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A tale of two voles: A response to Rosenberg 2019

ABSTRACT

In this article we respond to a recent paper in which Rosenberg (2019) suggested that red tree voles (*Arborimus longicaudus*) were just as common as western red-backed voles (*Myodes californicus*) and implied that federal management agencies should consider dispensing with field surveys of red tree voles in favor of an unspecified adaptive management approach. Our primary purpose in writing this response is not to debate how management agencies should manage red tree voles. Our objective is to demonstrate that Rosenberg's (2019) attempt to compare the distribution and relative abundance of red tree voles and western red-backed voles was fundamentally flawed. The data that he used to compare the two species are not analogous because they are based on different metrics, biased samples, and different sampling techniques. Rosenberg (2019) also failed to include data from numerous studies that suggest that, compared to red tree voles, western red-backed voles are much more uniformly distributed in the coniferous forests of western Oregon. In addition to assessing the methodological flaws and inconsistencies in Rosenberg's (2019) analysis, we review additional data that we think are useful for understanding differences in the distribution of tree voles and red-backed voles. We conclude that Rosenberg's (2019) analysis served little purpose except to muddy the waters regarding the actual distribution and abundance of red tree voles.

1. Introduction

During the development of the Northwest Forest Plan in 1993, a team of scientists and managers from multiple federal agencies formulated a list of potential management options for federal lands in the Pacific Northwest (Thomas et al., 1993a). As part of this process, Thomas et al. (1993a, b) compiled a list of native species that were thought to be associated with old forests and convened panels of experts to evaluate the likelihood of persistence of each species under different management options. Persistence scores ranged from 0 to 100 with 0 indicating no chance of persistence and 100 indicating a very high likelihood of persistence. Persistence scores were influenced by many factors, including life history attributes, distribution, abundance, dispersal capability, metapopulation structure, and the quality and quantity of data that were available (Thomas et al., 1993a; Meslow, pers comm., 2019).

Two mammal species evaluated by Thomas et al. (1993a) were the western red-backed vole (*Myodes californicus*) and red tree vole (*Arborimus longicaudus*), both of which were thought to be most abundant in old forests (Thomas et al., 1993b). Because the western red-backed vole was known to be relatively common and uniformly distributed in upland forests, the panel gave it a likelihood of persistence score of 90 based on the management scenario that ultimately became the Northwest Forest Plan. In contrast, the panel gave the red tree vole a persistence score of 73, primarily because of concerns regarding lack of data, limited dispersal capability, limited distribution, and the fact that red tree voles or their nests were either absent or uncommon in many areas (Thomas et al., 1993a; E. Charles Meslow, pers comm. 2019).

Because of its comparatively low persistence likelihood score, the red tree vole was the only mammal that was included on the list of "survey and manage" species that was adopted as part of the Northwest Forest Plan. Regulations added during the final development of the plan required federal land management agencies to conduct surveys for survey and manage species prior to conducting harvest activities and to protect those species if they were detected. For tree voles this meant that managers were required to protect a 4.05 ha buffer around occupied or recently occupied nest trees that were detected during preharvest surveys. Surveyors frequently encountered red tree vole nests in proposed harvest units, which made many proposed timber sales expensive and operationally unfeasible (Baker et al., 2005; Olson et al., 2007). Because of the impact of red tree vole management on timber harvest activities on federal lands, the Bureau of Land Management and US Forest Service sought to remove the red tree vole from the list of survey and manage species (USDA Forest Service and USDI Bureau of Land Management, 2001, 2004; USDI Bureau of Land Management, 2007). This effort failed in court and the Bureau of Land Management eventually extricated itself from the Northwest Forest Plan and developed a new management plan that did not require protection of red tree voles in most areas (USDI Bureau of Land Management, 2016a, 2016b).

