speculated that many generations of tree voles can live (sequentially) in the same tree. They emphasized that the large branch systems and organic accumulations on limbs of old-growth trees provide habitat for many species.


This paper provided no new data on tree voles, but the authors did report that many species occupy old-growth forests, including the red tree vole. They emphasized that managers should not overlook the important roles that large branch systems and organic accumulations play in providing habitat for species like tree voles.

These field notes included multiple references to Sonoma tree voles collected in 1981−1984 by William Gannon, Mike Webb, and others from areas east of Arcata, Humboldt County, California. We found most of these specimens in museum collections.


This species account included information on the distribution, habitat, food, nest characteristics, reproduction, chromosome number, and fossil record of the Sonoma tree vole. Like many before her, George gets it wrong when she says that tree voles eat the edge of Douglas-fir needles and discard the central vascular bundle.


The authors used a discriminant function analysis to compare morphometric characteristics of tree voles in three different regions. They concluded that populations of tree voles in California, which were then referred to as *A. longicaudus*, actually represented a distinct, as yet unnamed species. They concluded that populations of *Arborimus* in northern Oregon were subspecifically distinct from populations of *A. longicaudus* in the rest of Oregon. They proposed the subspecific name *A. l. silvicola* for tree voles in northern Oregon and *A. l. longicaudus* for tree voles in the rest of Oregon.


The authors used pitfall traps and snap-traps to sample small mammals in three different regions in the western Cascades in Oregon. They caught no red tree voles in snap-traps. They did catch tree voles in their pitfall traps, but their results were a bit confusing because the numbers in their tables did not always agree. In their summary of pitfall results in table 3, they say they caught two tree voles in mature forests and six tree voles in old forests, for a total of eight voles. In the same table, they say they caught six tree voles in mesic sites and three tree voles in wet sites for a total of nine tree voles. Why the two sets of numbers don’t add up to the same total is
unclear because the authors stated that all of the tree voles they captured were in mature and old forests. Regardless of this minor inconsistency, the upshot was that they caught voles in mature and old forests, but not in young forest, which was the same pattern observed in other pitfall studies conducted by Corn and Bury (1986). The authors qualified their results by saying that they caught so few tree voles they could not do meaningful statistical comparisons among forest age classes or moisture classes.


This study plan described a sampling method in which the authors proposed to search for red tree vole nests in trees that were felled by a Bureau of Land Management sampling crew. They suggested that this method was the only expedient and cost-efficient method available to study tree vole nests because they felt that tree climbing was unsafe and impractical on a large scale.


In this progress report, the authors reported that they changed their search methods from their original study plan after they found that they could only survey two felled trees per day using their original methods. Instead of doing an intense search of each tree, they started doing a less intense examination in which they walked along each felled tree “…pausing at intervals to look carefully amongst the foliage on either side of the trunk for red tree vole nests/sign.” They sampled a total of 93 trees, including 50 trees with the original intensive sampling method and 43 trees with the less intense method. Their searches were conducted 3 to 4 weeks after the trees had been felled. The proportion of trees with vole nests was 62 percent in the intensive sampling group and 44 percent in the less-intensive sampling group. Over 80 percent of the nest material found was collected during the intensive searches. The authors did not mention whether they could determine if nest fragments were from occupied or old vole nests, and they never saw any tree voles. They spent 39 days sampling 93 trees and collecting vegetation data. They did not discuss the potential impact of destructive sampling on vole nesting habitat.

Gillesberg and Carey argued that counting red tree vole nest fragments in felled trees was a more efficient way to document the presence of tree voles than other methods such as trapping or climbing trees. They examined 93 felled trees and found 117 pieces of tree vole nest material. They found that smaller nests usually consisted solely of resin ducts and fecal material, whereas larger nests contained resin ducts, conifer needles, twigs, lichens, feces, and other organic matter. Nests were found in a variety of locations, including hollow limbs, broken tops, and resting on branches. Nests were most often found in the lower one-third of the canopy, and larger trees (>100 cm diameter at breast height) were preferred over smaller ones.


Gillesberg and Carey concluded that searching felled trees was an effective method for finding nests of red tree voles. They examined 82 felled trees for evidence of tree vole nests in a 35.2-ha plot near Yoncalla, Douglas County, Oregon. All trees were in old-growth stands. A total of 117 nests or nest fragments were found in 50 of the 82 trees examined. Thirty-five trees contained 1 to 2 nests, and only 2 trees had more than 5 nests (9 and 11 nests, respectively). The actual number of nests represented by these fragments was unknown. Of the 117 nests or nest fragments located, 59 (50 percent) were in the lower third of the live crown, 34 (29 percent) were in the middle one-third, and 24 (21 percent) were in the upper one-third. Of 27 nests located in situ, 15 were out on branches and 12 were against the trunk. Two of four cavities examined had nests in them, one in a broken top and one in a hollow branch. Trees with nests tended to be taller and larger in diameter.

The authors did not examine felled trees in young stands but did review other literature in which researchers sampled multiple age classes. They concluded (pages 786–787) that “…live old-growth trees provide optimum habitat for the red tree vole because primary production is high and leaves are concentrated in old-growth, resulting in maximum food availability.”
They also stated (page 787) that the “…moist old-growth canopy functions as a climatic buffer and its high water-holding capacity maintains fresh foliage and provides free water to be licked from needles.”

The authors also said that they tried many other techniques for sampling tree voles, including visual searches from ground transects, Sherman live-traps, and pitfall traps, but did not catch any voles and only found nests in 4 of 77 stands in which they visually searched for nests on ground transects. However, they also said that “From searches in the stands in which we captured red tree voles, we did not locate any nests, despite the use of binoculars and hillside vantage points.” This is confusing because they also said that they never captured or observed any tree voles. We suspect they were referring to stands in which Corn and Bury (1991) captured tree voles in pitfall traps.


The authors analyzed effects of variable-retention harvest treatments on small mammals in the western Cascades, Lane County, Oregon. Their sample of 6,208 small mammals captured in pitfall traps included one red tree vole and one white-footed vole in 256,896 trap-nights. The authors said that the number of captures was too small to evaluate treatment effects on tree voles and white-footed voles, but they also speculated that tree voles require retention of large trees.


The authors found *Arborimus* remains in fisher scats in two of four study areas in northern California. In their Six Rivers Study Area in Humboldt and Trinity Counties, 14 of 152 scats (9 percent) contained remains of *Arborimus*. In their Hoopa Study Area in Humboldt County, 1 of 64 scats (2 percent) contained *Arborimus* remains. The authors did not differentiate between remains of tree voles and white-footed voles.

Gomez used pitfall traps to sample 15 different plots in five watersheds in the Coast Ranges of western Oregon in 1989–1990. He sampled three plots in each of five forest types (three shrub communities, three pole stands, three mature stands, three old-growth stands, and three deciduous stands). Each plot was sampled with an array of 60 pitfall traps. He captured 9,723 mammals and 917 amphibians/reptiles in 100,800 trap-nights. He caught 20 species of mammals, including 23 red tree voles and 59 white-footed voles (0.023 red tree voles and 0.059 white-footed voles per 100 trap-nights). He provided legal coordinates of his pitfall grids but did not say how many tree voles he captured at each grid. Of the 23 tree voles captured, 16 were in old-growth forests, 4 were in “large-saw timber,” 1 was in pole-size forest, 2 were in shrub vegetation, and none were captured in deciduous forest. Gomez concluded that “…tree voles were captured more frequently (P < 0.01) in old-growth than in each of the other forest types.” The number of tree voles captured in riparian transects versus upslope transects did not differ. More white-footed voles were captured in riparian (82 percent) than upslope (18 percent) habitat. White-footed voles were captured most frequently in areas of deciduous trees and shrubs.


In this published version of Doug Gomez’s thesis, the authors reported that they used pitfall traps to sample 15 plots in five watersheds in the Oregon Coast Ranges. They captured 9,764 small mammals and 917 amphibians/reptiles in 100,800 trap-nights. They caught 20 species of mammals, including 23 red tree voles and 59 white-footed voles. Capture rates for tree voles and white-footed voles were 0.023 and 0.059 per 100 trap-nights, respectively. They captured more tree voles in old-growth forest than in any other seral stages and concluded that red tree voles were most abundant in old forest. They reported capturing about equal numbers of tree voles in upland and riparian habitat. They suggested that white-footed voles were dependent on deciduous vegetation and not restricted to riparian areas as some have stated. This conclusion was in agreement with Voth et al. (1983) who also suggested that white-footed voles were closely associated with deciduous habitat.

This study was conducted in 1996 at Cape Meares National Wildlife Refuge, Tillamook County, Oregon. In 7,290 trap-nights using a combination of pitfall traps and Sherman live-traps, the authors captured four white-footed voles in young or wind-damaged forests and three red tree voles in old-growth forests. The capture rate per 100 trap-nights was 0.04 for tree voles and 0.06 for white-footed voles. The specimens were apparently discarded, as we could not find them in museums.


Gordon mentioned that the Columbia River was the northern limit of the ranges of the red tree vole and white-footed vole.


This was a short progress report on Nina Meiselman’s thesis on Sonoma tree vole nest surveys (see Meiselman 1992, Meiselman and Doyle 1996).


Of 3,686 prey items identified in barred owl (*Strix varia*) pellets collected west of Eugene, Lane County, Oregon, 2,387 were mammals, including 147 (4.0 percent) red tree voles.


The authors described several cases in which red tree voles were captured by owls or hawks in Douglas County, Oregon. In one case, Graham observed a female northern spotted owl as she captured a tree vole that was climbing down a tree trunk. Mires observed a northern pygmy-owl (*Glaucidium gnoma*) flying with a tree vole in its talons and also watched a red-tailed hawk (*Buteo jamaicensis*) as it tore into a tree vole nest and captured a tree vole.

Although there were no authors listed on this report, the sections on tree voles were written by Lowell Diller, Keith Hamm, Dave Lamphear, and Trent McDonald at the Korbel office of Green Diamond Resource Company (Lowell Diller, wildlife biologist, Green Diamond Resource Company, 1165 Maple Creek Road, Korbel, CA 95550). They identified 3,056 prey items in pellets collected from northern spotted owls in northwestern California in 1989–2004. The sample included 497 tree voles (16.3 percent).

The authors also used line transects to estimate the distribution and abundance of nests of Sonoma tree voles on Green Diamond lands from 2001–2004. They sampled 10-ha plots in four different forest age classes (20 to 29 years, 30 to 39 years, 40 to 50 years, and >50 years). They did not climb to verify nests but used time constraint sampling by searching for resin ducts on the ground below all nests detected. Tree vole nests were detected in 32 of 68 plots sampled (47 percent). The authors located a total of 129 tree vole nests (range = 0 to 19 per plot). Abundance of nests was positively correlated with forest age.

156. **Greenway, G. 2005.** Location of the historical Lierly Ranch in California. Email to Eric Forsman. (13 September). (Available upon request from the compilers).

In this email, Greg Greenway, an archeologist on the Mendocino National Forest, described the location of the historical Lierly Ranch on a 1917 map as T19 N R12W section 31 NE1/4 of the NW1/4. This is the location near Mount Sanhedrin where two Sonoma tree voles were collected in 1899 and 1913, respectively. However, Greenway conceded that the exact location could be problematic because the Lierly Ranch was also labeled as the Ascherman Ranch in section 30. Harry Lierly lived at the ranch until he died in 1924.


At the time he wrote this report, Grinnell noted that there was only one “long-tailed lemming mouse” record for California. This was a tree vole found dead in the road near Mount Sanhedrin in 1899, as described by Witmer Stone (1904).

Grinnell described the range and habitat of the tree vole and the “Pacific coast lemming mouse” (white-footed vole) in California.


In this romanticized and misleading account of tree vole biology, Grosvenor said that male tree voles were primarily terrestrial and were usually “…content to rummage under the debris on the forest floor.” He also said that juvenile tree voles “…take about a month to mature.” None of this is supported by the literature, and most of it is simply wrong.


The authors concluded that Phenacomys could not be used as an index fossil but was a good indicator of climate because of its association with the modern Hudsonian Life Zones of North America. They stated that Pliophenacomys Hibbard was the ancestral genus of modern Phenacomys and was recovered from late Pliocene deposits of the Great Plains. They emphasized that fossil Phenacomys voles were excellent indicators of boreal conditions because their molars were easy to identify. They stated that inter- and intraspecific variation in dentition was too great to allow identification of Phenacomys fossils to species. Thus all fossil forms had been identified as Phenacomys intermedius. They reported that remains of Phenacomys had been located at ≥20 Pleistocene to early recent sites in the United States, from the east coast to south central Idaho. Some of their taxonomy was a bit out of date. For example, they considered the dusky tree vole as a unique species.


The authors concluded that the World Conservation Union Red List Category was “data deficient” for the red tree vole and white-footed vole. They recommended conducting studies on the ecology of these species to determine if they were truly rare and threatened.

In table 1 on page 115, Hagar listed the white-footed vole as a species that forages on shrubs, understory vegetation, California hazel (*Corylus cornuta*), and red alder.


In this paper on *Euryparapisitus* mites of North America, the authors reported that mites were collected from eight white-footed voles in Lincoln, Benton, Curry, and Linn Counties, Oregon. They included the geographic coordinates for each collection.


In this revised edition of the Mammals of North America, Hall concluded that the subspecific status of the dusky tree vole was provisional owing to uncertainty about its relationship with the red tree vole.


In addition to a key to the *Phenacomys*, Hall and Cockrum provided range maps, specimen measurements, and skull drawings for the heather vole, red tree vole, dusky tree vole, and white-footed vole.


On pages 720–721, the authors provided external measurements, descriptions, and distributions for the white-footed vole, dusky tree vole, and red tree vole.


In this general species account, Hamilton described the red tree vole as a specialized feeder that lacks the ability to change food and will starve in the absence of their specialized foods (conifer needles). However, he also reported that Benson and Borell (1931) found that tree voles would sometimes eat other foods in captivity. He repeats much of the conventional...
wisdom regarding tree voles, including (1) when they feed on needles of Douglas-fir they discard the resin ducts before eating the medullary portion of the needle, (2) they seldom come to the ground except to reach some other tree, (3) many nests cannot be seen from the ground because they are hidden in dense foliage, (4) females build bigger nests than males, and (5) tree voles occasionally build their nests on top of abandoned squirrel nests.

Based on a single specimen, Hamilton concluded that the shape of the baculum of the tree vole was distinctive compared to all other genera of Arvicolinae.

Hamilton described the estrous cycle, ovulation, mating behavior, gestation period, postpartum estrus, growth rates, and feeding behavior of adult and juvenile tree voles. He and Don Roberts used over 50 adult animals in their laboratory experiments. Most of his findings were identical to the observations reported 2 years earlier by Clifton (1960). He reported that gestation of nonlactating females was 27.0 to 28.5 days. He presented data from a captive female with two young that bred when her young were 2 days old and produced a second litter 41.8 days later. He also suggested that adult females that produced litters 40 days after having previous litters was evidence of delayed implantation. He cited many papers indicating that postpartum estrus was common in voles. However, his tests of postpartum estrus were only successful in one of three cases in which males were introduced into cages with females that had just had litters. In two cases, the females were unreceptive. In the third case, the female mated with the male 27 to 28 hours after parturition but was not successful in weaning the young from the first litter. Hamilton said that the young were normally weaned at 30 to 40 days of age when they weighed approximately 17 g. He found that eyes opened on about the 21st day, at which point there was a spurt in daily weight gain as the young began to eat solid food. He said that Douglas-fir cells were found in fecal pellets of young in some nests as early as 17 days of age, 3 to 4 days before their eyes opened. He suggested this was due to ingestion of the mother’s fecal pellets (coprophagy), which was first witnessed on the 17th day. He said that, “When held in
the hand on this date the young avidly consumed all the feces they came upon.” This included voles eating their own fecal pellets. He suggested that coprophagy was necessary to inoculate the gut with micro-organisms needed for digestion of Douglas-fir needles. Juveniles were first seen eating needles when they were 25 days old, and by 27 days were removing resin ducts and eating needles like adults. He described a juvenile that escaped from its cage at 32 days of age and was found 3 days later in a nest that it had built in a pile of Douglas-fir limbs that were kept in the lab. It had continued to gain weight, indicating that it was able to survive on its own at this age. There is an excellent discussion of induced ovulation and adaptations to a low-energy diet, including a longer period of intrauterine development, small litter size, slow juvenile growth rates, and long period of female care. He suggested that these reproductive traits are primarily an adaptive response to a low-energy diet of conifer needles as opposed to adaptations for living in an arboreal environment. He suggested that tree voles were not able to live at high elevations because their arboreal nests were too small and exposed to keep them warm during winter.


We obtained these original notes from Don Roberts when we interviewed him at his home in Santa Cruz, California, in 2006. After transcribing the notes, we donated the originals to the Slater Museum of Natural History at the University of Puget Sound. These notes described the capture locations and laboratory histories of 248 tree voles that Roberts and Bill Hamilton used in their captive-breeding study of Sonoma tree voles from 1957 through 1961. Most of the specimens that they captured or bred in captivity are at the Slater Museum. Most of these specimens were captured near the Russian River in Sonoma County, California, but a few were collected in Mendocino and Humboldt Counties, California.


These notes included drawings that Wayne Hammer recorded when he captured a red tree vole near Vida, Lane County, Oregon, on 13 September 1967. Hammer was a government trapper who helped Chris Maser and Murray Johnson collect many tree voles in western Oregon.

Harris described and discussed tree vole biology in several sections of his book, citing Maser (1966), Johnson (1973), and Maser et al. (1981) as his primary sources of data. He described the loss of leader dominance in trees and resulting upturned branches that support nests of tree voles. He said that tree voles spend their entire life in the canopy and that many individuals may inhabit the same old-growth tree during the span of centuries. He said that tree voles are primarily restricted to mature Douglas-fir forests, although they do occur in other tree species and in younger successional stands. He describes the diet as restricted almost entirely to Douglas-fir needles. He repeated the oft-stated fact that the red tree vole is the most highly specialized vole in the world and the most arboreal mammal in North America. He also said that the white-footed vole is the smallest mammalian browser and perhaps the rarest vole in North America. He speculated that red tree vole home ranges average about 0.082 ha.


The authors assessed the taxonomic status of *Paranoplocephala bairdi*, a cestode flatworm found in heather voles and tree voles. Their results supported the independent status and conspecificity of specimens from heather voles and tree voles. They suggested that *P. bairdi* was a host-specialist parasite of tree voles and heather voles, with a wide geographical distribution in North America.


The authors modeled the ecological niche of tapeworms of voles in North America, including *Andrya neotomae* found in white-footed voles and *Anoplocephaloides cf. dentata* found in red tree voles.

These field notes described a field trip in 1995 during which John Hayes, Mike Murray, and others spent 2 days climbing trees to capture red tree voles northeast of Waldport, Lincoln County, Oregon. Of the six tree voles captured, two were melanistic (Hayes 1996). The six live specimens were sent to Milo Richmond at the Cornell Cooperative Wildlife Research Unit for captive breeding, where they all died. These were the first confirmed cases of melanism in the tree vole. Unfortunately, the specimens were lost or discarded.


In this species account, Hayes summarized knowledge of red tree voles as of 1996, including a reference to melanistic specimens that he collected in 1995. He pointed out that skulls of voles in the genus *Arborimus* could be distinguished from those of other arvicolines in the range of *A. longicaudus* by the shape of the deep reentrant angles of the lower molars. He described the rootless molariform teeth of juveniles that gradually develop roots as tree voles mature (Hooper and Hart 1962, Howell 1926). Rooted molars generally are considered to be an ancestral character for the subfamily. He reported that Johnson (1973) speculated that the genus *Arborimus* evolved in the Pacific Northwest during the Pliocene, but that this could not be confirmed because there are no known tree vole fossils.


John Hayes said that he sent six red tree voles (four normal, two melanistic) that he captured northeast of Waldport, Lincoln County, Oregon, to Milo (Mike) Richmond, the leader of the Cooperative Wildlife Research Unit at Cornell University. When contacted by Forsman, Richmond said he kept all six tree voles in the same cage and that they were all females because they never bred. He said that the voles lived about a year, but he did not remember what became of the specimens.


The authors reported that they caught an 18.9-g adult male white-footed vole in a Fitch live-trap in riparian habitat in the Oregon Coast Range. They did not specify where they captured the vole, but their four study sites were in Benton, Lincoln, and Douglas Counties.

One of the species they used in their distribution and habitat modeling exercise was the Sonoma tree vole.


In his notes, Hooper says that he prepared five Sonoma tree voles that were captured by Seth Benson and his wife Emma, and David Johnson between Monte Rio and Camp Meeker in Sonoma County, California. The two adult females and three juvenile females all died after a few days in captivity.


The authors described the glans penis of arvicolines, including tree voles. They viewed tree voles as a divergent form of the heather vole.


The authors used Sherman live-traps to sample small mammals along the South Fork of the McKenzie River in eastern Lane County, Oregon, 1968–1970. Of 3,630 small mammals captured, 3 were white-footed voles.


In 2013, the Bureau of Land Management (BLM) hired contractors to climb 206 trees in 10 remnant stands of old-growth and mature forest in the Marys Peak Resource Area of the Salem District of BLM. Trees were selected on the basis of visible nests or unique structure, such as broken tops, forks, or cavities. Climbers found evidence of tree vole presence in 132 of 206 trees climbed (64 percent), including 77 trees (37 percent) with evidence of recent activity. On the basis of this nonrandom sample, Hopkins concluded that tree voles were common in, “…every suitable patch of habitat that was surveyed, and some survey units showed abundant
evidence of vole presence regardless of habitat patch size.” He went on to infer that all of the late-successional forests in reserved allocations in the resource area (about 2171 ha) would have similar levels of vole presence. He concluded that tree voles were “…very common and likely abundant within all suitable habitat in the watershed.” And finally, he concluded that the proposed BLM timber sale would have “…a negligible effect on the vole population within the watershed…” There was no discussion regarding the validity of drawing general conclusions based on a nonrandom sample of trees selected specifically because they had visible nests or unique structure. There was also no discussion regarding the validity of population estimates that were based on nest counts as opposed to actual documentation of live animals.


A white-footed vole collected near Orick, Humboldt County, California, was compared to five other white-footed vole specimens. Howell concluded that “After studying the California species of Phenacomys, I can see nothing to be gained by adopting the subgenus Arborimus Taylor. Most of the characters on which it is based are either very slight, or inconsistent. It seems to me that the genus is an unusually well-defined one, and that nothing whatever can be gained by further division. However, if a subgenus must be recognized, let it contain only longicaudus, and be based upon the arboreal habits and hairy tail of that species, rather than on ill-defined characters that can be segregated only with considerable difficulty.”


Based on a single specimen collected near Tillamook, Oregon, Howell proposed a new species of tree vole (Forest lemming-mouse; Phenacomys silvicolum) that was darker and had smaller ears than the red tree vole. He concluded that the skull of this new species was longer with a narrower braincase that had more pronounced temporal ridges, and that the molariform teeth were structurally different (much heavier with a different occlusal pattern). Miller (1925) subsequently shortened P. silvicolum to P. silvicola.

Howell concluded that *Phenacomys longicaudus* and *P. silvicola* were definitely but not exclusively arboreal and probably had fewer predatory enemies to deal with when compared to terrestrial voles. He called these two species the “red tree mouse” and “forest tree mouse,” respectively. He suggested that the distribution of tree voles was discontinuous throughout the humid coastal belt of Oregon and California. He incorrectly speculated that tree voles could occur in Washington. He reported that tree voles descended to the ground to reach other trees and that the few ground nests that had been discovered had all been occupied by males. He stated that tree voles fed on the fleshy part of needles and on tender twig bark from green twigs. He said that tree voles were seldom found in isolated patches of forest and speculated that open expanses of nonforest may be barriers to dispersal. He incorrectly said that tree voles discarded the midrib of Douglas-fir needles. He estimated that a captive subadult tree vole ate 100 Douglas-fir needles an hour, day and night. He also noted that what appears to be good habitat can contain no tree voles. He stated that he usually selected forests of small (young) trees when searching for tree voles because nests were more accessible in small trees. He said that “Throughout their range these mice usually frequent the taller trees, and for this reason it is extremely difficult to estimate their numbers, for an immense Douglas-fir might harbor a dozen nests that cannot be recognized as such from the ground.” He reported that Harry Wilder found this to be the case when felling large trees on his Carlotta ranch. He claimed that on two consecutive mornings, Wilder and Irvine Clay captured 50 tree voles. We think the latter claim was an exaggeration on someone’s part, because museum specimens from Wilder and Clay never exceeded more than a few specimens in a day. Howell’s efforts to trap tree voles were unsuccessful, “As it is probably impossible to offer any bait that would attract the mice.” Like most tree climbers, he captured more females than males. He suggested that this was because males had smaller nests and eluded capture better than females. He stated, “Any opinion regarding the abundance of tree mice in a given area is little more than a haphazard guess.” He refuted
the claim that tree voles were colonial by stating, “One who is familiar with the tree mouse is prone to refer to an aggregation of individuals in any well-defined area as a colony; but the animals really have no colonizing tendency and are not at all sociable in the strict sense of the word.” He went on to say that, “In reality the mice are of a markedly solitary disposition, the females usually being truculent and intolerant of other individuals.” Howell also recounted an episode in which Wilder observed a Steller’s jay demolishing a tree vole nest.

Howell sent three white-footed vole stomachs to C.C. Sperry at the U.S. Biological Survey division of food habits research. The stomach contents were 100 percent pulverized roots of herbaceous plants. This is in contrast to other reports in which white-footed voles fed on leaves of herbaceous trees or shrubs (Forsman and Swingle 2006, Manning et al. 2003, Voth et al. 1983).

In this obituary, Howell described the life of Harry Wilder, who collected many tree voles at his ranch from 1913 to 1927. Wilder was born in 1865 in New Hampshire. He developed an interest in nature though his main income was as a beekeeper. In 1912, he and his wife Charlotte moved to a ranch near Carlotta, Humboldt County, California, where Wilder subsequently collected at least 46 Sonoma tree voles. Wilder collected an additional five Sonoma tree voles near Bridgeville in Humboldt County, and one Sonoma tree vole near Ruth in Trinity County. During 1913–1930, an additional 26 Sonoma tree vole museum specimens were collected at Wilder’s Ranch at Carlotta. At this time, just about everyone who was trying to collect tree voles in California stopped by to see Wilder, including Walter Taylor (1915), Brazier Howell (1926), Seth Benson (1931), Laurence Huey (1926), and Joseph Mailliard (1923).

The authors examined karyotypes of red tree voles collected from Coos and Benton Counties, Oregon. They reported a complex situation in which the diploid numbers ranged from 40 to 52 depending on locality.
190. Hubbard, C.A. 1940. A check list of the fleas of the Pacific Northwest (Washington, Oregon, northern California, and northwestern Nevada) with notes from southern California. Pacific University Bulletin. 37: 1–4. Hubbard reported that he collected a flea (*Megabothris quirini* Rothschild 1905) from a tree vole near Newberg, Yamhill County, Oregon, in 1935. We suspect this is one of the three tree vole specimens that he sent to the U.S. National Museum, but none of those specimens has a 1935 collection date.


192. Huey, L.M. 1926. Unpublished field notes. On file with: San Diego Natural History Museum, CA. These notes described a collecting trip in which Laurence Huey, a naturalist at the San Diego Natural History Museum, and Brazier Howell, from the Smithsonian Institute, drove up Highway 101 to the Trinidad whaling station in 1926 (http://www.sdnhm.org/about-us/our-museum/history/trinidad/). On this trip, they spent a day at the Wilder Ranch, near Carlotta, Humboldt County, California, where they collected one adult male and two juvenile Sonoma tree voles. In addition, Huey said that Howell collected six white-footed voles at Trinidad, Humboldt County, California.

193. Huff, M.H.; Holthausen, R.S.; Aubry, K.B. 1992. Habitat management for red tree voles in Douglas-fir forests. Gen. Tech. Rep. PNW-GTR-302. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 16 p. In this literature review, the authors cited Carey (1991) to support their contention that young forests were population sinks for tree voles. They did not mention the large number of specimens (including many breeding females) collected in young forests by previous researchers. They stated that red tree voles occurred almost exclusively in Douglas-fir forests but did not mention that tree voles along the coast in northwest Oregon occurred primarily in forests of western hemlock and Sitka spruce, as documented by previous researchers (Clifton 1960; Jewett 1920, 1930; Walker 1928, 1930). They stated that the only data available to describe habitat occupied by tree voles were data from pitfall studies conducted by
the U.S. Forest Service Pacific Northwest Research Station and their contractors from 1984 to 1986. They did not acknowledge the wealth of information on tree vole habitat in the earlier literature and in the unpublished notes of Murray Johnson (1957–1985), William Hamilton, III, and Don Roberts (1957–1961), Vernon Bailey (1914), Chris Maser (1967–1974), Seth Benson (1930–1956), Walter Taylor (1913), Walter Dalquest (1943–1944), and others. They suggested that suitable habitat for tree voles was mesic forests and that tree voles avoided dry environments. They discussed elevational limits based on data from pitfall studies and reported that they found no difference in the amount of old forest around stands in which tree voles were captured in pitfalls and stands in which no tree voles were captured in pitfalls. They proposed a model for evaluating habitat quality for tree voles based on basal area of Douglas-fir, density of large trees, height of live trees, stand age and size, site moisture class and elevation. They suggested that tree voles were vulnerable to local extirpations from fragmentation and loss of habitat, and that vole populations had undergone significant declines owing to cutting of old-growth forests.


195. Huff, R.; Van Norman, K.; Hughes, C.; Davis, R.; Mellen-McLean, K. 2012. Survey protocol for the red tree vole, Arborimus longicaudus (= Phenacomys longicaudus in the record of decision of the Northwest Forest Plan). Portland, OR: U.S. Department of Agriculture, Forest Service and U.S. Department of the Interior, Bureau of Land Management. 52 p. This was the fourth edition of the survey protocol used by the U.S. Forest Service and Bureau of Land Management to document presence of tree voles in proposed project areas. The first half of the report included a review of tree vole biology and distribution. The second half was a revised protocol for surveys.

The authors conducted surveys of Sonoma tree vole nests in 64 stands that were subdivided into three forest size classes, including pole (15 to 28 cm diameter at breast height [dbh]), young (29 to 60 cm dbh), and old (>61 cm dbh) forest. Each stand was surveyed with 500-m transects. Surveyors located 441 tree vole nests (215 “active,” 226 “inactive”). They located at least one tree vole nest in 89 percent of the stands surveyed, including 19 of 24 pole stands, 10 of 12 young forest stands, and 26 of 28 old-forest stands. Most (n = 302) of the nests were in old forest. The authors did not report if any of the young or pole stands had remnant old trees, but they did mention that old trees appeared to maintain suitable tree vole habitat in young stands. They did not report how many nests were identified based on tree climbing as opposed to visual observation from the ground.


The authors stated that Sonoma tree voles were relatively common on their forested lands. Their conservation strategy was a habitat-based approach in which they proposed to sustain viable populations of tree voles in each watershed by retaining some large old conifers. They suggested riparian management zones would provide dispersal corridors for tree voles.


This specimen catalog included notes describing one Sonoma tree vole specimen traded to the University of Illinois and one Sonoma tree vole and one red tree vole traded to the U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Arcata, California.


In the abstract, the authors stated that red tree voles were normally associated with older forest. They suggested that leaving old Douglas-fir trees in harvest areas might provide habitat for tree voles in young forests that reestablish on cutover areas.

In this short species account, Ingles described nests of tree voles and accurately described how they removed resin ducts from Douglas-fir needles before eating the rest. He said that tree voles breed throughout the year and suggested that weasels, martens, small hawks, and owls were important predators of tree voles.


Ingles provided brief species accounts of red tree voles and white-footed voles. Most of the information presented is correct, except that Ingles errs when he says that tree vole nests include the mid-ribs and resin ducts of Douglas-fir needles. Mid-ribs of Douglas-fir needles are never found in tree vole nests, because they are consumed.


In this analysis, the Institute of Natural Resources science advisory team criticized the Oregon Department of Forestry (ODF) analysis of the effects of management on red tree voles, northern spotted owls, and aquatic amphibians. They argued that (1) tree voles required a more robust spatially explicit management strategy than was proposed by ODF, and (2) that the ODF analysis failed to account for the distinctive conservation challenge presented by the dusky tree vole. They proposed an alternative approach for analyzing the effects of management on tree voles.


In this paper on foraging behavior of spotted owls the authors incorrectly listed the red tree vole as a major prey item of California spotted owls (*Strix occidentalis occidentalis*) in the Sierra Nevada, where tree voles do not occur.

There was nothing specific about tree voles in this paper, but the information about factors that influence needle growth in old-growth Douglas-fir may be important for understanding relationships between tree voles and their habitat.


There was nothing specific about tree voles in this paper, but the description of epicormic branching in Douglas-fir will be of interest to anyone interested in the ecology or management of tree voles.


This newspaper article described a field study in which researchers were collecting tissue samples for a genetic study of tree voles in western Oregon in 2000.


This photocopy of Jewett’s unpublished specimen catalog lists 21 tree voles and 3 white-footed voles collected by Jewett from 1917 through 1936. He also listed six additional red tree voles that he received from other collectors. The original copy of this specimen catalog and Jewett’s original field notes were sent to the San Diego Museum of Natural History, where they were either lost or discarded.


Jewett described the second white-footed vole known to science and the first in Oregon. He captured the vole in a mouse trap baited with oatmeal on 18 May 1914. The location was a riparian area of dense salmonberry
(Rubus spectabilis) and sword fern (Polystichum munitum) near the McKenzie River about 3.2 km downstream from Vida, Lane County.


Jewett introduced this paper with a somewhat poetic sentence, “In the dense forests of the Pacific Northwest, where the sun seldom penetrates the heavy growth of firs and spruces to mother earth, live two species of the most interesting of our small mammals, Phenacomys longicaudus in the tree tops, and Phenacomys albipes on the moss-covered floor of the forest.” He then provided a wealth of information on the habitat and distribution of the tree vole. He described lots of nests, and suggested that, “…the lower Rogue River watershed in Curry County is the center of abundance of these little tree mice.” He obviously was aware that tree vole nests can be confused with nests of woodrats and squirrels and made it clear that the nests he observed were indeed tree vole nests. He also mentioned that some of the larger nests that he observed were, “…evidently built by woodrats and later occupied by these mice.” He said that most nests, “…are located in Douglas-fir, but several have been noted in Sitka spruce near the coast.” He described two large nests “…in the barn yard…” at the John Adams Ranch in Curry County that were about 3 m above ground and 8 m apart where he caught a male and female, respectively. He said that, “Mr. Adams told me the nests had been there ten years to his knowledge, and as far as he could remember were the same as when he located his buildings on the ground.” He discussed escape behavior, including running out on limbs, climbing down trees head-first, and jumping and free-falling to the ground. He also described a case where a vole hid among the limbs when a small boy was induced to climb a likely looking nest tree at the Lowry Ranch on the Rogue River. He described a number of nests in young forests and talked about young boys who kept tree voles as pets. He also mentioned that tree vole nests had been found near Bonneville in Multnomah County, and Forest Grove in Washington County, but did not provide details. He described feeding behavior but didn’t quite get it right in terms of how the voles removed resin ducts from Douglas-fir.


Jewett provided a second-hand account of a case in which Elmer Williams captured a female tree vole and her three newborn young near Agness,
Curry County, Oregon, on 22 May 1921. The nest was about 12 m up in a Douglas-fir. Jewett said that Williams did not measure or save the specimens.


Jewett and his family found a tree vole nest 5 m up in a Douglas-fir tree while walking through the woods near the beach at Netarts, Tillamook County, Oregon, on 14 August 1929. He had his 12-year-old son climb to the nest, at which point a vole ran out and jumped to the ground and escaped despite a search by the entire Jewett family. They returned the next morning and Jewett sent his son up the tree again, at which point the vole began to climb down the bole headfirst and was shot. The vole was an adult female that had recently given birth, but they did not find young in the nest. He said that she was a slow and cautious climber. He provided measurements of the type specimen of dusky tree vole collected by Alex Walker at Tillamook in 1916 and concluded that the species was indeed arboreal, as was previously documented by Howell 1926. He described the center of the nest as a, “…well matted mass of dissected leaves of fir.”


Jobanek provided a detailed account of the 1914 expedition in which Vernon Bailey travelled to Oregon to try to capture a tree vole. Bailey met with Alfred Shelton in Eugene and they spent several days climbing trees on Spencer Butte before finally catching a tree vole. Jobanek provided many interesting details about personalities, correspondence between people, campsites, methods, maladies, and modes of travel in 1914. This is an excellent read for anyone interested in the early history of mammalogy in Oregon.


Johnson’s catalog described a case in which an arboreal salamander was collected in a Sonoma tree vole nest 4.8 km east of Duncans Mills, Sonoma County, California, on 1 March 1936. The specimen number for the arboreal salamander is MVZ19144.

Johnson observed a case in which a female Sonoma tree vole gave birth in captivity shortly after being captured with two large young. He did not take note of the fact, but this was another record that documented post-partum mating. He described the general appearance of the two neonates and used a microscope to observe five distinct mystacial rows of vibrissae. Johnson did not say so in his notes, but the voles \( (n = 10) \) he described were collected on field trips with Seth and Emma Benson.