In a recent publication Rosenberg (2019) seems to be arguing that red tree voles should never have been included on the list of survey and manage species in the first place or, at the very least, are sufficiently common to warrant removing them from that list. Instead, he argues for a more flexible approach that would be based on some kind of unspecified "adaptive management." Although we agree with Rosenberg (2019) that adaptive management techniques should be considered with regard to management of red tree voles (or any species), we argue that his analysis was largely flawed based on methodological issues associated with the very different natural histories and functional roles of these two species in forests of western Oregon and northwestern California. Moreover, he disregarded many studies that demonstrate that, compared to red tree voles, western red-backed voles are much more common and more evenly distributed. For these reasons, we did not find his analysis particularly enlightening or appropriate. Here we provide specific comments on our concerns and highlight where we think Rosenberg (2019) failed in effectively comparing these species.

1.1. Commonness-rarity argument and its influence on management of red tree voles

Rosenberg's (2019) conclusions were predicated upon the assertion

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that the tree vole's position along the commonness-rarity spectrum was a prominent factor in determining its conservation status in the Northwest Forest Plan (Thomas et al., 1993a; USDA Forest Service and USDI Bureau of Land Management, 1994), and that this may be a flawed method for evaluating the likelihood of species persistence. Rosenberg (2019) implied that the commonness-rarity criterion was largely responsible for the differences in conservation status between tree voles and red-backed voles in the assessment conducted by Thomas et al. (1993a).

Although Rosenberg (2019) conceded that other factors were taken into account in the conservation assessment conducted by Thomas et al. (1993a), he asserted that there is, in general, an over-emphasis on rarity in natural resource management (Caughley, 1994; Flather and Sieg, 2007) and that this likely influenced the decision to list the tree vole as a survey and manage species in the Northwest Forest Plan. This premise was never examined or evidenced by Rosenberg (2019), though it appeared to be the primary motivating factor behind his manuscript. In an apparent attempt to demonstrate that tree voles are just as abundant as the relatively common red-backed vole, Rosenberg (2019) spends much of his manuscript comparing data from a variety of different studies that were based on completely different metrics. It is in comparing those metrics that his analysis was flawed, as we will discuss below.

1.2. Apples and oranges – Unique natural histories

Although the red tree vole and western red-backed vole are both members of the subfamily Arvicolinae, that is about where their similarities end. In brief, the red tree vole is a highly specialized arboreal species that feeds exclusively on conifer needles and twig bark or underlying cambium (Maser, 1966; Forsman et al., 2016), and is a candidate for listing as a threatened or endangered species in part of its range (USDI Fish and Wildlife Service, 2011). In contrast, the western red-backed vole is a terrestrial species that spends most of its time underneath rotting logs or rooting about in the duff layer on the forest floor, searching for hypogeous fungi (truffles; Maser, 1988; Maser et al., 1978; Ure and Maser, 1982). Western red-backed voles (hereafter "red-backed voles") belong to a circumboreal genus of 12 species with a combined range that includes most of northern North America, Europe and Asia (Musser and Carlton, 2005), whereas red tree voles (hereafter "tree voles") belong to a genus that includes just three species that occur only in western Oregon and coastal northwestern California (Verts and Carraway, 1998; Bellinger et al., 2005; Forsman et al., 2016). These differences in natural history and ecology have profound impacts on methods used to study these two species and on any reasonable comparisons one wishes to make.

The dramatic differences in survey methodologies for tree voles and red-backed voles are the primary reason that no studies have been conducted on both species simultaneously. Tree voles are virtually impossible to capture using conventional small mammal sampling methods (Swingle et al., 2004; Swingle and Forsman, 2016:148–149) and most studies of tree vole distribution and abundance have been based on signs of tree vole activity (e.g., nests) rather than direct captures of individuals. Thus, despite over a century of extensive efforts in which researchers climbed many thousands of trees to search for tree voles, no studies have produced capture histories suitable for density estimation and virtually nothing is known about annual or spatial variation in tree vole populations (Swingle and Forsman, 2016).