In this white paper on forest management on lands administered by the Bureau of Land Management, Johnson and Franklin proposed that monitoring of red tree voles be replaced by assessments using experimental treatments of vole habitat. They also suggested that the survey and manage mitigation standards for tree voles in the Northwest Forest Plan be replaced by designating the tree vole as a sensitive species. Johnson and Franklin did not say so, but if adopted, their recommendations would eliminate requirements to protect tree voles in areas proposed for harvest.


Murray Johnson's catalog included a list of tree voles and white-footed voles that he collected or that were born in his captive breeding colony. It also included many specimens that he obtained from others.


Murray Johnson was a biologist and thoracic surgeon whose avocation was searching for and studying tree voles. He published only a few papers, but his field notes, lab notes, and letters fill several file drawers and a large stack of three-ring binders. These notes described extensive field trips to collect tree voles in Oregon and California, as well as many pages of lab notes on tree voles that he kept in captivity. These notes document the history of 367 tree voles (\textit{Arborimus longicaudus}, \textit{A. pomo}, and their hybrids) that Johnson collected or bred in captivity as well as 169 tree voles that he obtained from others, including Doug Bake, Bill Rowland, Ricky
Brown, Chris Maser, Wayne Hammer, and Harry Schoenborn. A warning to anyone wanting to look at these notes—Murray’s handwriting was terribly difficult to read, and his lab notes were not well organized. But, hidden away in these notes are many interesting stories, including trials and tribulations involved in keeping tree voles in captivity, field trips when he was chased out of trees by bees, interactions with hostile landowners, bouts with poison oak (Toxicodendron diversilobum), and mysterious stomach ailments.


These unpublished notes consist of detailed histories of the individual tree voles that Murray kept in captivity, including records of breeding attempts, birth and death dates, and outcomes of hybrid crosses between red tree voles and Sonoma tree voles.


Murray Johnson wrote to Dorland Hammer on 15 March 1967 notifying him that all three red tree voles collected on their field trip a few weeks previous to Bills Peak, Coos County, Oregon, were males. Murray wrote Dorland on 7 March 1969 asking him to keep an eye out for tree voles in Coos County, Oregon, as there were few data from that area.


Johnson used electrophoretic analyses of proteins in sera and hemoglobin to compare two heather voles and 16 red tree voles. The albumin migration was slightly faster for Arborimus when compared to Phenacomys. Based on these results, Johnson proposed combining the named forms of Arborimus longicaudus into a single species, and separating the genera Arborimus and Phenacomys.


Based on differences in juvenile development, numbers of mammary glands, bacula, phallus, testes, dentition, skulls, and skeletal morphology, Johnson suggested that tree voles should be placed in the genus Arborimus, whereas the heather vole should be retained in the genus Phenacomys. He suggested that differences in many morphological and physiological
attributes indicated a major evolutionary divergence between *Arborimus* and *Phenacomys*. He also speculated that the genus *Arborimus* evolved in the Klamath Mountains during the Pliocene.


In this book chapter, Murray described the utility of biochemistry and immunological data analysis as a taxonomic tool. He cited his previous analysis (Johnson 1968) as evidence that the subgenus *Arborimus* should be separated from the genus *Phenacomys*.


In a letter dated 30 August 1988, Murray thanked Doug Bake for his interest, opinion, and data on tree voles in Sitka spruce and western hemlock forests. As described in Forsman and Swingle (2010), Doug provided Murray with many tree vole specimens from northwest Oregon. In another letter, Murray sent a memo to the other authors of the “Tree voles of Douglas-fir forests” manuscript stating that Martin Raphael had been asked to be a third technical editor. He also mentioned that an additional chapter on the heather vole was being added to the manuscript as a companion to the chapter on the white-footed vole.


Based on karyotypic and anatomical differences, Johnson and George proposed splitting the tree vole into two species, the red tree vole in Oregon and the Sonoma tree vole in California. They suggested that low reproductive success of crosses between red tree voles and Sonoma tree voles indicated that there was a “strong reproductive barrier between Oregon and California populations.” The reproductive crosses referred to in this manuscript were all based on captive breeding experiments conducted by Johnson from 1955 through 1986. Unfortunately, the details are buried in his voluminous lab notes and were never published.

In a letter dated 10 February 1966, Wayne Hammer told Murray Johnson that he just got back from gathering data on an underground tree vole nest. There is a color picture of this nest in Murray’s files. To our knowledge, this is the only ground nest of a tree vole ever discovered in Oregon. In another letter, Wayne stated he had two captive tree voles.


Murray Johnson and his wife Sherry briefly mentioned red tree voles and white-footed voles in this excellent species account of North American *Microtus*.


Mike Kesner sent a letter to Murray Johnson thanking him for providing two tree voles that Kesner used for his papers on myology and manus musculature of microtines (Kesner 1980, 1986). Kesner was planning on conducting field work on tree voles and asked Johnson where he should go to obtain specimens. Johnson responded by providing a long list of sites where he had collected tree voles. He also warned Kesner to beware of poison oak when climbing tree vole nest trees and said that he had to be especially careful about poison oak “because of my own sensitivities.”


This exchange of letters reflected a difference of opinion between Murray Johnson and Bill Lidicker over who should be in possession of the Sonoma tree voles collected and raised in captivity by Don Roberts and Bill Hamilton, III when they were graduate students at University of California, Berkeley. Lidicker wanted the specimens housed at the University of California, Berkeley, Museum of Vertebrate Zoology (MVZ) where the work was done, whereas Murray felt they should stay at the Slater Museum of Natural History in Tacoma, Washington, which was where Hamilton and Roberts donated them. In a letter dated 22 September 1977, Johnson acknowledged that the work was done while Roberts and Hamilton were students at Berkeley, but he disagreed with Lidicker that the specimens should be housed at MVZ because the study that Roberts and Hamilton conducted on tree voles was independent of their graduate work. Lidicker
did not argue further but did respond in a letter on 26 October 1977 in which he mentioned that an additional 16 tree voles that were from Roberts and Hamilton at the MVZ were sent to the Slater Museum. We believe these were the 16 uncataloged specimens that we found at the Slater Museum when we visited the museum in 2011.


Johnson and Maser proposed changing the genus of the white-footed vole from *Phenacomys* to *Arborimus*. They based this recommendation on differences in morphological characteristics and the number of diploid chromosomes.


In this letter, Murray Johnson and Chris Maser updated their coauthors on the tree vole book that they were working on. They discussed possible funding from the U.S. Forest Service and mentioned that they had approached Martin Raphael about becoming a technical editor.


This working draft of a book on tree voles was never completed. It included chapters on fossil history, taxonomy, anatomy, distribution, forest ecosystem, field methods, habitat, nests, behavior, food and water requirements, reproduction, juvenile development, demography, parasites, captives, white-footed voles, and heather voles.


This outline was developed for a book that Murray and his coauthors wanted to write. There were at least three versions of the outline. The book was started but never finished.

In 17,600 trap-nights, Aaron Johnston did not capture a single red tree vole or white-footed vole in live-traps on the Cascade-Siskiyou National Monument east of Ashland, Jackson County, Oregon.

234. Jollie, M. 1945. Unpublished field notes and specimen catalog. On file with: University of California, Berkeley, Museum of Vertebrate Zoology. In his field notes and specimen catalog, Malcolm Jollie reported that he collected four adult and six juvenile tree voles from Jenner and Anchor Bay in Sonoma County, and Laytonville in Mendocino County, California. Two of the juveniles were from a site 1.6 km east of Jenner. We suspect that the latter site was the “Poison Oak Knoll” location on the Russian River, where Seth Benson, Don Roberts, William Hamilton III, Murray Johnson, Alan Ziegler, and others (including us) collected tree voles. Jollie said that he caught a female tree vole in a snap-trap 12.9 km southwest of Laytonville. The snap-trap was set on a log between two Douglas-fir trees. He also said that he looked for tree vole nests farther inland between Willets and Ukiah in Mendocino County, without success.

235. Jones, C.; Hoffmann, R.S.; Rice, D.W.; Engstrom, M.D.; Bradley, R.D.; Schmidly, D.J.; Jones, C.A.; Baker, R.J. 1997. Revised checklist of North American mammals north of Mexico, 1997. Museum of Texas Tech University Occasional Papers. 173: 1–20. The authors reported that Johnson and George (1991) applied the generic name *Arborimus* to the white-footed vole and red tree vole, and that Johnson and George (1991) further proposed that the Sonoma tree vole was distinct from the red tree vole. The authors did not say whether they agreed or disagreed with these changes.

236. Jones, J.M. 2003. Habitat associations and ecology of the Sonoma tree vole (*Arborimus pomo*) in northwestern California. Arcata, CA: Humboldt State University. 55 p. M.S. thesis. Jones used distance sampling methods to compare relative abundance of Sonoma tree vole nests in different forest size classes. She concluded that tree vole nests were significantly more abundant in mature forest (>61 cm diameter at breast height [dbh]), than in pole forest (15 to 28 cm dbh) or young forest (29 to 61 cm dbh). She also modeled relationships between habitat variables and nest abundance at 61 sites. The best predictive models included percentage basal area of Douglas-fir, dbh of dominant trees, total basal area, percentage slope, and slope position.

In this published abstract, the authors compared relative abundance of Sonoma tree vole nests in three size classes of Douglas-fir forest on lands owned by The Pacific Lumber Company (currently, Humboldt Redwood Company) in northwestern California. Vole nests were significantly more abundant in mature than in young or pole forests, but there were no significant differences between young and pole stands. The authors also evaluated associations between landscape-level habitat attributes and Sonoma tree vole abundance within Humboldt Redwoods State Park, Redwood National Park, and the Angelo Coast Range Reserve in northwestern California. Sixty-one sites were searched for tree vole nests using line transects, and nest densities were estimated using program DISTANCE. Nest densities were positively correlated with diameter at breast height of the dominant trees, percentage basal area of Douglas-fir, and slope position. Total basal area and percentage slope were also important predictors of nest density.


The authors compared conservation status rankings of red tree voles by four different conservation organizations. Nature Serve/Natural Heritage Network Ranks listed the red tree vole as rare, uncommon, or threatened but not immediately imperiled. Oregon Department of Fish and Wildlife listed the red tree vole as vulnerable in the Coast Ranges. The U.S. Fish and Wildlife Service listed the red tree vole as a species of concern, and the Oregon Biological Information Center listed the red tree vole as a species of conservation concern.

The authors updated conservation status rankings for the red tree vole and the white-footed vole from their 2010 version. The rankings were identical except that the U.S. Fish and Wildlife Service listed the red tree vole for the north Oregon coast as endangered or threatened.


On pages 124–125, the authors provided a brief description of red tree voles and Sonoma tree voles.


The authors found that terpenoids were located exclusively in the resin ducts in Douglas-fir, Sitka spruce, and western hemlock needles. They concluded that tree voles were able to largely avoid exposure to terpenoids in Douglas-fir and western hemlock by discarding the resin ducts. They reported that resin ducts in Sitka spruce were discontinuous and sometimes absent entirely. How tree voles avoided ingesting terpenoids when feeding on Sitka spruce was not documented.


Kesner dissected and compared the masticatory musculature of 12 species of voles, including 2 red tree voles and 2 heather voles. Based on myological differences, he suggested that *Arborimus* was a distinct genus from *Phenacomys*.


In this first publication from his dissertation, Kesner said that the tree vole had one of the more derived microtine digastric muscles.


Kesner examined the structure of the forearm and hand in voles and mice. He concluded that the tree vole manus had a combination of primitive and derived characters that included the most highly developed “clasping” trait of the arvicolines sampled.

This newspaper report described a talk given by Portland Parks and Recreation wildlife biologist John Deshler on 7 November 2012. Deshler suggested that the gray fox (*Urocyon cinereoargenteus*), dusky-footed woodrat (*Neotoma fuscipes*), and red tree vole would be good candidates for reintroduction to Forest Park in Portland, Oregon.


Mary Koford reported that she, Marietta Voge, Anita Pearson, and Lois Taylor searched for tree vole nests on 19 May 1949 near Fort Ross, Sonoma County, California. They captured an adult female that gave birth to four young the next day in captivity.


Kritzman provided a short life-history account of the red tree vole.


Krohne used the red tree vole as an example of one of many species of arvicolines in which neonate birth weights were negatively correlated with litter size (Hamilton 1962).


Lamb reported that he and Harley Watson captured three tree voles in northwest California near Mad River, Trinity County, and one tree vole near Bridgeville, Humboldt County.


Larrison briefly described red tree voles and white-footed voles.

In this book chapter, Lawlor suggested that tree voles may respond differently to logging of old-growth forests in different parts of their range. To support this hypothesis, he cited studies in Oregon in which authors found that tree voles were strongly associated with old-growth forests (Aubry et al. 1991, Corn and Bury 1991, Gilbert and Allwine 1991) and papers in California in which the association with old forests was less conclusive (Meiselman 1992, Meiselman and Doyle 1996, Raphael 1988, Thompson and Diller 2002).


The authors ranked forest amphibians, birds, and mammals according to their perceived risk of local extinction in western Oregon and Washington. Of 93 species examined, red tree voles and white-footed voles ranked near the top.


The authors listed fleas that had been found on white-footed voles, including *Catallagia scullen scullen*, *Epitedia scapani*, *Hystrichopsylla occidentalis occidentalis*, *Megabothris (Amegabothris) abantis*, and *Rhadinopsylla sectilis goodi*.


In this obituary, Little said that he accompanied Howell to Alton, Humboldt County, California, to collect tree voles in 1923. He said that in late summer, Howell collected five tree voles at Harry Wilder’s Ranch near Carlotta. We found evidence from museum specimen tags that Howell kept three of those voles in captivity and that one of them produced one young. We could not find Howell’s field notes, but we did find museum specimens of 18 Sonoma tree voles and 5 white-footed voles that he collected.

These notes described minutes of a meeting in which Sue Livingston of the U.S. Fish and Wildlife Service discussed the taxonomic status of red tree voles and dusky tree voles with Mark Miller, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center. Miller stated that his paper (Miller et al. 2006) did not address the subspecies issue and that he did not work on the Bellinger et al. (2005) paper, so he could not say if his paper enhanced or contradicted Bellinger et al. (2005). Miller et al. (2006) found that there were genetically discrete populations in the north Coast Ranges and North Cascades compared to the rest of the tree vole population farther south. This north-south discontinuity has also been observed in plants (Soltis et al. 1997; Plant Systematics and Evolution 206: 353–373) and the southern torrent salamander (*Rhyacotriton variegatus*; Miller et al. 2006 Journal of Heredity 6: 561–570).


In this unpublished agency report, Livingston discussed the subspecific taxonomy of tree voles in Oregon based on comments she received from Mark Miller and Sue Haig at the U.S. Geological Survey Forest and Rangeland Ecosystem Science Center in Corvallis, Oregon. Miller and Haig suggested that the north/south genetic discontinuity between tree voles could possibly support subspecies designation.


Maguire used pitfall traps to sample small mammals at four locations in the central Cascades in Douglas and Lane Counties in Oregon. There were 6 replicate trapping grids at each location, for a total of 24 sampling grids. Tree voles were captured at three of the four locations (four at Little River,
three at Layng Creek, and one at Dog Prairie). White-footed voles were captured at only one location (Layng Creek), where they were captured in three of six stands sampled.


In 1921, Joseph Mailliard, Chester Lamb, and Irvine Clay collected two adult and three juvenile Sonoma tree voles at Kneeland, southeast of Arcata, Humboldt County, California. In 1926, Mailliard and Raleigh Borell collected 11 Sonoma tree voles at the McClellan Ranch near Bridgeville, Humboldt, County, and one tree vole from Harry Wilder’s ranch near Carlotta, Humboldt County, California. One of the tree voles was collected by shooting the nest. Mailliard also said that Borell found the head and shoulders of a tree vole under a tree, and that Harry Wilder told him that he and Irvine Clay collected 50 tree voles in one day. The latter story was repeated by Howell (1926), but we found no evidence that it was true.


In autumn 1921, Joseph Mailliard, Chester Lamb, and Irvine Clay conducted field work in northwestern California. Mailliard wrote, “Mr. Clay not only led the way to Kneeland, but gave several demonstrations along the road through the fir forest of how to capture the long-tailed tree mouse. In fact, if it had not been for this practical demonstration of just how to proceed in the matter, it is doubtful any mice would have been secured by the field party. At least in part of the springtime, the larger nests contain one female with (usually) two or three young, while the male has a small nest of his own, probably often in another tree nearby, as no nests of males were discovered in the small sapling fir trees in which the females’ nests were found. In each case, there were branches interlocking from adjacent trees that could furnish means of communication with the family nest. But few nests discovered by us were occupied, and these only in forest that had been extensively thinned out by wood cutting. Careful watch was kept for the nests of this mouse in every locality visited by us, but the only ones discovered were on the road between Eureka and Kneeland Post Office.” Later on in the paper Mailliard wrote, “A sharp watch was kept in all suitable forest country for nests of the long-tailed tree mouse as outlined
elsewhere in this paper, but very few nests were found, and of those discovered in accessible situations the great majority appeared deserted.” His comment about occupied nests being found only in stands that had been heavily thinned by woodcutters is interesting because we found no other references in which researchers found tree voles in heavily thinned stands.


Manning used Sherman live-traps to sample small mammal populations in the Sterling Creek watershed 10.0 km southeast of Ruch, Jackson County, Oregon. Of 593 small mammals captured, none were tree voles or white-footed voles. His study adds to the considerable body of evidence that tree voles do not occur east of the Applegate River.


Manning and Edge used Sherman live-traps to sample small mammals in Salmonberry Creek and Little Lobster Creek, approximately 9.5 km southwest of Alsea, Lincoln County, Oregon. They captured 926 small mammals but did not state the number of trap-nights sampled. No red tree voles or white-footed voles were captured.


This was the published version of Jeff Manning’s thesis. They used Sherman live-traps to sample small mammals in Jackson County, Oregon. They captured 538 deer mice and 248 red-backed voles (Myodes californicus) but did not state how many trap-nights or what other small mammals they captured. Why the numbers differ from his thesis is not clear.


Manning and Maguire reported that they captured a 24-g male red tree vole in a pitfall trap at 1600 m elevation near Dog Prairie Creek in the central Cascades, Douglas County, Oregon. However, when we contacted Tom Manning to ask for details, he said that the elevation in the published
note was wrong and that the elevation of the capture site was actually 1500 m. This record represented a considerable range expansion.