In contrast, red-backed voles are relatively easy to capture with a variety of standard sampling methods used for small mammals. Due to ease of capture and commonness of red-backed voles, the literature on their distribution and habitat associations in the Pacific Northwest is extensive, including many studies where researchers used pitfall traps, snap traps, or live traps to compare the relative abundance of red-backed voles among regions, forest age classes, forest types, or silvicultural treatments (e.g., Gashwiler, 1970; Hooven and Black, 1976; Corn and Bury, 1991; Gilbert and Allwine, 1991; Gomez and Anthony, 1998; Rosenberg et al., 2003; Suzuki and Hayes, 2003; Weldy et al., 2019). As a result, there is a great deal more certainty regarding the regional distribution and numeric abundance of red-backed voles than there is for tree voles.

1.3. Distribution of tree voles and red-backed voles

Rosenberg (2019) correctly pointed out that tree voles occur in forested areas throughout much of western Oregon but what he failed to emphasize was that virtually all studies of tree voles have indicated that their distribution is very uneven both within and among different geographic regions (Dunk and Hawley, 2009; Forsman et al., 2016; Rosenberg et al., 2016). For example, in the extensive study designed by Rittenhouse et al. (2002), tree vole nests were found in only 43% of the 2 ha plots surveyed within their contemporary range (Forsman et al., 2016:25), even though most plots (70%) were located in old-growth coniferous forests that were thought to be optimal habitat (Dunk and Hawley, 2009).

In his study of tree vole nest detection rates in the central and southern Oregon Coast Ranges, Marks-Fife (2016) found tree vole nests in all of the 26 mature and old-growth forest plots that he examined, but found no tree vole nests in 5 of the 10 young forest stands that he examined, despite the fact that he placed all plots near known tree vole locations in the region where tree voles are most abundant (Forsman et al., 2016). Although most of the stands that he surveyed had evidence of tree vole presence (nests), Marks-Fife (unpubl. data) only observed tree voles in 9 of 36 stands (25%), despite the fact that he searched all nests to determine if they were occupied. This study, which was designed to maximize the likelihood of encountering tree vole nests, again suggests that tree voles were very unevenly distributed, even in the central and southern Coast Ranges where they are thought to be most abundant (Forsman et al., 2016)

In contrast to the uneven distribution of tree voles, red-backed voles have been captured in > 90% of the small mammal trapping studies conducted in western Oregon across many forest types that varied by age and tree species composition (Appendix 1), including studies conducted in extensive areas of young forest in the northern Coast Ranges of Oregon, where tree voles appear to have largely been extirpated by wildfire and logging (Suzuki and Hayes, 2003; Price et al., 2015; Forsman et al., 2016). Rosenberg (2019) did not provide any means for evaluating distributional patterns of red-backed voles as he considered only a narrow subset of studies in which researchers used live traps to sample red-backed voles in the Cascades and Klamath Mountains. In our view this represents a serious flaw in his attempt at a comparison of the relative distribution and abundance of tree voles and red-backed voles.

1.4. Density of red tree voles

Based on the data that he presented in Tables 1 and 2, Rosenberg (2019) suggested that tree voles occur at similar or higher densities than red-back voles. We found numerous problems with his comparisons. Firstly, density is a commonly estimated population metric (individuals per unit area) that in recent decades has been estimated with ever-more sophisticated models in which researchers use capture histories and ratios of marked and unmarked animals to estimate densities in closed populations (Otis et al., 1978; White et al., 1982). Full capture-recapture histories are required for density estimates and most researchers take great care to avoid biases in estimating density. Credible papers also provide measures of statistical uncertainty in density estimates. Unfortunately, the lack of capture history data for both tree voles and red-backed voles did not deter Rosenberg (2019) from presenting numerous point estimates (with no measure of statistical uncertainty) of minimum vole "density" that were based on biased samples or indices of density derived from biased samples, as described in the following sections.