Based on a sample of 13 white-footed voles captured in pitfall traps in the Oregon Cascades, the authors described a southward range extension. They concluded that the species was semiarboreal based on presence of hazel pollen from unopened catkins in fecal pellets. Capture sites were associated with brushy areas of red alder and California hazel, further supporting the hypothesis that this species tends to be associated with thick brush and shrubs. In stomach samples, the authors found that green plant tissues were present in 9 to 91 percent of the fields viewed under a microscope (mean = 50 percent), and that arthropods were present in 3 of the 13 samples examined. Spores from hypogeous fungi were present in all but one sample.


On 25 and 26 August 2009, the U.S. Fish and Wildlife Service convened a four-person listing advisory panel workshop for the red tree vole. The panel listened to reports from research scientists on management status, genetics, biology, distribution, and habitat associations of the red tree vole. Using a modified Delphi scoring method, the panel then ranked the distinct population segment of tree voles in the northern Oregon Coast Ranges as threatened (67 percent), not warranted (32 percent), or endangered (1 percent). The panel identified the following evidence in their decisionmaking process: loss of area and connectivity of old-growth forests from harvesting and fire, low reproductive potential, high predation rate, lack of guidelines and management, and isolated populations.

Marcot and Molina reported that much research had been conducted on the distribution and biology of the red tree vole subsequent to the adoption of the Northwest Forest Plan and that federal land managers were frustrated because the requirement to protect red tree vole nests found during predisturbance surveys was interfering with timber harvest.

In this brief species account, the authors stated that tree vole diets contained 0.5 to 2.0 percent Douglas-fir seeds. We found no evidence supporting this statement.

Karl Martin used pitfall traps to sample small mammals in the Oregon Coast Ranges (Nestucca River, Lobster Creek, and Drift Creek drainages) from 1995 through 1996. He captured 16,892 small mammals, including 42 red tree voles and 85 white-footed voles. The number of individuals captured per 100 trap-nights was 0.033 for tree voles and 0.066 for white-footed voles. Although capture rates were highest in forests with large trees (>53 cm diameter at breast height), none of the differences among forest size classes were significant. Most of Martin’s tree vole specimens were donated to the University of Alaska, Fairbanks, Museum of the North. Martin captured an additional 16 tree voles in pitfall traps during a pilot study near Prairie Mountain, Benton County, Oregon in 1994. We found the skulls of those specimens in a freezer at Oregon State University; they are currently housed at the U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Corvallis, Oregon.

These museum files contained several letters and specimen lists from Karl Martin to Conroy and Cook regarding the capture locations of 38 red tree voles and 74 white-footed voles that Martin captured in Oregon and donated to the museum.

This was the published version of Karl Martin’s dissertation. The authors captured 42 red tree voles and 85 white-footed voles in pitfall traps. They concluded that tree vole capture rates were positively associated with
mature conifer forests and were negatively affected by decreasing patch densities of large sawtimber (fewer individual patches).


Martin described Propliophenacomys parkeri, a new genus and species that represented the oldest known member of the lineage leading to Pliophenacomys, and possibly to Phenacomys.


Martin found eight arvicolid species at a site in South Dakota, including Pliophenacomys. He compared the teeth of these fossil voles to the teeth of heather voles, white-footed voles, and red tree voles.


These notes included a large binder with original field data forms describing red tree vole nests that Chris Maser found in Oregon.


Maser’s specimen catalog listed 99 red tree voles and 1 white-footed vole collected in Oregon from 1963 through 1972.


Maser reported remains of one Phenacomys silvicola and one Phenacomys spp. that he found in owl pellets at 610 m elevation on the north side of Marys Peak, Benton County, Oregon, in 1963.


On 19 February 1965, Maser shot an adult female northern spotted owl with a pellet rifle on Oregon State University’s McDonald Forest, a few kilometers north of Corvallis, Benton County, Oregon. The stomach of the owl contained remains of two adult tree voles. The skulls are in the Oregon State University collection (can No. 256). Maser described the habitat as a dense stand of young Douglas-fir. The owl was roosting about 60 m southeast of a nest in which Maser found a female tree vole and two newborns.

This thesis included an extensive literature review on tree voles, white-footed voles, and heather voles, as well as a wealth of information that Maser collected personally, including observations on nest attributes, reproduction, sex ratios, escape behavior, feeding behavior, and habitat. Based on a single ground nest located by Wayne Hammer, Maser speculated that tree voles might live underground during part of the year. He stated that stick size was not a valid criterion to determine which species built a nest because tree voles sometimes cut twigs that were nearly as large as those cut by squirrels or woodrats. He described the free-fall position that tree voles assume when jumping from their nests. He observed tree voles licking water off needles in captivity and suggested that tree voles also lick water off needles in the wild.

In April through June 1965, Maser conducted a population density study of tree voles. He searched a 12.4-ha area of young forest for tree vole nests and dissected all nests that he detected to determine the number of voles in each nest. He captured 40 voles, including 12 adults, 3 subadults, and 25 juveniles. Thus adult density was 0.96 per hectare. This was a minimum estimate, as he did not know how many voles went undetected. The study plot was located in Benton County, 7.3 km SW of Monroe.


These field notes described Maser’s collecting activities in western Oregon from 1967 through 1974. He collected tree voles with Rita Maser, Jack and Rob Booth, Ruth and Damon Smith, Wayne and Dorland Hammer, Ron Nussbaum, and Eric Forsman. He also obtained four tree vole specimens from Bill Harvey (a logger) who collected them while clearcutting an old-growth forest on Prairie Mountain, Benton County, Oregon.


On pages 219–225, Maser described the appearance, distribution, habitat, diet, feeding behavior, reproduction, dispersal, nests, predators, escape behavior, and crypsis of red tree voles. He described pelage color variation
of red tree voles from north to south. He stated that young trees were not structurally able to fulfill nesting requirements or offer much protection from weather. He called the tree vole one of the most specialized arboreal mammals in the world. He said that young and tender conifer needles are sometimes eaten whole and that some twigs are split, apparently to obtain their pithy center. He said that tree voles typically construct their nests at or above the height of the first live branch, and that female tree voles may leave their young and disperse to a new nest once the young become capable of fending for themselves [definitely not true in most cases]. He speculated that many hundreds of generations of tree voles can live in one large Douglas-fir.

Maser considered the white-footed vole (pages 218–219) one of the rarest voles in North America because only 72 had been captured prior to 1974. He said that white-footed voles feed on deciduous leaves and forbs. He concluded that white-footed voles nest and forage on the forest floor, but also forage in the forest canopy.


In this court deposition, Maser gives a passionate defense for the protection of old-growth forests as habitat for tree voles.


This checklist was based on 3 months during which Chris and Rita Maser conducted field work at Cascade Head Experimental Forest in Tillamook County, Oregon, in winter 1971–1972. Maser called the white-footed vole the rarest member of the vole family in North America. He captured white-footed voles primarily in riparian alder forests along small streams. Maser called the red tree vole the most highly specialized vole in the world. He speculated that tree vole populations were widely scattered and disappearing as a result of land development. He reported that tree vole nests were found from 2 to 47 m above ground in the live crowns of Douglas-fir, Sitka spruce, western hemlock, and grand fir. He stated that tree voles fed on
conifer needles and tender bark removed from conifer twigs. He stated that known predators were the northern spotted owl, great horned owl (*Bubo virginianus*), long-eared owl (*Asio otus*), and northern saw-whet owl.


Maser and Johnson described morphology, distribution, habitat, and diet of the white-footed vole based on their field work and examination of museum specimens. They described the white-footed vole as blunt-nosed, with white feet contrasting with the overall brown pelage. They presented all known white-footed vole locations in the text and map figure. They described finding herbaceous plant material in stomachs of white-footed voles. One white-footed vole was captured underground in a trap set for mountain beaver (*Aplodontia rufa*).


Much of the information on tree voles and white-footed voles in this book repeated information previously presented in Maser’s master’s thesis. The authors suggested that “Since red tree voles seldom inhabit trees less than 25 years of age, clearcut logging decimates entire populations and is responsible for the disappearance of tree vole populations in many areas, and in large measure, for their widely scattered present distribution.” They cited Johnson (1968) in stating that there were two subspecies of red tree voles in Oregon (*A. longicaudus longicaudus* and *A. l. silvicola*), and speculated that tree voles and white-footed voles evolved in the ancient Klamath Mountains of southwest Oregon. They quoted Johnson (1973: 240), who said that “Geologic history provides data for an attractive hypothesis; *Arborimus* evolved in this region from some primitive microtine during the Pliocene, adapting to a habitat of mixed deciduous and coniferous forest during a time of moderate temperature and high rainfall; consistent climatic conditions along the Pacific Coast have maintained the restricted habitat.”

This excellent (but out-of-print) key included detailed drawings by James Cloutier of the skulls of all vole species that occur in Oregon and Washington, plus species accounts and distribution maps for each species.


Mayer reported the maximum length of guard hairs for red tree voles and white-footed voles. He concluded that, “The most difficult genera to distinguish from one another, due to overlapping measurements in length, width, and medullary width, are the Phenacomys [= Arborimus], Clethrionomys [= Myodes], and Microtus.”


Mazurek and Zielinski reported that they detected a Sonoma tree vole at a remote camera station in Mendocino County, California, in 2002. A Trailmaster TM550 infrared Trail Monitor 35mm camera located at the base of a tree was triggered by motion and heat sensors.


This was the published version of their final report. They set cameras at the base of paired legacy trees and nearby control trees in young forest. They detected an adult Sonoma tree vole at one of the legacy trees.


The authors used pitfall traps to sample small mammals in three stands of 40- to 50-year-old red alder with scattered residual Douglas-fir and western redcedar (Thuja plicata) in Benton, Lincoln, and Coos Counties in Oregon. They did not give exact numbers but said that they captured <10 tree voles in 28,800 trap-nights. All tree voles were captured in upland stands of pole-size conifers.

In 1988, the authors used pitfall traps and snap-traps to sample six mature stands in Drift Creek, Lincoln County, Oregon. In 31,200 trap-nights, they captured 2,562 mammals and 288 amphibians. They captured two red tree voles (0.006 per 100 trap-nights) and 11 white footed voles (0.035 per 100 trap-nights). Of the white-footed voles, 10 were captured along streams and 1 was captured in upslope habitat.


McLellan reported collecting several tree vole specimens and their nests from “cat spruce” that were growing along rivers in tidal marsh near Gardiner, Douglas County, Oregon, in 1894. The specimens were captured in traps that were set on limbs beside nests. We do not think these were tree voles for two reasons. First, McLellan says that the nests were constructed mostly of moss and marsh grass, and second, we did not find any tree vole specimens listed in McLellan’s collecting catalog.


McNab hypothesized that tree vole energetics may differ from other voles because tree voles have small litters, slow development of young, and a long gestation period.


McNab examined body temperature and basal metabolic rates in 24 species of arvicolid rodents, including six Sonoma tree voles. The tree voles eventually died because he could not obtain adequate food for them in Florida. He concluded that there was “...little variation in the precision or level at which body temperature of arvicolid rodents is regulated.” Body temperatures for most arvicolids ranged between 37.4 and 38.3 °C, and
there was no evidence that any species ever went into torpor. He speculated that the high metabolic rate of arvicolids may allow them to breed throughout the year and produce large litters. He concluded that arvicolid rodents are “specialists in maximizing production, which permits them to live in generally harsh environments characterized by cool to cold temperatures.”


Meiselman located 79 tree vole nests in 9 stands near Branscomb, Mendocino County, California. The majority of nests (57 percent) were in mesic old-growth/mature stands. She found that nests tended to be located on the south side of the tree on south-facing slopes. She suggested that tree voles may select southern exposures to take advantage of solar warming in winter. She discussed the error in calling this species “colonial” in a concise and succinct manner. She stated that nests were significantly more abundant in old-growth stands than mature or young stands. She also suggested that tree vole nests were more difficult to detect in old-growth forests and that this could bias comparisons among forest age classes.


This is the published version of Meiselman’s thesis. She conducted surveys for tree vole nests in 100- by 1670-m strip transects in three forest age classes (<100 years, 100 to 200 years, >200 years) with three replicates in each category. Of 149 potential nests detected on transects, 79 (53 percent) were tree vole nests. Of the 79 tree vole nests, 39 (49 percent) were in >200-year-old stands, 22 (28 percent) were in 100- to 200-year-old stands, and 18 (23 percent) were in stands that were <100 years old.


Merriam described four new species, including *Phenacomys intermedius, P. celatus, P. latimanus,* and *P. ungava.* He noted that the molars of these voles were rooted, with two divergent roots. This was one year before True (1890) published the first description of *Phenacomys longicaudus.*

Merriam described the type specimen of the white-footed vole that was collected on 24 May 1899 by Walter Fisher near Arcata, Humboldt County, California. He compared it with the two red tree vole specimens collected by Aurelius Todd in Oregon. He said that the white-footed vole was very different when compared to the red tree vole. Specifically, the tail was more slender and scantily furred, the skull was narrower and longer, the zygomatic were narrower and less spreading, the braincase was narrower and longer, the rostrum and nasals were longer, the bullae were larger, and the fossa was longer and squared-off at the anterior end as opposed to rounded or angular.


The authors listed the red tree vole as a species that finds its optimal habitat in old-growth forests, but no data were presented.


Michel and Winter suggested that dense, misshapen branches of Douglas-fir provided good cover and support for tree vole nests.


Based on data obtained from Hamilton (1962), Millar concluded that juvenile red tree voles were 65 percent of adult size at weaning, which is relatively large for an arvicoline.


In appendix 1, Millar listed reproductive characteristics of tree voles, as follows: adult weight = 0.023 kg, birth weight = 0.0024 kg, gestation period = 27 days, fetal growth rate = 0.008/day, and litter size = 2.5. He cited his previous paper (Millar 1977) as the source for this information, although the data actually came from Hamilton (1962).

Miller found a tree vole skull in the stomach of a female northern spotted owl collected along the Eel River, 16.1 km north of Garberville, Mendocino County, California, on 26 May 1932. He suggested that spotted owls might be an important predator on tree voles, a fact that has since been documented in many different studies.


Miller said that he captured a white-footed vole on the bank of a stream on the Dollar Ranch on Maple Creek, 1.6 km north of the confluence with the Mad River, Humboldt County, California, on 9 September 1942. He and Ward Russell also visited the Wilder Ranch near Carlotta, Humboldt County, California. At the time of their visit on 17 September 1942, Harry Wilder had been dead for 7 years, but they talked with Mrs. Wilder and examined Wilder’s collection of ≥300 specimens. According to Miller, Mrs. Wilder expressed interested in giving the specimens to a museum. We located 52 Sonoma tree vole specimens that Wilder collected from 1913 to 1927 in the collections of 5 museums.


Miller revised the genera and subgenera of voles and lemmings based on morphological differences in the skull and teeth. He reported that Phenacomys voles differed from other voles in that the teeth were rooted and the reentrant angles on the lingual side of the tooth were much deeper than on the labial side. He noted no pronounced external differences between Phenacomys spp. and other voles, except that the tail of Phenacomys longicaudus was proportionally longer than in other species.


Miller presented a key to the species of Phenacomys and described the status, characteristics, and distribution of six forms of Phenacomys, including the tree vole. He stated that nothing in the external appearance distinguished Phenacomys from small species of Microtus except for the long tail and arboreal behavior of the tree vole. He described the type specimen of the tree vole and also mentioned an isabelline specimen that was collected on 13 April 1891 at Meadows, Lane County, Oregon. The latter specimen was pale yellowish drab on the head, back, and sides, with the venter grayish white. This specimen is at the U.S. National Museum (USNM030649).

Miller listed 11 species of *Phenacomys*, including the red tree vole and white-footed vole.


Miller listed 12 species of *Phenacomys*, including the red tree vole, white-footed vole, and dusky tree vole. He shortened the species name from *Phenacomys silvicolus* (Howell) to *P. silvicola*, but did not say why he made this change.


Miller and Kellogg listed the species of *Phenacomys* in North America, including the red tree vole, white-footed vole, and dusky tree vole.


Miller and Rehn listed nine forms of *Phenacomys* from North America, including the red tree vole and white-footed vole. They noted that two species of *Phenacomys* were added to the list since their 1901 paper.


Based on an analysis of mitochondrial control region sequences in red tree voles, the authors concluded that there were two haplotype groups corresponding to the northern and southern regions of the range. Spatial genetic analyses demonstrated a primary genetic discontinuity separating northern and southern sampling areas, while a secondary discontinuity separated northern sampling areas into eastern and western groups on opposite sides of the Willamette Valley.

The authors analyzed patterns of size-associated morphological variation of red tree voles. They concluded that there were subtle, but significant, morphological differences across the boundary that had been proposed to delimit the ranges of the dusky tree vole and red tree vole. However, the morphological characters examined had virtually no diagnostic utility for distinguishing between the two putative subspecies.


Miller and Haig found strong spatial genetic structure in red tree voles in Oregon, with genetic distances greater in the north. They suggested that habitat fragmentation during the last glacial maximum constrained dispersal, resulting in greater genetic diversity in the north than the glacial free south.


The authors briefly mentioned the red tree vole in their discussion of the Survey and Manage Program, which was adopted as part of the Northwest Forest Plan.


On pages 221–225, Murie summarized information about nests, feeding behavior, and distribution of red tree voles. He also told a story about climbing to what he thought was a hawk’s nest near Forest Grove, Washington County, Oregon, only to find that it was filled with shredded fir needles. He did not realize it was a tree vole nest until years later. He suggested that tree voles may consume young terminal needles without removing the resin ducts.


These notes described Murray’s field trips to collect tree voles used in the genetic analysis in his master’s thesis. He collected 12 Sonoma tree voles in Humboldt, Mendocino, and Sonoma Counties, California. He also collected nine red tree voles, including five in Del Norte County, California and four in Lincoln County, Oregon. The four tree voles in Oregon were collected
with the help of John Hayes at Oregon State University, at the same location where Hayes (1995) later captured two melanistic red tree voles.

Based on a comparison of restriction enzyme sites of mtDNA, Murray concluded that there were two main groups of tree voles in California, red tree voles north of the Klamath River and Sonoma tree voles south of the Klamath River.


In this critique of the survey and manage guidelines, Richard Nawa, staff ecologist for the Siskiyou Project, argued that line transect surveys were grossly inadequate for surveys of red tree voles because many nests went undetected.

318. **Nelson, D.W.; Thompson, D.R.; Paez, R.A. 2006.** Klamath Siskiyou Wildlands Center; Umpqua Watersheds; Cascadia Wildlands Project v. Lynda Boody, in her official capacity as Glendale Field Manager and Bureau of Land Management, an agency of the U.S. Department of the Interior; Katrina Symons, in her official capacity as Glendale Field Manager; William Haigh, in his official capacity as South River Field Office Manager on the Roseburg District, BLM; D.R. Johnson Lumber Company. No. 06-35214. D.C. No CV-03-03124-JPC opinion. U.S. Court of Appeals for the Ninth Circuit, San Francisco, CA.
In this ruling, the Ninth Circuit Court reversed an earlier district court judgment and placed an injunction on the Cowcatcher and Cottonsnake timber sales on the Roseburg and Medford Districts of the Bureau of Land Management. The court ruled that the U.S. Forest Service and Bureau of
Land Management violated federal law in downgrading the survey and manage classification for the red tree vole.