In his Table 1, Rosenberg (2019) presented tree vole density estimates based on studies in which researchers searched for tree vole nests in the forest canopy (Maser, 1966; Biswell and Forsman, 2010; Marks-Fife, 2016) or in felled trees (Gillesberg and Carey, 1991). Two of the four studies cited (Biswell and Forsman, 2010; Gillesberg and Carey, 1991) could only be used to estimate minimum densities of tree vole nest trees because detection probabilities and occupancy rates of nests were not determined. No tree voles were observed in these studies, so at best these estimates are an index of tree vole nest abundance with unknown relationship with true abundance of tree voles. There is no way to compare these estimates with the minimum density estimates of red-backed voles that Rosenberg (2019) presents in Table 2 because the latter estimates were all based on captures of individual red-backed voles.

With regard to the tree vole study conducted by Maser (1966), the 12.4 ha study area was not selected randomly and sampling occurred over a long time period (75 days) during which the population could not be considered "closed," a necessary assumption in estimates of density (Otis et al., 1978). Selection of the study area happened after Maser and one of his colleagues (Wayne Hammer) found a high concentration of tree vole nests in a young forest of Douglas-fir (*Pseudotsuga menziesii*) in which arboreal nests were easy to see and trees were small and easy to climb (Maser, pers comm. 1968). Only then was the decision made to use the area for what Maser (1966:170) referred to as a "population study." The data from the Maser study area represented an unusual concentration of tree voles in an open population that was sampled over a period of nearly three months. It cannot be assumed that the post hoc density estimates that Rosenberg (2019) calculated based on the Maser study are representative of average conditions for tree voles and any comparison between densities of tree voles captured in the Maser study area and red-backed voles captured in randomly or systematically placed trapping grids is almost certainly not representative of the relative abundance of the two species.

In the main body of Table 1, Rosenberg (2019) displayed a density estimate of 3.3 tree voles per ha based on the fact that Maser (1966:217) captured a total of 40 tree voles in his 12.4 ha study area. Only by searching through the text and reading the footnotes to Table 1 can one discover that the majority of voles captured by Maser (1966) were nestlings and that he captured only 15 non-juveniles (12 adults, 3 subadults) within his study area (1.2 per ha). This is an important fact because none of the estimates of red-backed vole density that Rosenberg (2019) cited in Table 2 included nestling juveniles. The only comparison that makes any sense is one that is limited to adults and dispersal age subadults. Thus, Rosenberg's (2019) use of methodologically biased estimates from the Maser (1966) study is even more misleading because he emphasized one estimate in the table and relegated the more applicable estimate to fine print in a footnote. However, even that comparison is invalidated based on the problems outlined in the previous paragraph.

Rosenberg (2019) presented multiple point estimates of density in Table 1 that were reported in Marks-Fife (2016). Only one of those estimates (mean $\pm$ SE = 1.91 $\pm$ 0.97 tree voles per ha) was based on actual observations of tree voles and Marks-Fife (2016:79) was careful to point out that this estimate only applied to occupied stands in the non-random sample of stands that he surveyed. Marks-Fife (2016) observed so few tree voles during his study (10 voles in 113 occupied or recently occupied nest trees) that he could not calculate separate estimates of density in different forest age classes based on live animals. Because of this problem Marks-Fife (2016:72) generated an index of density that he referred to as "the number of adult tree vole home ranges per ha." He calculated this index by dividing his estimates of the number of occupied or recently occupied nest trees by the mean number of nest trees used by radio-collared tree voles in a previous study (Marks-Fife, 2016:79; Swingle, 2005). This index was the source of the high estimates of density that Rosenberg (2019:167) erroneously referred to as "adult vole" density in Table 1 and that he argued were the most reliable estimates of tree vole density. Unfortunately, Rosenberg (2019) failed to recognize that these estimates were based on several unsupported assumptions, one of which was that all recently occupied nests that were present at time zero were built by voles that were present at time zero. That is not a valid assumption because tree vole nests persist for years and accumulate over time. Thus, the nests that are present at any point in time are the product of multiple generations of tree voles, many of which are already dead as few tree voles survive more than a few months (annual survival = 0.15, 95% CI = 0.06–0.31; Swingle et al., 2010). This means that the index developed by Marks-Fife (2016) probably greatly overestimated the abundance of tree voles. To suggest that density metrics derived from the Marks-Fife (2016) study are comparable with density estimates based on live-trapping studies of red-backed voles is a perfect example of comparing apples and oranges and is almost guaranteed to lead to erroneous conclusions.