In this popular article, Nelson apparently got most of his information on tree voles from Walter Taylor and Harry Wilder. He described the “tree mouse” as the most aberrant member of the genus *Phenacomys*. He briefly described the range, habitat, nests, diet, nocturnal habits, and litter size of tree voles.


Nowak and Paradiso provided a brief summary of the taxonomy, habitat, nests, and life history of the red tree vole. Like others before them, they said that tree voles were slow and cautious climbers (but see Forsman et al. 2009). They repeated previous speculation that male tree voles lived primarily in burrows or debris piles, but presented no data to support this contention.


Nussbaum and Maser found remains of one *Arborimus* spp. among 227 prey items in 143 scats collected from bobcats (*Lynx rufus*) in the Oregon Coast Ranges from 1970 to 1972. They were unable to determine the species.


Olson and Burnett speculated that habitat contiguity may be essential for red tree voles.


In this review, the authors reported that strategic surveys of red tree voles were expensive and that protection of red tree voles made it difficult to conduct timber sales.

Olterman reviewed the literature and examined specimens deposited in museums and personal collections. He interviewed mammalogists, game biologists, naturalists, trappers, and outdoorsmen to ascertain current distribution and abundance of mammals. He classified the white-footed vole as rare based on the small number of specimens that he found in museums \((n = 46)\), but conceded that they could be more common than indicated by specimens. Olterman concluded that the red tree vole was neither rare nor endangered because he located 233 specimens, most of which were collected by Murray Johnson and Chris Maser.


Olterman and Verts presented a range map based exclusively on red tree vole museum specimens and concluded that the species occupied a large range in western Oregon. They did not consider tree voles rare or endangered. Based on the few specimens in museums, they concluded that white-footed voles were rare.


Olterman and Verts found 284 red tree vole specimens in various collections and provided a detailed list of where those specimens were housed. This list is now out of date because many specimens have been collected since it was published.


The Oregon Department of Fish and Wildlife listed the red tree vole as “vulnerable” in the Oregon Coast Ranges. They defined vulnerable as facing one or more threats to the population or habitat. Species on this list are not currently threatened with extirpation but could become so with continued or increased threats to their population or habitat.

The Oregon Board of Forestry directed the Oregon Department of Forestry to identify specific strategies to maintain, enhance, and restore fish and wildlife habitat for species of concern on the Clatsop and Tillamook State Forests, while at the same time meeting timber harvest targets. In response to this request, the Oregon Department of Forestry modeled forest trends on the state forests and concluded that the rarity of complex late-successional forest habitat was a limiting factor for red tree voles and that young forest was a barrier to dispersal of tree voles.


The Oregon Natural Heritage Information Center (ORNHIC) compared species status listings by different agencies in Oregon. The U.S. Fish and Wildlife Service listed the red tree vole, dusky tree vole, and white-footed vole as species of special concern. The Oregon Department of Fish and Wildlife listed the white-footed vole as a sensitive species. The ORNHIC listed the dusky tree vole as threatened throughout its range and the white-footed vole and red tree vole as species of conservation concern.


The authors used quantitative methods to classify vegetation types into habitats for 420 wildlife species, including the red tree vole.


Owings used laboratory experiments to compare predator avoidance behavior of red tree voles and gray-tailed voles (*Microtus canicaudus*). His predator avoidance hypothesis was that arboreal rodents would rely on quickness and agility to escape while terrestrial rodents would freeze unless attacked. He also hypothesized that terrestrial rodents would become more aggressive when attacked. He found no difference in freezing behavior. Gray-tailed voles were more aggressive toward attackers than tree voles.

In their habitat conservation plan, the Pacific Lumber Company (currently the Humboldt Redwood Company) proposed to provide habitat for tree voles on their lands by managing at least 10 percent of each watershed as late-seral forest.


This strategic survey on the Salem District of the Bureau of Land Management was completed, but we are unaware of any report that followed. Contractors conducted targeted surveys for red tree vole nests to add information on distribution and abundance. Bureau of Land Management staff selected survey sites, but methods were not described in the proposal.


This leaflet included information on capture methods, distribution, and behavior of Sonoma tree voles.


In these field notes, Pearson said that he talked with a “tough hombre” who recognized tree vole nests around his place near Coyote Peak, west of the Hoopa Valley Indian Reservation, Humboldt County, California. In our tree vole specimen database, there are two Sonoma tree voles that were collected by Pearson. One was at French Camp on 23 August 1949 near Coyote Peak, Humboldt County, California. The other was 11.3 km north of Fort Ross, Sonoma County, California, on 20 May 1949.

In her summary judgment, Judge Pechman ruled that the U.S. Forest Service and Bureau of Land Management failed to comply with the National Environmental Policy Act in preparing their 2004 final environmental impact statement to remove or modify the Northwest Forest Plan’s survey and manage measure. Pechman also ruled that the federal agencies failed to analyze the impacts of moving survey and manage species (including the red tree vole) to the sensitive species status program. She also ruled that the agencies failed to thoroughly analyze their assumption that late-successional reserves would protect survey and manage species.


In this ruling, Judge Pechman set aside the 2004 Record of Decision to eliminate the survey and manage measure from the Northwest Forest Plan. She ordered the U.S. Forest Service and Bureau of Land Management to reinstate the 2001 Record of Decision for the amendment to the survey and measure guidelines.


In this court order, Judge Pechman ruled that federal timber sales or habitat disturbing activities that were proposed in the 2004 Record of Decision could only go forward if they were in compliance with the 2001 Record of Decision. This decision meant that federal agencies had to continue to survey for and manage red tree voles in old forests. However, Judge Pechman allowed several exemptions to this decision, one of which was that thinning projects in forests <80 years old could be conducted without surveying and managing for tree voles. This exemption had large implications for the conservation of red tree voles because it meant that federal agencies no longer had to survey or manage for red tree voles in forests that were <80 years old.

In this court order, Judge Pechman denied a motion in which the U.S. Forest Service and Bureau of Land Management had requested relief from the injunction placed on their 2007 Record of Decision (ROD) to remove the survey and manage measures. Pechman concluded that the federal agencies failed to establish that the 2001 ROD for the amendment to the survey and manage standards and guidelines was unworkable, and that they failed to show they entered into the 2006 stipulation in good faith or made a reasonable effort to comply with it before modifying the document. She also ruled that the federal agencies failed to show that the 2007 ROD complied with all appropriate law. The final argument for relief was also denied as the court ruled that it did not matter how much money or time the agencies spent preparing the 2007 document.


In this cross-motion, the Bureau of Land Management requested a summary judgment to allow the Rickard Creek timber sale to proceed. They argued that the administrative record indicated that the timber sale area was not a high-priority site for tree voles.


Phillips and Chrostowski summarized the status, distribution, habitat, reproduction, behavior, home range, food habits, and management recommendations for red tree voles and white-footed voles. They stated that tree voles require fog condensation on canopy needles as a water source and that male tree voles nest primarily, if not exclusively, on the ground.


On page 320, Pratt briefly described tree voles and white-footed voles.

Price and Landon found two adult clouded salamanders 75 m up in a cavity in the top of a Douglas-fir that was 78 m tall. The cavity also contained copious amounts of red tree vole fecal pellets. The location was in western Douglas County, adjacent to the tallest Douglas-fir in Oregon, the 99-m Brummit Fir (since renamed “Doerner Fir”).


In this excellent literature review, the authors described the distribution, morphology, genetics, physiology, reproduction, development, ecology, feeding habits, behavior, mortality, aging, economic status, and management and conservation of *Microtus*. They only mentioned the red tree vole once when they reported the negative effects of hybridization between sibling species of *Arborimus*. We assume that they were referring to Murray Johnson’s hybrids between *A. pomo* and *A. longicaudus*. Johnson and George (1991: 4) stated that hybrid crosses had a much higher rate of pregnancy-related deaths and suggested that this was indicative of a reproductive barrier between the two species.


Quay described two white-footed vole specimens collected by Harold Broadbooks on 17 June 1942, 1.6 km east of Newport, Lincoln County, Oregon. The skulls and skins of these specimens were originally misidentified as *Microtus* until Quay corrected this misidentification at the University of Michigan Museum of Zoology.


Quay compared the number and size of the meibomian (tarsal) glands in the eyelids of voles and lemmings, including the red tree vole. He suggested that the reduction in gland number and increase in gland size in more advanced fossorial species may be the result of a reduction in eye size.

Quay described the morphology of the diastemal palate in many different voles, including red tree voles. The diastemal palate is the region of the skull between the incisors and molars.


Quay compared the sebaceous and sudoriferous glands of the mouth of many different mammals, including red tree voles. Regarding the significance of these differences he said that “Little if anything can be offered as definitive evidence of the functions or functional significance of the oral sebaceous or sudoriferous glands.”


Quay compared the development and location of sebaceous glands in many different voles, including red tree voles. He discussed taxonomic differences and possible functions of sebaceous glands in communication.


The authors used pitfall traps, live-traps, and snap-traps to sample 47 forest stands in southwestern Oregon and northwest California from 1984 through 1985. They captured 22 tree voles in 141,120 trap-nights (0.016 per 100 trap-nights). All tree voles were captured in pitfalls. The samples were apparently too small to test relationships between capture rates and forest age or structure. Near Cave Junction, Oregon, they captured five red tree voles in 43,200 trap-nights (0.012 per 100 trap-nights). Near Willow Creek, California, they captured nine Sonoma tree voles in 48,960 trap-nights (0.018 per 100 trap-nights). Near Branscomb, California, they captured eight Sonoma tree voles in 48,960 trap-nights (0.016 per 100 trap-nights). The authors did not mention age or sex ratios of tree voles captured in pitfalls, but we examined 13 of their museum specimens and found that they were all males (5 adults, 7 subadults).
Annotated Bibliography of the Red Tree Vole (*Arborimus longicaudus*), Sonoma Tree Vole (*A. Pomo*)...


In his specimen catalog for 1981–1983, Raphael listed 13 Sonoma tree voles (4 males, 9 females) captured in pitfall traps in Humboldt County and western Trinity County, California. We found 11 of these specimens at the Museum of Vertebrate Zoology.


From 1981 through 1983, Raphael used pitfall traps with drift fences to sample small mammals and amphibians in six seral stages of forest within 80 km of Willow Creek, Humboldt County, California. He captured 19 Sonoma tree voles in 899,431 trap-nights (0.002 tree voles per 100 trap-nights). Relative abundance of tree voles did not differ among forest age classes, but the power to detect differences among age classes was low because of the small number of voles captured.


Raphael’s essay included the red tree vole as an ancient forest species. He said that the tree vole was highly specialized because it was the only arboreal mammal in North America that fed exclusively on conifer needles.


Rausch and Johnson reported that the cecal villi of the heather vole closely resembled the cecal villi of the red tree vole and differed only slightly from the cecal villi of the white-footed vole.


In this 15 January 1985 letter to Murray Johnson, Repenning said that he did not agree with Johnson that the red tree vole should be in the genus...
Arborimus instead of Phenacomys. Repenning’s opinion was based on his interpretation of paleontological data.


Repenning suggested that microtines evolved so rapidly that they could be correlated to specific climatic events in North America. He noted that current Phenacomys voles were limited to subarctic and temperate forests, and suggested that Phenacomys voles evolved in Beringia from a Eurasian ancestor.


The authors discussed a recently discovered fossil of Phenacomys intermedius from the late Pliocene (2.5 million years ago) that was discovered in northern Alaska. The oldest P. intermedius fossil in the conterminous United States was 0.8 million years old and confined more or less to Beringia. They cited a personal communication from Walter Dalquest who suggested that some P. intermedius were 1.6 million years old based on unpublished data. They described the rooted hypsodont teeth of Phenacomys. Though they used Phenacomys instead of Arborimus for the red tree and white-footed vole, they said that they did so without opinion. They said that there were two pre-Pleistocene Phenacomys (P. deeringensis), one from Alaska and one from Siberia. The Alaskan P. deeringensis was more primitive and had very low dentine tracts compared to P. deeringensis from Siberia. The first lower molar of the extinct P. deeringensis was essentially identical to living P. intermedius. Repenning also named P. gryci located from the northern Alaskan site.


Repenning and Grady named Paraphenacomys as a new subgenus that they said was closely related to Phenacomys and the Arborimus subgenus. They included P. deeringensis and P. intermedius (living) in the new subgenus while noting three unnamed species. In the subgenus Paraphenacomys, Repenning and Grady included P. albibipes, P. brachyodus, and P. gryci. They said that the only known white-footed vole fossil was an uncataloged
first lower molar at the University of Arizona from the 13,000-year-old Smith Creek Cave fauna, White Pine, Nevada. *P. brachyodus* was a new species from the Cheetah Room, West Virginia. Unfortunately, the Repenning (in press) paper that was cited several times by the authors was never published because it was one of the chapters in the unfinished tree vole book that Murray Johnson was working on when he died.


Reynolds collected 104 regurgitated pellets from a pair of nesting long-eared owls (*Asio otus*) 16.1 km north of Corvallis, Benton County, Oregon. The pellets contained 153 prey items, one of which was a red tree vole.

360. **Richards, R.L. 1986.** Late Pleistocene remains of boreal voles (Genera *Phenacomys* and *Clethrionomys* [= *Myodes]*) from southern Indiana Caves. *Proceedings of Indiana Academy of Science.* 95: 537–546.

Richards suggested that the presence of heather vole fossils indicated that southern Indiana was once covered by boreal forests. There was nothing specific about tree voles in this paper, but it is pertinent to the evolutionary history of the genus *Phenacomys*.


In western hemlock, needles in the upper outer crown were thicker and had more vascular tissue than needles in the lower inner crown. The authors did not report whether resin ducts also varied in size depending on position within the crown. There was nothing specific about tree voles in this paper, but within-species or within-tree variation in needle structure may play an important role in habitat selection and foraging behavior of tree voles.


This study plan described the methods used to collect data on density of red tree vole nests in a stratified random sample of plots in western Oregon...
and northwestern California (Dunk and Hawley 2009). The primary goal was to compare the relative abundance of red tree vole nest trees in different forest age classes and land use categories on federal lands within the range of the species. The original plan was to survey a square 1-ha plot at each of 400 randomly selected Current Vegetation Survey/Forest Inventory Assessment plots. However, an additional 1-ha plot was added at each location after the start of the survey to increase the probability of detecting nests. The second plot was installed on the north side of the first plot. Within each plot, contractors visually searched for nests in trees while walking along linear transects that were spaced 25 m apart. Potential nests seen from the ground were climbed to determine if they were vole nests and to estimate their occupancy status. In plots where no tree vole nests were detected during ground surveys or where the forest canopy was so complex that nests were hard to detect, contract climbers climbed five randomly selected large trees (>61 cm diameter at breast height) to see if they could find nests. When they analyzed the data from this study, Dunk and Hawley (2009) only used data from the original sample of 1-ha plots because they were concerned that the second plot at each location was not selected randomly and might be in a different cover type or land use allocation than the first plot.


This phylogenetic analysis indicated that Dicrostonyx, Phenacomys, and Arborimus formed a monophyletic clade. The authors proposed this clade be given a new tribal classification name, Dicrostonychini Kretzoi 1955.


Roest described a juvenile red tree vole that was collected in the “guide shack” at Oregon Caves National Monument in August 1948. This specimen is in the Oregon State University Fisheries and Wildlife collection (OSUFW844). Roest did not say how the vole was captured.


In this published version of his 1949 thesis, Roest said that the juvenile red tree vole that was captured in the guide shack at Oregon Caves National Monument was killed, but he did not say how.

The authors analyzed prey remains in regurgitated pellets of northern spotted owls on the Blue River and McKenzie Ranger Districts on the west slope of the Cascade Range, Lane County, Oregon. Pellets were collected from 1987 through 1996. The mean number of spotted owl territories where pellets were collected per year was 16.6 (range = 4 to 17). The mean ± SE percentage of tree voles in the diet was 6.7 ± 1.2 percent based on prey numbers, and 3.7 ± 0.8 percent based on prey biomass. The authors also used Sherman live-traps to sample small mammals from 1988 through 1996. They did not report the total number of trap-nights but did report using 100 Sherman live-traps each year for 8 consecutive days. They captured 1,501 deer mice and 303 red-backed voles but did not report capturing any other small mammals.


The authors listed the red tree vole as a species of special interest or concern to forest managers because the species was difficult to study and the patterns of abundance or occurrence were poorly understood.


In 1942, Russell collected eight Sonoma tree voles by placing snap-traps baited with walnuts on top of tree vole nests at Maple Creek east of Arcata, Humboldt County, California. He captured four adult females, two adult males, and two subadult males. He also collected a northern spotted owl at the same location. The owl had four tree vole skulls in its ventriculus. Russell also collected two additional Sonoma tree voles in 1968 near Kneeland, Humboldt County, California.


The authors reported that they found fossil remains of *Phenacomys/ Arborimus* in cave sediments at Oregon Caves National Monument.


Semken and Wallace described qualitative and quantitative methods used to identify arvicoline molars from archaeological and paleontological sites. They included the heather vole in their key but not tree voles or white-footed voles. They cited Guilday and Parmalee (1972) in support of the assertion that the four living *Phenacomys* vole species cannot be distinguished by dentition alone.


The authors cited Denison (1973), Zentner (1977), and Gillesberg and Carey (1991) as sources indicating that red tree voles used lichens as nest material and possibly as food.


Alfred Shelton and Charles Camp collected a Sonoma tree vole at the Lierly Ranch in 1913. This photo provides some context, but it is unclear if the area in the photo was near where the vole was collected or not.


In his field notes for the North Coast Counties Expedition of 1913, Shelton concentrated on birds while fellow expedition member Charles Camp (1913) dealt with mammals. However, Shelton listed two Sonoma tree vole specimens in his field notes, a subadult male collected at Mendocino City, and an adult female collected at the Lierly Ranch 12.9 km north of Hearst, Mendocino County, California.

Shelton’s field notes included several references to red tree voles. In February 1914, he and John Bovard captured three large juveniles 33 m up in a “tall fir” at Spencer Butte, south of Eugene, Lane County, Oregon. In June 1914, he described a specimen that Vernon Bailey chased out of a nest and shot off a limb while tree climbing on Spencer Butte (see Bailey 1914, 1915; Jobanek 1988). In October 1914, he described a tree vole that eluded capture in a grove of large Douglas-fir on the Curry Estate where the North and South Forks of the Umpqua River join west of Roseburg, Douglas County, Oregon. He also says that he found a cluster of tree vole nests near the community of Mable in the Mohawk Valley, Lane County, Oregon.