1.5. Density of red-backed voles

We identified a number of issues that made it difficult to evaluate the density estimates that Rosenberg (2019) presented for red-backed voles in his Table 2. For example, without consulting the original publications we could not tell if the estimates were all based on post hoc calculations by Rosenberg (2019) or included some estimates that came directly from the original papers. By reading the original papers we eventually figured out that all of his estimates were post hoc because none of the original reports included density estimates for red-backed voles. This problem could have been avoided with a few footnotes to the table and a clear statement in the methods section that all reported density estimates were calculated by Rosenberg (2019).

In some cases we could not replicate Rosenberg's (2019) estimates in Table 2, and in other cases we questioned whether his estimates were valid. For example, he presented a post hoc estimate of 7.5 red-backed voles per ha based on a study by Hooven and Black (1976) who conducted trapping sessions at monthly intervals for 7 months each year (April–October) in 1968–1970. Hooven and Black (1976) did not conduct a mark-recapture analysis, did not report captures for each sampling occasion, and did not always sample the same number of days in each trapping session (Hooven, 1971:56). We concluded that there was no way to estimate density based on the Hooven and Black (1976) data because they sampled an open population for 7 months each year without providing any information on monthly capture histories. Any attempt to estimate density based on their data is hopelessly confounded by mortality and recruitment. In his dissertation, Hooven (1971:50) even emphasized that statistical analysis of his data relative to density was meaningless.

Rosenberg's (2019) post hoc estimate of red-backed vole density from Waters and Zabel (1998) was based on a study that was conducted outside the distributional range of the red tree vole. Waters and Zabel (1998) did not estimate density of red-backed voles and limited their analysis to a comparison of capture rates among silvicultural treatments (shelterwood harvest) and forest age classes (mature, old-growth). It is questionable whether density estimates from this study with 40 m spacing between trap stations is comparable with the other studies cited in Table 2, all of which had 15–20 m spacing between stations. The methodological shortcomings of this study as a density study of red-backed voles exemplifies the lack of rigor and documentation in Rosenberg's post hoc approach to estimates, a process that he did not provide sufficient details to replicate.

We also note that Rosenberg (2019) failed to cite two papers in which Doyle (1985:52) and Rosenberg et al. (2003:1720) reported densities ($\bar{x} \pm SE$) of 7.3 $\pm$ 0.8 and 1.9 $\pm$ 0.3 red-backed voles per ha in upland coniferous forests in western Oregon. Although these estimates are not comparable with indices of tree vole abundance, for the reasons described earlier, they are additional examples of the fact that red-backed voles are common residents in coniferous forests in western

Oregon.

A more fundamental concern regarding the density estimates that Rosenberg (2019) presented on red-backed voles is that he restricted his review to a small number of studies in which researchers used live traps to sample small mammals in coniferous forests in the Cascades and Klamath Mountains. He ignored the much more extensive literature in which researchers used pitfall traps or snap traps to compare the relative abundance of small mammals at many different locations, including the Coast Ranges of western Oregon (Appendix 1). He argued that those data should not be used in a discussion of population density because of the likelihood that new animals will enter the population as previous residents are removed. Actually, this same argument could be applied to live-trapping studies as well, because trap mortality of red-backed voles tends to be high (Gashwiler, 1970; Hooven, 1971). But regardless of that problem, we argue that, if the objective is an unbiased comparison, one should consider all available literature and not ignore the numerous studies in which pitfall traps and snap traps were used to sample small mammals in western Oregon. If nothing else, these studies are useful for evaluating patterns of distribution of red-backed voles within and among forest types and regions. The results in most of these studies indicated that red-backed voles were one of the most abundant rodents in upland coniferous forests and were captured in nearly every published study that we could find (Appendix 1). The results could not be more striking when compared to the tree vole nest survey that was designed by Rittenhouse et al. (2002). In the latter study the majority of plots that fell within the range of the tree vole had zero evidence of tree vole presence (Dunk and Hawley, 2009; Forsman et al., 2016) and the minimum density of nest trees was typically < 1 per ha (Forsman et al. 2016:27–28). While all tree vole nest surveys are almost certainly biased low because of false negatives (no nests detected when some are actually present), the Rittenhouse et al. (2002) survey protocol was designed to reduce the likelihood of false negatives by having climbers inspect a stratified random sample of trees in plots in which few or no nests were detected from the ground. Based on this protocol, Dunk and Hawley (2009:632) estimated that the proportion of false negatives from ground surveys in the Rittenhouse et al. (2002) study was only 6.0%, and that this bias had a "…negligible effect on our findings and conclusions."

2. Application of imperfect data to management

Although it is never clearly stated, Rosenberg (2019) seems to be arguing that tree voles are sufficiently abundant to drop them from the list of species that require any special management consideration in Oregon with the possible exception of the northern Coast Ranges, where there is little federal land, and where tree voles are particularly rare (Price et al., 2015; Forsman et al., 2016). In some respects, this is a moot point, because the Bureau of Land Management has already removed itself from the Northwest Forest Plan and has stopped surveying for tree voles on their lands in western Oregon, with the exception of forests that are > 80 years old in the northern Coast Ranges, where the tree vole is a candidate for listing under the Endangered Species Act (USDI Fish and Wildlife Service, 2011; USDI Bureau of Land Management, 2016a, b). In the rest of western Oregon, the US Forest Service is no longer required to conduct tree vole surveys in forests < 80 years old (Pechman, 2006; Connaughton and Shepard, 2011), and is currently implementing a new management approach that will focus on protection of tree vole habitat in "high-priority" sites in fifth-field watersheds, thereby reducing the need for tree vole surveys in old forests (Huff, 2016). Management and habitat protection for tree voles is restricted to federal lands in Oregon because the Oregon Department of Forestry does not require that state or private landowners conduct any management specifically aimed at tree voles (Oregon Department of Forestry, 2010).

In responding to Rosenberg (2019), our primary intent is not to argue whether federal and state agencies or private landowners should be required to survey for or protect tree voles. Our intent is to argue that an unbiased and sound scientific analysis of the facts matters, especially when there are implications for resource management. Here we provide evidence that Rosenberg (2019) presented a misleading and confusing summary of the science regarding the distribution and relative density of tree voles and red-backed voles. His suggestion that tree voles are as common and evenly distributed as red-backed voles is not supported by the available data. He largely ignores the dramatically different life history characteristics and subsequent survey design limitations associated with both species. Whereas data from red-backed voles come almost exclusively from animals captured on systematically placed trapping grids, data from tree voles comes primarily from indices based on density of nest trees with unknown relationships with the number of live individuals. Because a single tree vole can utilize multiple nests which may persist for years and which accumulate over multiple generations, it is incredibly difficult to establish relationships between nest abundance and density of tree voles (Marks-Fife, 2016). Rosenberg (2019) also minimized or ignored other limitations of the data, including the fact that some study areas were non-randomly selected because they were in areas with high relative abundances of tree voles and some estimates were not comparable because they included juvenile tree voles.

Based on our review, we conclude that tree voles and red-backed voles differ not only in terms of their life history attributes, but also in terms of their distribution on the landscape. The red-backed vole is a fairly common species, distributed throughout the coniferous forests of western Oregon and northwestern California, including many areas outside the range of the tree vole (Verts and Carraway, 1998:298; Waters and Zabel, 1998; Manning, 2002; Johnston, 2006). Although the red-backed vole tends to be most abundant in old forests (Rosenberg et al., 1994), it is typically found in nearly every area that is sampled in coniferous forests in the Coast Ranges of Oregon, including young forests in the Tillamook Burn region of northern Oregon where tree voles have largely been extirpated (Suzuki and Hayes, 2003; Price et al., 2015; Forsman et al., 2016). In contrast, extensive surveys conducted in western Oregon indicate that the distribution of tree voles is extremely uneven, and that they have been virtually eliminated in many areas as a result of wildfires and logging (Forsman et al., 2016).