While conducting field work for his thesis in 1968, Sherrell captured a male white-footed vole at Brush Creek, 1.6 km from the ocean and 12.1 km south of Port Orford, Curry County, Oregon. He caught the vole in a museum special trap that was placed under a thicket of salmonberry in the floodplain of Brush Creek.


Sherrell captured an adult male white-footed vole in a museum special trap at Brush Creek (Sherrell 1969). This was only the second white-footed vole documented in Curry County. Sherrell did not capture any tree voles, but he did review the literature and corresponded with Murray Johnson and others to come up with locations for 19 tree voles in Curry County, most of which were collected by or given to Stanley Jewett.


Silovsky and Pinto listed the red tree vole as having a moderate dependence on snags in their table on the native wildlife of the Siuslaw National Forest. They suggested that tree voles would be adversely affected by forest management methods that were prevalent in 1974 (clearcut and burn).

Simberloff and Cox cited Soulé and Simberloff (1986) to support the hypothesis that red tree voles would avoid riparian corridors between stands of mature Douglas-fir. They provided no evidence that this was actually the case.


The authors found remains of four Sonoma tree voles in 140 scats collected from fisher on the Hoopa Valley Reservation, Humboldt County, California, from 2004 through 2008.


The authors reviewed the literature on taxonomy, distribution, feeding habits, water consumption, reproduction, predators, nests, and habitat of red tree voles and Sonoma tree voles. They found no published data on movements, estimates of home range size, longevity, or survival of tree voles. They also found no published documentation of ecological differences between red tree voles and Sonoma tree voles, and discussed general ecological characteristics that they assumed to be common to both species.


Smoluk analyzed the geographic distribution of prey items identified in northern spotted owl pellets on the H.J. Andrews Experimental Forest in Lane County, Oregon, 1988–2009. Of 4,183 prey items identified in pellets, 272 (6.5 percent) were red tree voles. Based on their abundance in owl diets, Smoluk concluded that tree voles were more abundant at low elevations and in steep canyons. She reported that red tree voles were rare in pellets collected at owl territories above 1000 m elevation.

The authors reported that potential red tree vole habitat was rare in the Trask River watershed, except for a few stands of old-growth in the Upper Trask River. They stated that red tree voles required large blocks of contiguous habitat or connecting corridors of suitable habitat. This may be true, but they did not cite any papers or present any data to support this statement. They do cite Carey (1991) to support their claim that stands <100 years old cannot support viable populations of tree voles, but they do not acknowledge that Carey never actually monitored vital rates or population trends of tree vole populations.


In this addendum to tree vole survey data that were sent to the Medford District of the Bureau of Land Management by the Northwest Ecosystem Survey Team, Sobb emphasized that many red tree vole nests were not detected during ground-based surveys.


In this guidebook to mammals of Oregon State University’s McDonald Forest, Sondenaa considered the white-footed vole as rare and limited primarily to riparian areas. She stated that red tree voles occurred primarily in Douglas-fir forests and built their nests of twigs and discarded resin ducts on dense branches.


The authors suggested that tree voles would not use riparian corridors between patches of mature Douglas-fir forest. They did not explain why they thought this to be the case.
Spade took these pictures of a Sonoma tree vole nest at Ten Mile River north of Fort Bragg, Mendocino County, California in 2012. The forest consisted of Douglas-fir and redwood. The pictures included a picture of the nest in the tree as well as pictures of nest materials on the ground under the nest.

This paper was mainly about arboreal behavior of wandering salamanders (*Aneides vagrans*), but the authors also reported that they found clouded salamanders (*A. ferreus*) in three nests that were built by western gray squirrels (*Sciurus griseus*) in the Coast Ranges of Oregon. This report was confusing because the authors said that they were studying red tree voles and that the salamanders were found in nests that contained fecal pellets of rodents that had recently left the nests. This left us unsure whether the nests occupied by the clouded salamanders were squirrel nests or vole nests. The authors also incorrectly listed the species name of the red tree vole as *Arborimus pomo*.

The authors modeled consequences of forest management policies on biological diversity, carbon, and timber production in the Coast Ranges of western Oregon. Their habitat model was based on tree diameter, percentage of Douglas-fir, canopy closure, and canopy heterogeneity.
They concluded that under current management policy, there would be an increase in areas dominated by old forest and that red tree vole habitat would increase by 25 percent. If thinning of plantations on federal lands ceased, their model predicted it would have little effect on the amount of red tree vole habitat.


The authors modeled potential biodiversity in the Oregon Coast Ranges province under the current federal policy (Northwest Forest Plan) and two alternative strategies. The red tree vole was one of their focal species. Variables used for modeling suitable habitat for tree voles were percentage of Douglas-fir basal area, quadratic mean diameter, percentage canopy cover, and canopy heterogeneity. They included an appendix that explained the assumptions made in building a habitat capability index for the red tree vole.


The nest material in this picture contained Bishop pine (Pinus muricata) resin ducts from the nest of a Sonoma tree vole. This was a different record than the cases reported by Wooster and Town (2002).


Stein argued that the primitive digit feature that Kesner (1978) suggested was a derived and primitive characteristic may just be variation. Stein found the same finger feature in 2 of 12 Clethrionomys [= Myodes] she examined.


On page 123, Stephens described the “redwood lemming mouse,” which was another name used for the recently described white-footed vole.

In his field notes, Stone said that nests of tree voles were common at the headwaters of Ryan Creek, 9.7 km north of Willits, Mendocino County, California. However, all of the nests he examined were deserted, and he speculated that this was due to fragmentation of the stand from logging. He did not say how he determined that the nests were tree vole nests.


On page 578, Stone explained how the Academy of Natural Sciences of Philadelphia (currently the Academy of Natural Sciences of Drexel University) obtained a tree vole specimen collected by A.S. Bunnell at the Lierly Ranch, near Mount Sanhedrin, Mendocino County, California. The adult female specimen (ANSP11625) was found dead on a road in 1899. Stone described the specimen and gave measurements. He noted that the teeth were heavily worn, indicating that the vole was very old.


Storer reported that fossil *Phenacomys* spp. were found at Cape Deceit, Alaska.


On 13 February 1944, Storer and Walter Dalquest collected an adult female tree vole and two fairly large juveniles from a nest 3.2 km north of Occidental, Sonoma County, California.


Strong discussed mammals of Labrador, including information from Native Americans. He wrote, “The picture of the red-backed mouse (*Clethrionomys*) was likewise identified as a-pu-wish-ish, and that of the rufous tree mouse (*Phenacomys*) as an-i-suk-i-sash…” Strong concluded that this was an erroneous identification because the red tree vole only occurs in the Pacific Northwest.

Sturges collected two white-footed voles in riparian habitat adjacent to a small stream at 305 m elevation at Connors Camp on Marys Peak.


Suzuki used pitfall traps and museum special snap-traps to sample small mammals in riparian habitats in Drift Creek, Lincoln County, Oregon. In 19,300 trap-nights, he captured 14 white-footed voles (0.07 captures per 100 trap-nights) and no red tree voles.


Suzuki used pitfall traps to sample thinned and unthinned stands. In his experimental study, he sampled four replicate plots of 35- to 45-year-old forest in the Tillamook Burn between Tillamook and Forest Grove. In addition, he sampled eight “observational” sites with paired plots (thinned vs. unthinned plots) at each site. The latter stands were the same age for each paired sample, with ages ranging from 52 to 100 years old. Observational plots were scattered over a large area from Tillamook County south to northern Coos County in the Coast Range. On the experimental sites, he captured 9,016 vertebrates in 75,600 trap-nights but did not capture a single red tree vole. He did report 0.05 white-footed vole captures per 100 trap-nights, which we back-calculated to equal 38 individuals. In 2 years of sampling at the observational sites, he accumulated 64,000 trap-nights and captured 5,094 vertebrates. He reported that he caught less than 30 red tree voles and white-footed voles, but he did not provide any information on the age of the stands in which they were captured or whether those stands were thinned or unthinned. In his dissertation, there were no tables showing the locations of the actual sample plots or the numbers of animals captured in each stand. We could not find any of his specimens in museums.


In this published version of Suzuki’s dissertation, the authors reported that they captured 38 white-footed voles on their experimental plots and five white-footed voles on their retrospective plots (the latter plots were called
“observational plots” in the dissertation). They caught no tree voles in the experimental plots but did report capturing nine tree voles in the retrospective plots. They did not describe forest stands in which they captured tree voles.


Swingle radio-collared 61 red tree voles at 2 study areas in Douglas County, Oregon. He reported home range size, number of nests used, activity patterns, estimated survival, nest attributes, and nest detectability from ground-based observers. He also reported on sexual differences in body mass and movements, nest fidelity, nest size, subadult dispersal, predators, reproduction, and terrestrial activity. Of 61 voles collared, 6 were melanistic.


In western Oregon, data from 61 radio-collared red tree voles were used to estimate home range areas, behavior and survival rates. Predators of the radio-collared tree voles were weasels, owls, and a gopher snake (Pituophis catenifer).


The authors estimated home range size of radio-collared red tree voles. Estimates of home ranges ranged from one tree to 10,672 m².


The authors analyzed the movements of 15 male and 30 female red tree voles. Tree voles were primarily active at night. One of the individuals tracked, 17 used multiple nests (range = 7), and 18 occupied just single nest. Estimated mean home range size was 1,732 m² (median = 760 m²). Home range size did not differ between males and females except in late
winter and spring when home ranges of males were larger than those of females. There was no evidence of ground nesting by any of the voles.


The authors estimated that the annual survival rate of 50 radio-collared red tree voles was 0.15. There were no strong effects of sex, vole age, or forest age, and little effect of mass at initial capture on survival. Of 25 mortalities attributed to predators, 15 were attributed to weasels (*Mustela* spp.). The majority (93 percent) of tree voles killed by weasels were females. Other predators included owls, a gopher snake, and a domestic dog (*Canis familiaris*).


The authors placed 8- by 8- by 25-cm Havahart double-door live-traps on limbs next to 19 red tree vole nests. Based on observation of fresh tree vole nest material, all of the nests were either occupied or recently occupied. Traps were “baited” with fresh resin ducts collected from nearby tree vole nests, and pieces of apple were wired inside most of the traps (130 of 184 trap-nights). Three red tree voles were captured in 184 trap-nights (1.6 tree voles per 100 trap-nights). The number of tree voles captured per 100 trap-nights was much higher than from published studies using pitfall traps and live-traps placed on the ground. In addition to the voles captured in live-traps, the authors captured two adult tree voles when nests were probed with a thin metal rod when the traps were removed. Although voles were captured in live-traps, the method was labor-intensive because trees had to be climbed frequently to check sprung traps.


These notes described Walter Taylor’s activities while he was a member of the 1913 North Coast Counties Expedition, sponsored by the University of California, Berkeley, Museum of Vertebrate Zoology. Taylor said they found no sign of tree voles at the start of the expedition, but then Gordon Ferris talked to some boys at Mendocino City who told him they knew how to catch tree voles. The boys then led Taylor and Ferris out into the woods and showed them how to climb trees and catch tree voles. This experience
provided background material for several subsequent papers published by Taylor (1915a, 1915b, 1961).


Taylor pointed out that six of eight adult tree voles collected during the 1913 North Coast Counties Expedition were females. In addition, they captured “…8 young males and 14 young females.” We assume he meant juveniles captured in their maternal nests. Based on the small number of adult males captured, he suggested that the mice were either polygamous or that females were easier to catch because they were less inclined to flee the nest when nests were torn apart. An alternative, and we think more likely, explanation is that females are easier to find because their nests are bigger and more conspicuous than male nests. Still another hypothesis is that male tree voles are harder to find because they nest on the ground; there is little evidence to support this hypothesis and much evidence to the contrary.


In this seminal paper, Taylor provided a wealth of information on the life history and behavior of tree voles. This information was gleaned from his own field work during the 1913 North Coast Counties Expedition, as well as conversations with other tree vole experts such as Harry Wilder and Aurelius Todd. Taylor thought tree voles were fairly abundant and widely distributed and that the lack of abundance in museum collections was due to the lack of knowledge about their habitat. He stated that all of the tree vole nests located near Mendocino City were in grand fir and that those tree voles were feeding on grand fir. He said that nests had also been found in Douglas-fir and Sitka spruce. He noted a Bishop pine cutting in a tree vole nest in a grand fir but did not speculate that tree voles were feeding on Bishop pine. He discussed colonial relationships, clustering of nests, locomotion, climbing behavior, docile behavior, home range, hibernation, nest height, nest construction, male and female nests, and much more. He said that tree voles do not have any extraordinary agility or quickness, and though they are not slow, they are a little clumsy. He pointed out that it is the midrib that is eaten from Douglas-fir and grand fir needles, and that some previous observers had obviously mistaken the uneaten resin ducts
for the midrib. He said that tree voles were primarily arboreal, perhaps exclusively so. He did note that Harry Wilder thought that tree voles must come to the ground occasionally because some trees with nests did not have intertwining branches with other trees.

Taylor said tree voles were relatively docile when handled, but that a few had bitten their captors hard enough to draw blood. He said that green conifer cuttings were typically present in occupied nests and that tree voles occurred in the humid coastal zone of frequent fog and moderately heavy rainfall. In discussing home range, Taylor wrote, “It is not improbable that the tree mouse ranges freely through the foliage of several trees in the vicinity of his home nest tree.”

Taylor said that the majority of tree vole nests were located against or around the bole on branch whorls and that tree voles sometimes built their nests on top of abandoned nests of western gray squirrels. Net lichen (Ramalina reticulata) was found mixed with resin ducts in some nests. He said that green cuttings found on the ground were indicative of occupied nests [actually, we have found that green cuttings on the ground are often indicative of predated nests]. Regarding the composting action that takes place inside tree vole nests, Taylor wrote “Below the level of the used portion of the nest there was usually found a mass of decaying matter, sweating and steaming like a pile of old manure or like green feed in a silo.” Taylor thought that large nests were the result of years of occupancy by tree voles, and that the type of supporting foundation was the most important factor determining the form of the nest.

Taylor said that Aurelius Todd told him that nests were frequently changed or deserted, and that Harry Wilder reported that tree voles abandoned disturbed nests. Taylor suggested that small boys might be a major cause of abandonment of nests, but also acknowledged that some nests became uninhabitable when they were dislodged by storms. He did not seem to consider the obvious fact that voles are short-lived animals that usually die from predation, and that this is the primary cause of nest abandonment.

Regarding reproduction, Taylor said that young may be born any time of the year but that most reproduction occurred in late winter, spring, and summer. He said that nests were typically occupied by a single adult female and her young or by solitary adult males and females. Taylor reported that female maternal nests were much larger than male nests and that male nests were higher in trees and thus harder to detect. He also
reported that large maternal nests were more likely to be climbed to and dissected. He cited one instance in which two adult males were collected from the same tree but did not say if they came from the same nest.


Taylor discussed his relationship with Joseph Grinnell and described his first introduction to the tree vole by small boys in northwestern California. He finished with a succinct summary of his previous papers on tree voles (Taylor 1915a, 1915b).


From 1952 through 1954, Tevis sampled small mammals using snap-traps near Sayler, Humboldt and Trinity Counties, California. He captured 1,033 small mammals but did not capture any tree voles or white-footed voles. We cite this paper because it is just one more piece of evidence that terrestrial snap-traps are ineffective for sampling tree voles and white-footed voles.


The Interagency Scientific Committee reviewed the literature and concluded that tree voles were positively associated with stand age based on pitfall-trapping data and may reach highest densities in old-growth forests. They conceded that the data were too limited to suggest trends in abundance based on geography or elevation. In table J1, they erred by including the tree vole as a prey of spotted owls in Washington, where tree voles do not occur.


The Scientific Analysis Team included the red tree vole in the list of species that they evaluated. They assessed species viability under five alternative planning scenarios and discussed mitigation options to ensure species viability.


The Forest Ecosystem Management Assessment Team used an expert panel process to estimate the outcomes of various management options on tree voles (pages IV-171–174). They concluded that, “...habitat for red tree voles will be sufficient and well distributed under Options 1, 3, 4, and 5, but lower under options 7, 8, and 9.” On page IV-176, they say that “Little is known about the red tree vole. Studies are needed to better understand its basic ecology, including its habitat associations and dispersal capabilities. Further genetic research is needed to determine whether Phenacomys pomo and P. longicaudus are distinct species.” In Appendix Table IV-C-1, they estimated the area of the range of the red tree vole in Oregon and California and estimated how much of the range was in areas protected from harvest.


The authors listed the red tree vole as a species that uses old-growth forest disproportionately to its occurrence.


Thompson and Diller used line transects to estimate density of Sonoma tree vole nests in six stand-age classes (10 to 19, 20 to 29, 30 to 39, 40 to 49, 50 to 59, ≥60 years). The density of occupied or recently occupied nests increased with increasing stand age. Median persistence time of nests was 28.6 months (95 percent CI = 25.8 to 34.8 months). They found a few nests in stands as young as 10 to 16 years old, but suggested that tree voles
usually do not start to occupy young stands until trees are about 20 years old. The authors located one terrestrial nest in a 38-year-old stand below a small Douglas-fir.


In this paper, Aurelius Todd described the events surrounding his discovery of the type specimen of *Phenacomys longicaudus*, which was collected by L.J. Cornelius near Coos Bay, Oregon, in 1890 (USNM 19071/25883). Todd said that the type specimen was not the first tree vole he had seen. He captured another tree vole in the headwaters of Elk Creek, about 7 miles east of Yoncalla, Douglas County, Oregon, in 1886, but the specimen was lost in transit on its way to the National Museum.

Todd suggested that tree voles were almost exclusively arboreal. He said that, “The nest is a novelty in itself, being about the size of a robin’s nest, and built after the usual manner of mice in shape, but almost exclusively of the leaves of the tree in which it lives, which are split into threads from end to end, forming very slender filaments, seldom broken, and each leaf is frequently split twice or more, making from two to four threads of each leaf. These threads are soft, dry and apparently warm, and they show much ingenuity in the general make-up of the whole nest. Rarely has a few unsplit leaves, moss and twigs on the outside of the nest been found.” The split leaves that Todd referred to were obviously discarded resin ducts from the needles of Douglas-fir.


Toweill found remains of white-footed voles in 2 of 484 bobcat (*Felis* [= *Lynx*] *rufus*) scats and 3 of 844 coyote (*Canis latrans*) scats in the Cascade Range of Oregon. He also found remains of heather voles in three coyote scats. He did not say how he was able to distinguish remains of white-footed voles from red tree voles.


True described the type specimen of *Phenacomys longicaudus*, which was collected by L.J. Cornelius near Coos Bay, Oregon, and sent to the U.S. National Museum by Aurelius Todd. The specimen (USNM 19071/25883) included a dried skin and crushed skull. True described the bright rusty
brown color of the vole and said that the molars were rooted and resembled those of the heather vole. He referred to the new species as a “mouse” but did not give it a common name.

421. **U.S. Department of Agriculture, Forest Service. 1996.** Survey and manage inventory report: Mount Hood National Forest 1995. Sandy, OR. 105 p. This report described the results of red tree vole surveys on the Mount Hood National Forest from 1995 through 1996. In 1995, surveyors located eight trees with tree vole nests in the Bull Run watershed and one nest in the South Fork of Eagle Creek. Not all trees were climbed so it is not clear how the observers confirmed the species that built the nests. In 1996, three red tree vole nests were confirmed by tree climbers in Eagle Creek, and 22 more were classified as potential red tree vole nests that were not climbed.

422. **U.S. Department of Agriculture, Forest Service. 2007.** Notice of availability (NOA) Record of Decision (ROD) for the final supplement to the 2004 supplemental environmental impact statement to remove or modify the survey and manage mitigation measure standards and guidelines. Federal Register. 72: 41288–41289.

In this announcement in the Federal Register, the U.S. Forest Service said that the Northwest Forest Plan had made it difficult for the Forest Service and Bureau of Land Management to meet goals for timber harvest, hazardous fuels treatment, and ecosystem restoration. They proposed to solve this problem by removing the tree vole from the “survey and manage” requirements in the Northwest Forest Plan. As an alternative, they proposed to change the tree vole to a “special status species,” which does not require specific surveys or protections except in limited areas.

423. **U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management. 1994a.** Final supplemental impact statement on management of habitat for late-successional old-growth forest related species within the range of the northern spotted owl, Volume 1. Portland, OR. [Irregular pagination]. The agencies concluded that the “Survey and Manage” standards and guidelines would help in providing a well-distributed population of red tree voles. In table 3 and 4-30 (page 3 and 4-184), they estimated the likelihood that tree voles would remain well-distributed within their historical range under each of the different land management alternatives in the draft supplemental environmental impact statement. Under alternative 9 (the selected alternative), the red tree vole was given a 73 percent likelihood
of remaining well distributed, a 25 percent likelihood of becoming locally restricted, a 2 percent likelihood of becoming restricted to refugia, and a 0 percent likelihood of extirpation. Under alternative 9, the Sonoma tree vole was given a 78 percent likelihood of remaining well distributed, a 23 percent likelihood of becoming locally restricted, and a 0 percent likelihood of becoming restricted to refugia or going extinct.


In table B11-1 (page B-160), the red tree vole was the only mammal included on the list of “survey and manage” species. It was designated as deserving surveys prior to ground-disturbing activities.


The Species Analysis Team reviewed the panel notes from Thomas et al. (1993) and did not find support for further mitigation to meet the screening criteria for the Sonoma tree vole under alternative 9. The red tree vole failed to pass the screens because of its association with old forest, limited dispersal capabilities, and general lack of data on distribution, habitat requirements and population status. But the main concern for the red tree vole was that forest fragmentation and spatial isolation of old forests would prevent gene flow and demographic movement between metapopulations. The Species Analysis Team concluded that past management had fragmented red tree vole habitat and that timber harvesting practices had reduced tree vole numbers. The team concluded that more information was needed on dispersal and abundance of tree voles, especially in young forests. They also discussed the need for connectivity of old forest in reserves to facilitate movement.

This record of decision was based on alternative 9 from the final environmental impact statement. The standards and guidelines established the Survey and Manage Program that required surveys for red tree voles prior to ground-disturbing activities and management of known sites.

427. U.S. Department of Agriculture, Forest Service; U.S. Department of the Interior, Bureau of Land Management. 1994e. Standards and guidelines for management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl: attachment A to the Record of Decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl. Portland, OR. [Irregular pagination].

The Forest Service and Bureau of Land Management concluded that they should conduct surveys to determine if red tree voles were present prior to conducting ground-disturbing activities. This decision added the tree vole to the so-called list of “survey and manage species.” The tree vole was the only mammal on the survey and manage list, which also included many plants, invertebrates, amphibians, and birds.


In this first attempt to develop a survey protocol for red tree voles on federal lands, the Tree Vole Working Group reviewed literature and unpublished reports to summarize what was known regarding the taxonomy, distribution, biology, and habitat of the red tree vole. They concluded that red tree vole habitat consisted primarily of moist Douglas-fir forests and that the network of old forest reserves established in the Northwest Forest Plan would support a well-distributed population of tree voles.

This supplemental environmental impact statement listed the life-history traits and habitat requirements that led to the listing of the red tree vole as a “survey and manage” species in the Northwest Forest Plan. It also defined the interim survey protocol for red tree vole nests and summarized surveys conducted to date. The anonymous authors reported that few or no tree voles were found in the north Cascades and northern Coast Ranges of Oregon. They cited pitfall trapping studies and one nest survey (Meiselman and George 1996) in support of the conclusion that tree voles were significantly more abundant in old forest than in young forests. They mentioned but did not specifically cite a distance sampling study (Biswell unpublished data) in the central Coast Ranges where tree vole nests were more abundant in old forest than young forest (0.83 vs. 0.18 nests per hectare). They also reported that surveyors found 0.07 tree vole nest trees per hectare in predisturbance surveys in northern Josephine County, Oregon.


This literature review included information on reproduction, ecology, nests, distribution, habitat, threats, information needs, and management recommendations of red tree voles. The anonymous authors used the term “active” to describe tree vole nests that were either occupied or recently occupied. The term “active” tree vole nest from different versions of the tree vole survey protocol (Biswell et al. [2000], 2002; Huff et al. 2012) was defined as nests containing green resin ducts, green fecal pellets, and/or green cuttings.

The agencies described and compared four management alternatives for “survey and manage” species, including the red tree vole. They concluded that all four alternatives would provide sufficient habitat but would differ in the degree of certainty regarding persistence of tree voles.


This document included background material for the analyses that were presented in the companion volume 1, including a long section that included responses to reviewer questions.


The agencies concluded that the red tree vole would have enough habitat to maintain stable populations under all of the proposed alternatives except for alternative 2.


This record of decision amended the “survey and manage” guidelines by increasing or decreasing levels of protection afforded different species. It included a recommendation that the agencies conduct strategic surveys of tree voles to learn more about their distribution and abundance. An annual species review process was established to evaluate new information on whether species should be added or removed from the list of survey and manage species.

In this 2003 draft supplement to the 2000 final supplemental environmental impact statement for the northern spotted owl, the agencies presented three alternatives that would either remove or modify the “survey and manage” standards and guidelines that were adopted as part of the Northwest Forest Plan. The stated reasons for doing the analysis were that (1) it was costing too much money and time to survey and protect species like tree voles, and (2) the survey and manage standards and guidelines were making it difficult to meet the resource management goals and objectives set forth in the Northwest Forest Plan. Of the three alternatives considered, the preferred alternative was to get rid of the survey and manage standards and guidelines. If adopted this would mean that the agencies would no longer be required to survey for tree voles in most areas proposed for harvest.


This report described the process that field units were supposed to use to evaluate whether a site could be classified as a “non-high-priority site” for surveys of tree voles in central Coast Ranges and central Cascades of Oregon. Determination of non-high-priority sites was to be conducted at two scales: the watershed scale and survey polygon scale. The four criteria for determining non-high-priority sites were (1) the percentage of federal lands within a watershed, (2) habitat quality, (3) survey effort, and (4) number of “active” tree vole nests located. For watersheds with high amounts of reserves and red tree vole habitat, these criteria could be used to programmatically release areas from “survey and manage” measures for the red tree vole.


In this followup to the 2003 draft supplemental environmental impact statement, the agencies announced that their preferred alternative was to remove the “survey and manage” standards and guidelines from the Northwest Forest Plan. Under this alternative the tree vole would be classified
as a Special Status Species on federal forest lands in the northern Coast Ranges. The stated reasons for retaining the tree vole as a Special Status Species in the northern Coast Ranges were low population numbers and lack of federal lands.


This document included background material for the analyses that were presented in Volume 1 of the 2004 final supplemental environmental impact statement (FSEIS). There is a large section in which the agencies responded to questions raised by reviewers during preparation of the FSEIS, including specific questions regarding tree voles on pages 243–246.


In this March 2004 Record of Decision the agencies announced their decision to remove the “survey and manage” mitigation measure from the Northwest Forest Plan. This decision would allow the agencies to conduct timber sales without protecting tree vole nest sites or conducting surveys to determine if tree voles were present.


This notice informed the public that the U.S. Forest Service and Bureau of Land Management had completed a final supplemental environmental impact statement in which they proposed to remove the “survey and manage” mitigation measure from the Northwest Forest Plan. Instead, they proposed to manage species like tree voles using, “…other elements of the Northwest Forest Plan and their existing Special Status Species Programs….”

In this notice, the U.S. Forest Service and Bureau of Land Management announced that they would prepare a supplemental environmental impact statement (SEIS) to respond to a court order in the case of Northwest Ecosystem Alliance v. Rey, dated August 1, 2005. In this case, Judge Pechman ruled that the 2004 SEIS was deficient for several reasons. In this notice, the agencies stated that they would address these deficiencies in a new SEIS.


This draft supplemental environmental impact statement (SEIS) was prepared in response to the August 1, 2005, court order in the case of Northwest Ecosystem Alliance v. Rey. It was not a stand-alone document. It specifically addressed deficiencies in the 2004 final environmental impact statement that were identified by the court. It included sentences or sections that replaced or expanded on sections in the 2004 final SEIS. The section on red tree voles (pages 87–92) briefly summarized new research. The agencies continued to argue that they could drop the “survey and manage” standards and guidelines, but they acknowledged that the proposed action might not provide for stable populations of some species within the area of the Northwest Forest Plan. In the case of the red tree vole (pages 87–92), they acknowledged that the preferred alternative would not provide enough habitat to support stable populations in some parts of the range of the species.

In this supplement to the supplement, the U.S. Forest Service and Bureau of Land Management added a no-action alternative that attempted to address the 2006 U.S. 9th Circuit Court ruling that they violated federal law in their attempt to remove or modify “survey and manage” mitigation for the red tree vole.


In yet another final supplemental environmental impact statement, the U.S. Forest Service and Bureau of Land Management stuck to their guns and selected a preferred option that removed the “survey and manage” mitigation measure from the Northwest Forest Plan. The expected effects of the various options on tree voles were discussed on pages 285–297.


In this annual report, the agencies reported that they found tree vole nests in 1,239 predisturbance surveys. They also announced plans to start a new survey in which a contractor would conduct tree vole surveys in 400 randomly selected plots starting in 2002.


Little new information on tree voles was presented in this report, but the authors did mention that a radio-tracking study of red tree voles was being conducted.


In this record of decision, the Under Secretary of Land and Minerals Management for the U.S. Department of the Interior (C. Stephen Alfred) announced his decision to remove the “survey and manage” mitigation
measure standards and guidelines as they applied to Bureau of Land Management lands in the Northwest Forest Plan. He specifically addressed the red tree vole on pages 22–23 where he said that the Bureau of Land Management would discontinue predisturbance surveys for tree voles in all areas.


The red tree vole and white-footed vole were listed as species of concern in Oregon. However, the U.S. Fish and Wildlife Service also concluded that more information was needed to determine the status of both species.


The U.S. Fish and Wildlife Service announced that they had received a petition requesting that they list the dusky tree vole as endangered or threatened. They concluded that the petition had merit and announced that they would start the evaluation process to determine if listing was warranted.


After 3 years of review, the U.S. Fish and Wildlife Service concluded that listing of the tree vole in the northern Coast Ranges of Oregon was warranted, but they declined to begin the listing process because other species had priority.


Verts compiled the maps for the mammal section in this atlas, including the red tree vole. These maps are now out of date.


This document included a morphological key and range maps for Oregon mammals, including the red tree vole and white-footed vole.
453. Verts, B.J.; Carraway, L.N. 1995. White-footed vole: *Phenacomys albi-
pes*. Mammalian Species. 494: 1–5.
This species account described the taxonomy, distribution, habitat, food, behavior, and reproduction of the white-footed vole.

In this incredibly detailed book, the authors provided a wealth of information on all land mammals in Oregon, including the red tree vole and white-footed vole. They presented data on morphological measurements, distribution, habitat, geographic variation, reproduction, ontogeny, mortality, behavior, and taxonomy. They limited their analyses of distribution primarily to data from museum specimens.

Voge listed a cestode parasite (*Andrya* spp.) collected from a Sonoma tree vole 0.8 km east of Stewarts Point, Sonoma County, California.

Voge and Bern found that the red tree vole, white-footed vole, and heather vole all had large numbers of hair-like villi in the cecum, whereas voles in the genus *Microtus*, *Clethrionomys [= Myodes]*, *Lagurus*, *Lemmus* and *Ondatra* did not have such villi. They suggested that these villi could slow the passage of food through the cecum, but did not say whether they thought these villi could increase the nutrient absorption of the organ. They suggested that the structure of the tree vole cecum might be an adaptation to the specialized diet.

Voge and Bern compared the cecal villi of the American pika (*Ochotona princeps*) and *Phenacomys* spp. The cecal villi of the pika were shorter, wider, and flatter. Unlike the red tree vole, the epithelium of the cecal villi in the pika did not show intense alkaline phosphatase activity, suggesting that villi in the cecum did not serve the same function in both species.

The authors examined the stomach contents and fecal pellets of 21 white-footed voles captured in snap-traps in riparian habitats in the Oregon Coast Ranges. Based on the percentage of occurrence, the diet consisted entirely of leaves from vascular plants, including 41 percent red alder, 9 percent red willow (*Salix lasiandra*), 15 percent shrubs, and 23 percent forbs. They found no seeds, fruits, fungi, or invertebrates in the diet. They concluded that the white-footed vole was a browser with a niche that extended from the ground into the forest canopy.


In his field notes for 8 to 10 July 1979, Vrieze described a field trip in which he, Brian McNab, and McNab’s two sons collected three adult Sonoma tree voles east of Arcata, Humboldt County, California. We think McNab (1992) may have used these tree voles in his analyses of energetics and then discarded the specimens, as we did not find the specimens in any museums.


Vrieze examined the horizontal and vertical distribution of tree vole nests in young forests (≤50 years old) east of Arcata, California. He found that the horizontal distribution of nests did not significantly deviate from random. On the vertical axis, tree voles appeared to build their nests near the lowest branches with green needles. He concluded that differences in nest height between study areas were due to differences in the heights of the lowest green branches in the various study areas. Vrieze climbed to all nests to document activity and species of cuttings on nests. He classified tree vole nests as “active” if they had fresh conifer cuttings, fecal pellets, and resin ducts, and he assumed that “active” nests were occupied by one or more tree vole. This was the first reference we are aware of that classified tree vole nests as “active” or “inactive.” Unfortunately, this has led to a great deal of confusion because all subsequent groups that have used the term “active” to refer to tree vole nests have used the term to include any nest with evidence of recent use, regardless of whether the nest is actually occupied. As a result, none of the surveys conducted using the “active” or “inactive” classification data can be used to estimate the actual density of tree voles.

462. **Walker, A. 1928.** Some Oregon *Phenacomys*. Journal of Mammalogy. 4: 254–255. Walker said that the only prior collections of dusky tree voles were the type of specimen collected near Tillamook in 1916 and a female and four young collected near Corvallis by Wight (1925). He described an interesting case in which loggers near Tillamook used dynamite to remove a hollow western hemlock snag, only to find four or five dazed tree voles staggering about in the hole left by the stump. Peter Walker captured one of the injured voles and gave it to his brother Alex. When Alex visited the site the next day, he found another mangled tree vole in the hole. He suspected that the voles had been nesting inside the base of the snag and were left in the hole when their nest was blasted apart. Fragments of a nest were found in the depression where the snag had stood. The site was on a hillside covered by a forest of large Douglas-fir and western hemlock. The trees in the immediate vicinity of the nest were exclusively hemlock and had just been felled and were still lying on the ground. The two voles that were collected were an adult male and female. This episode is puzzling because adult tree voles are rarely found together in the same nest, and it was unclear if there were multiple nests or if the nest was located in the stump of the snag (i.e., a ground nest), or fell from a location higher up in the snag.

463. **Walker, A. 1930.** Notes on the forest *Phenacomys*. Journal of Mammalogy. 11: 233–235. Walker reported that a logger brought him a live dusky tree vole that was captured on Cape Meares, Tillamook County, Oregon, in 1929. The vole was captured in the branches of a Sitka spruce that had just been felled. The logger saw another vole at the same time, but did not catch it. Walker kept the vole alive for several months and described its behavior, including climbing and dangling by one foot. The vole preferred to eat western hemlock and would ignore spruce and Douglas-fir if hemlock was available. Walker stated that fresh young tips of limbs were preferred.
Walker also described a trip that he and his brother Peter made to Cape Lookout, Tillamook County, Oregon, in 1929. On that trip they found four tree vole nests in young Sitka spruce trees and captured one adult female and two young, all of which died soon after capture. They also found a nest in a western hemlock that had fresh nest material, but was unoccupied. All nests in Sitka spruce were 12 to 15 m above ground and had spruce cuttings on top. The nest in the western hemlock was 4.5 m up in a bushy tree and had hemlock cuttings on top.


The authors used ecological niche models to explore spatially explicit hypotheses regarding past geographic patterns of distribution. They predicted three phylogeographic refugia for the red tree vole during the last glacial maximum: Oregon Cascades, Oregon Coast Ranges, and northwestern California Coast Ranges.


James (Pat) Ward identified 495 prey items from nine northern spotted owl territories near Dinsmore, Humboldt County, California. Of the 495 prey items, 8.9 percent were tree voles. Ward also used Sherman traps and Tomahawk live-traps to sample prey (30,980 trap-nights) but did not capture any tree voles, even though many traps were placed on tree trunks.


The authors reported that Sonoma tree voles were important prey items of northern spotted owls in northwestern California but could not be effectively sampled with Sherman live-traps that were placed on the ground.


From 1995 through 1996, the authors used pitfall traps to sample small mammals and amphibians near the border of Humboldt and Trinity Counties in northwestern California. They reported capturing Sonoma tree voles at greater than 7 of the 42 streamside sites they sampled, but they did not
report the actual number of tree voles captured or what they did with the specimens.


Watson said that he collected an adult female and juvenile tree vole at the Reilley Ranch in the South Fork Mountains, Trinity County, California, in 1932. He was working with Chester Lamb (1932).


Webb’s field notes for 1981–1982 described trips in which he, Bill Gannon, Doug Kelt, Tim Lawlor, and Doug Kain collected Sonoma tree voles east of Arcata, California. We found eight tree vole specimens in museums that were collected by Webb, but his field notes only listed four.


Weng and Jackson described the structure and placement of resin ducts in Sitka spruce needles, which are an important food source for tree voles in the northern Coast Ranges of Oregon. They found that Sitka spruce needles had discontinuous resin duct canals, which the authors referred to as resin duct sacs. Sitka spruce had an average of 4.9 mm of resin duct sacs per needle. In figure 5, they showed a cross section of a Sitka spruce needle that had a single resin duct sac on one side of the needle.


Whitaker and Maser found that 15 of 17 red tree voles examined had mites, including at least 5 different species. All but 1 of 33 white-footed voles had mites, including 7 different species. The authors concluded that the damp arboreal nests of tree voles and subterranean nests of white-footed voles were ideal habitats for mites.

The red tree vole was host to *Radfordia arborimus* and *Haemogamasus reidi*. The white-footed vole was host to *Eulaelaps stabularis*, *H. ambulans*, *H. occidentalis*, and *Macrocheles praedafimetorum*. Both the red tree vole and white-footed vole were hosts to *Glycyphagus hypudaei*, *Androlaelaps fahrenholzi*, and *Quasilistrophorus microticolus*.


Whitaker and Wilson reported that the white-footed vole was host to the mite *Haemogamasus reidi* and the red tree vole was host to the mite *Androlaelaps fahrenholzi*.


On his study area in the Oregon Coast Ranges, David Wiens identified 179 tree voles in pellets of spotted owls and 155 tree voles in pellets of barred owls. Tree voles accounted for 14.7 and 4.6 percent of prey items identified in the pellets of spotted and barred owls, respectively.


This was the published version of the information in Wiens (2012).


On a zoology field trip led by Howard Wight in 1924, a student climbed a tree and found a nest that contained four juvenile tree voles near Corvallis, Oregon. The nest was about 14 m up inside the broken top of a 60-cm Douglas-fir. The young were removed and three snap-traps were placed on top of limbs radiating out from the nest. The next morning the adult female was found caught by a leg and hanging from one of the traps. Though the young were fed a mixture of cow and goat milk, they all died within a week and were preserved in alcohol. The female was preserved as a study skin. Her stomach contained fir needles, bark and lichen, all in a finely pulverized state.

In this report, Howard Wight listed the red tree vole as a snag-dwelling mammal. He got it right, because tree voles do occasionally nest in snags that are in contact with the limbs of live trees (Swingle 2005: 29).


The California Department of Fish and Game listed the red tree vole as a species of concern owing to habitat loss. In this report, Williams gave a species account that included information on distribution, population status, and habitat. He suggested that selective logging may be less detrimental to tree voles than clearcutting. Williams stated that red tree voles have “a spotty pattern of dispersion,” citing Taylor (1915) as his source. Williams said that little was known about white-footed voles, especially distribution and habitat.


Wilson and Forsman suggested that opening up the forest canopy by thinning in young stands was detrimental to tree voles because it eliminated arboreal pathways between trees and reduced the availability of trees that had good structure for nest support.


Witmer and deCalesta examined seasonal variation in the frequency of occurrence of prey in scats of bobcats and coyotes on Elliott State Forest in the Oregon Coast Ranges. *Arborimus* voles occurred in 0 to 4 percent of coyote scats and 0 to 8 percent of bobcat scats. The authors did not attempt to differentiate between remains of red tree voles and white-footed voles.

Wooster found 224 Sonoma tree vole nests from 1991 through 1994, during surveys of areas slated for harvest in northwestern California. He provided no analysis of the data, but made the following assertions: (1) When one nest is found in a stand, many others would be found; (2) there was no pattern of nest tree selection by size or age; (3) nests were placed in trees that received more light; (4) tree voles girdled trees; and (5) tree voles were associated with valley bottoms. He also questioned the assertion that tree voles are weak dispersers because he found one case where tree voles were able to reinvade forests growing on an area that had been harvested. He concluded that Sonoma tree voles were quite common in previously logged areas and that the California Forest Practices Rules provided sufficient protection of tree vole habitat.


In this wide-ranging discussion regarding habitat and behavior of tree voles in California, Wooster concluded by saying that his surveys indicated that tree voles were very adaptable and were thriving in numerous young-growth stands. It is difficult to interpret his results because he provided no quantitative comparisons between young and old forests or between thinned and unthinned stands. But this uncertainty does suggest the need for long-term studies of tree vole persistence and population density in managed forests.


Wooster handed out this unpublished manuscript at a meeting of tree vole biologists at Jackson Demonstration State Forest, California on 3 March 2005. The paper described a survey of tree voles at one site in Mendocino County, California. Wooster and Town suggested that forest capacity to hold water could be more important than forest age in providing suitable habitat for tree voles.

Wooster and Town reported that they found four nests in which tree voles were living and feeding on Bishop pine in Mendocino County, California. They stated that tree voles that fed on Bishop pine mechanically removed the resin ducts in the edges of the needle, just as they do with Douglas-fir. Taylor (1915) also observed a Bishop pine cutting in a tree vole nest along with grand fir cuttings but did not speculate that tree voles were feeding on pine. Stagnaro (2008) also reported evidence of tree voles feeding on Bishop pine.

In this article intended for a lay audience, the authors described the interesting little mouse that lived in the trees, complete with illustrations.

In this short species account, Yensen suggested that the rarity of white-footed vole specimens could be due to the difficulty of capturing them. The World Conservation Union Red List Category lists the white-footed vole as data deficient because so little is known about its distribution and abundance.

The authors reported that red tree voles made up 36 percent of prey items identified in 84 pellets collected from northern spotted owls near the Chetco River, Curry County, Oregon. At another study area near Mad River, Humboldt County, California, Sonoma tree voles comprised 12 percent of 581 prey items in spotted owl pellets. No tree voles were located in 76 spotted owl pellets collected in the Klamath Mountains, 48 km west of Happy Camp, California.

Zahler described the woolly flying squirrel (*Eupetaurus cinereus*), a species native to northern Pakistan, that appeared to feed primarily on conifer
needles. Other than tree voles, this is the only other mammal that we are aware of that feeds heavily on needles of conifers.


Zahler and Khan analyzed fecal samples from four woolly flying squirrels and found that 92 to 100 percent of the fecal material was from pine (*Pinus* spp.) needles. They concluded that the woolly flying squirrel was highly specialized for feeding on pine needles. They suggested that free water may be a limiting factor for woolly flying squirrels in the arid region of northern Pakistan because they assumed that wooly flying squirrels required lots of water to counteract and purge the volatile secondary compounds in pine needles.


Zentner reported that he located 53 Sonoma tree vole nests in northwestern California from 1973 to 1977. He reported that nests in small (<30 cm dbh) Douglas-fir trees were usually located in the upper third of the live crown, whereas nests in medium Douglas-firs (30 to 60 cm dbh) were usually located in the top half of the crown, and nests in larger Douglas-fir trees (>60 dbh) were located throughout the live crown. Zentner described the shape and size of nests and concluded that large trees had larger nests. He stated that twigs and cuttings in vole nests were 8 to 30 cm long and that nest cores consisted of shredded Douglas-fir bark. He also reported that 14 percent of the inner nest core was the outer edges of fir needles. He described the inner chamber as being located in the center of the nest and lined with “finely-chewed material.” He said that he documented tree voles removing snow from their nests, but he never said how he documented this. Zentner said that if he climbed nest trees, the voles would abandon their nests for 2 to 7 days or longer, and that just walking to within sight of a nest usually caused desertion for 1 to 3 days. We think he could not have
documented any of this without dissecting nests to see if they were actually occupied.

The most perplexing part of this thesis is that Zentner claimed to have found tree vole nests much farther inland in northern California than any previous researchers. Based on these records, he put forth the hypothesis that tree voles in northern California had been forced to expand their range eastward in response to logging of their habitat near the coast. Given the improbability of a mass exodus of tree voles from logged areas into a previously unoccupied region, and the negative results of recent surveys for tree voles in the inland regions where Zentner claimed to have found tree vole nests, we think a much more likely scenario is that Zentner mistook nests of other species for tree vole nests, and tree voles did not occur there in the first place. But this needs further investigation.
Appendix 1—Number of tree voles (Arborimus longicaudus, A. pomo) or white-footed voles (A. albipes) captured during trapping studies conducted in western Oregon and northwestern California

<table>
<thead>
<tr>
<th>Citation</th>
<th>Trap-nights</th>
<th>Trap type</th>
<th>Tree vole</th>
<th>White-footed vole</th>
</tr>
</thead>
<tbody>
<tr>
<td>8—Anthony et al. (1987)</td>
<td>10,800</td>
<td>ST</td>
<td>0</td>
<td>9 (0.083)</td>
</tr>
<tr>
<td>11—Aubry et al. (1991)</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>PF</td>
<td>&gt;1</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>44—Borrecco (1973)</td>
<td>63,360&lt;sup&gt;e&lt;/sup&gt;</td>
<td>LT</td>
<td>1 (0.002)</td>
<td>0</td>
</tr>
<tr>
<td>53—Bury and Corn (1987)</td>
<td>38,800</td>
<td>PF</td>
<td>17 (0.044)</td>
<td>0</td>
</tr>
<tr>
<td>82—Cole et al. (1998)</td>
<td>50,256</td>
<td>PF, LT</td>
<td>1 (0.002)</td>
<td>1 (0.002)</td>
</tr>
<tr>
<td>87—Corn and Bury (1986)</td>
<td>38,800</td>
<td>PF</td>
<td>18 (0.046)</td>
<td>0</td>
</tr>
<tr>
<td>88—Corn and Bury (1988)</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>PF</td>
<td>18</td>
<td>0</td>
</tr>
<tr>
<td>89—Corn and Bury (1991)</td>
<td>108,864</td>
<td>PF</td>
<td>13 (0.012)</td>
<td>0</td>
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<tr>
<td>90—Corn et al. (1988)</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>PF</td>
<td>17</td>
<td>0</td>
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<tr>
<td>102—Dizney et al. (1985)</td>
<td>65,600</td>
<td>PF, LT</td>
<td>0</td>
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<td>103—Doyle (1985)</td>
<td>92,904</td>
<td>LT</td>
<td>0</td>
<td>1 (0.001)</td>
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<tr>
<td>104—Doyle (1990)</td>
<td>40,152</td>
<td>LT</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>108—Fisher (1942)</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>ST</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>110—Fontaine (2007)</td>
<td>8,900</td>
<td>LT</td>
<td>1 (0.011)</td>
<td>0</td>
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<tr>
<td>141—Gilbert and Allwine (1991)</td>
<td>165,310&lt;sup&gt;e&lt;/sup&gt;</td>
<td>PF, ST</td>
<td>9 (0.005)</td>
<td>0</td>
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<tr>
<td>145—Gillesberg and Carey (1991)</td>
<td>2,310&lt;sup&gt;e&lt;/sup&gt;</td>
<td>LT</td>
<td>0</td>
<td>0</td>
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<tr>
<td>146—Gitzen et al. (2007)</td>
<td>256,896</td>
<td>PF</td>
<td>1 (&lt;0.001)</td>
<td>1 (&lt;0.001)</td>
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<tr>
<td>148—Gomez (1992)</td>
<td>100,800</td>
<td>PF</td>
<td>23 (0.023)</td>
<td>59 (0.059)</td>
</tr>
<tr>
<td>149—Gomez and Anthony (1998)</td>
<td>100,800</td>
<td>PF</td>
<td>23 (0.023)</td>
<td>59 (0.059)</td>
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<tr>
<td>150—Gomez et al. (1997)</td>
<td>7,290</td>
<td>PF</td>
<td>4 (0.055)</td>
<td>4 (0.055)</td>
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<tr>
<td>178—Hayes et al. (1996)</td>
<td>14,400</td>
<td>LT</td>
<td>0</td>
<td>1 (0.007)</td>
</tr>
<tr>
<td>182—Hooven and Black (1976)</td>
<td>15,750&lt;sup&gt;e&lt;/sup&gt;</td>
<td>LT</td>
<td>3 (0.019)</td>
<td>0</td>
</tr>
<tr>
<td>208—Jewett (1915)</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>ST</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>233—Johnston (2006)</td>
<td>17,600</td>
<td>LT</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>257—Maguire (2002)</td>
<td>86,400&lt;sup&gt;e&lt;/sup&gt;</td>
<td>PT</td>
<td>&gt;1</td>
<td>&gt;1</td>
</tr>
<tr>
<td>260—Manning (2002)</td>
<td>23,760&lt;sup&gt;e&lt;/sup&gt;</td>
<td>LT</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>261—Manning and Edge (2004)</td>
<td>2,400&lt;sup&gt;e&lt;/sup&gt;</td>
<td>LT</td>
<td>0</td>
<td>0</td>
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<tr>
<td>262—Manning and Edge (2008)</td>
<td>23,760&lt;sup&gt;e&lt;/sup&gt;</td>
<td>LT</td>
<td>0</td>
<td>0</td>
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<td>263—Manning and Maguire (1999)</td>
<td>21,168</td>
<td>PT</td>
<td>1 (0.005)</td>
<td>0</td>
</tr>
<tr>
<td>264—Manning et al. (2003)</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>PF</td>
<td>0</td>
<td>13</td>
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<tr>
<td>268—Martin (1998)</td>
<td>127,900</td>
<td>PT</td>
<td>42 (0.033)</td>
<td>85 (0.066)</td>
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<tr>
<td>270—Martin and McComb (2002)</td>
<td>127,900</td>
<td>PF</td>
<td>42 (0.033)</td>
<td>85 (0.066)</td>
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<tr>
<td>288—McComb et al. (1993a)</td>
<td>28,800</td>
<td>PF</td>
<td>&lt;10</td>
<td>0</td>
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<tr>
<td>289—McComb et al. (1993b)</td>
<td>31,200</td>
<td>PF, ST</td>
<td>2 (0.006)</td>
<td>11 (0.035)</td>
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<tr>
<td>350—Ralph et al. (1991)</td>
<td>141,120</td>
<td>PT, ST, LT</td>
<td>22 (0.016)</td>
<td>0</td>
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<tr>
<td>352—Raphael (1988)</td>
<td>899,431</td>
<td>PF</td>
<td>19 (0.002)</td>
<td>0</td>
</tr>
<tr>
<td>366—Rosenberg (2003)</td>
<td>36,000&lt;sup&gt;e&lt;/sup&gt;</td>
<td>LT</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Appendix 1—Number of tree voles (*Arborimus longicaudus*, *A. pomo*) or white-footed voles (*A. albipes*) captured during trapping studies conducted in western Oregon and northwestern California (continued)

<table>
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<tr>
<th>Citation</th>
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<th>Trap type</th>
<th>Tree vole</th>
<th>White-footed vole</th>
</tr>
</thead>
<tbody>
<tr>
<td>368—Russell (1942)</td>
<td>16&lt;sup&gt;e,f&lt;/sup&gt;</td>
<td>ST</td>
<td>8 (50)</td>
<td>0</td>
</tr>
<tr>
<td>375—Sherrell (1969)</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>ST</td>
<td>0</td>
<td>1</td>
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<td>376—Sherrell (1970)</td>
<td>5,585&lt;sup&gt;e&lt;/sup&gt;</td>
<td>ST</td>
<td>0</td>
<td>1 (0.018)</td>
</tr>
<tr>
<td>398—Sturges (1955)</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>PF, ST</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>399—Suzuki (1992)</td>
<td>19,300</td>
<td>PF, ST</td>
<td>0</td>
<td>14 (0.073)</td>
</tr>
<tr>
<td>400—Suzuki (2000)</td>
<td>139,600</td>
<td>PF</td>
<td>&gt;1</td>
<td>&gt;1</td>
</tr>
<tr>
<td>401—Suzuki and Hayes (2003)</td>
<td>139,600</td>
<td>PF</td>
<td>9 (0.006)</td>
<td>432 (0.0310)</td>
</tr>
<tr>
<td>407—Swingle et al. (2004)</td>
<td>184&lt;sup&gt;f&lt;/sup&gt;</td>
<td>LT</td>
<td>3 (1.6)</td>
<td>0</td>
</tr>
<tr>
<td>412—Tevis (1956)</td>
<td>3,400&lt;sup&gt;e&lt;/sup&gt;</td>
<td>ST</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>461—Waldien (2005)</td>
<td>52,800</td>
<td>LT</td>
<td>0</td>
<td>0</td>
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<tr>
<td>467—Waters et al. (2001)</td>
<td>NR&lt;sup&gt;d&lt;/sup&gt;</td>
<td>PF</td>
<td>&gt;1</td>
<td>0</td>
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<tr>
<td>476—Wight (1925)</td>
<td>1&lt;sup&gt;e,f&lt;/sup&gt;</td>
<td>ST</td>
<td>1(100)</td>
<td>0</td>
</tr>
</tbody>
</table>

<sup>a</sup> Bibliography number precedes citation.

<sup>b</sup> PF = pitfall trap, ST = snap trap, LT = live-trap.

<sup>c</sup> Captures per 100 trap-nights are in parentheses and were estimated from the data if not reported in the original manuscript.

<sup>d</sup> NR = not reported.

<sup>e</sup> Trap-nights were estimated based on data presented in the methods section.

<sup>f</sup> Traps were placed on top of nests.
Subject Index by Bibliography Number

Bolding and underlining indicate species referred to in each reference, as follows:

Bold numbers without underlining = tree voles

Bold numbers with underlining = both tree voles and white-footed voles

Underlined, but not bolded = white-footed voles

Not bolded or underlined = references that do not specifically mention either species.


Behavior

Activity patterns ...........................................................................................................................................131, 402, 405

Arboreal ........................................................................................................................................................59, 264, 279, 410, 453, 454, 458

Climbing/movements ........................................14, 15, 28, 80, 85, 131, 186, 217, 277, 284, 319, 320, 331, 334, 374, 408, 410, 454

Female aggression towards male ..............................................................80, 170, 218, 224

Foraging ..........................................................................................................................................................131

Gnawing .........................................................................................................................................................80

Solitary behavior ........................................29, 80, 130, 131, 176, 186, 195, 209, 277, 279, 341, 380, 402, 408, 410, 430, 450, 454, 485

Temperament ..................................................................................................................................................15, 28, 80, 170, 186, 209, 217, 277, 283, 408, 454, 463

Vocalizations ..................................................................................................................................................80, 170, 217, 408, 410

Captive voles ................................................15, 28, 29, 48, 63, 79, 80, 98, 122, 126, 129, 161, 169, 170, 175, 176, 177, 180, 186, 214, 216, 217, 218, 224, 225, 227, 231, 246, 277, 278, 331, 410, 450, 463, 476

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