Rosenberg (2019) argues that evaluation of population viability improves management of species more broadly than assessment of rarity alone. We agree, and that is exactly why the Forest Ecosystem Management Assessment Team (Thomas et al., 1993a) took into account other factors when they evaluated persistence of tree voles and red-backed voles. Although we currently know a great deal more about the distribution of tree voles than we did when Thomas et al. (1993a) conducted their analysis, there is still a great deal of uncertainty regarding population density, demographic trends, population cycling, metapopulation function, and distributional patterns of this enigmatic species. Forsman et al. (2016) concluded that the distribution of tree voles was extremely uneven and that they were rare or absent in many areas that had experienced extensive wildfire or logging. This interpretation differs from Rosenberg's (2019:169) decidedly rosy conclusion that "Surveys conducted on red tree voles since its designation as a survey and manage species demonstrate that this species is much more abundant and well-distributed than initially believed…"

Although there is no doubt that survey and manage requirements for tree voles have constrained harvest of old forests on federal lands in western Oregon, it is also important to emphasize that those constraints were implemented not just because tree voles were thought to be rare. Tree voles are incredibly difficult animals to study, and there is still a great deal of uncertainty regarding their ability to persist in intensively managed forests or in old forest refugia that gradually become isolated in landscapes dominated by young, intensively managed forests (Forsman et al., 2016). The fact that their distribution is not at all uniform and that they are absent or rare in many areas that have been subjected to recent wildfires or logging is good reason to be concerned about the long-term persistence of tree voles. Contrary to Rosenberg (2019), we suggest that there are many reasons to manage proactively for tree voles, especially in regions where they are least abundant, perhaps with survey and management guidelines or some other form of adaptive management. But one thing seems certain – a comparison of disparate types of data from two species that are as different as red tree voles and red-backed voles is not helpful for informing management decisions that are likely to impact red tree voles.

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Appendix 1

Percentage of western red-backed voles (*Myodes californicus*) captured in trapping studies conducted in western Oregon and northwestern California. Last column (Percent MYCA) indicates percentage of red-backed voles in the total sample of all rodents captured.

Source	Forest type[a]	Region[b]	Trap nights	Trap type[c]	Total rodents[d]	Percent[d] MYCA
Anthony et al. 1987	CON	Cas (C)	10,800	ST	519	3.28
Bury and Corn 1987	CON	Cas (C)	38,880	PF	320	51.56
Cole et al. 1998	HDW	Coa (C)	50,256	PF, LT	2981	0.10
Corn and Bury 1991	CON	Coa (C)	108,864	PF	824	77.79
Corn et al. 1988	CON	Coa (C)	NR[e]	PF	303	54.13
Cross 1985	MCON	Kla, Cas (C)	6240	PF, ST, LT	462	48.27
Dizney et al. 2008	CON	Coa (N), Cas (N)	65,600	PF, LT	2098	0.00
Doyle 1985	CON	Cas (C)	92,904	LT	8617	6.19
Fontaine 2007	MCON	Kla	8900	LT	85	2.35
Gilbert and Allwine 1991	CON	Cas (N, C)	165,310[d]	PF, ST	1177	72.13
Gitzen et al. 2007	CON	Cas (C)	256,896	PF	2946	41.17
Gomez and Anthony 1998	CONHDW	Coa (C)	100,800	PF	1911	22.82
Gomez et al. 1997	CON	Coa (N)	7290	PF	247	6.07
Hayes et al. 1996	HDW	Coa (C)	14,400	LT	789	0.13
Hooven and Black 1976	CON	Cas (C)	15,750[c]	LT	2640	3.52
Johnston 2006	MCON	Kla	17,600	LT	831	0.48
Manning 2002	MCON	Kla	23,760[d]	LT	501	23.95
Manning and Edge 2004	CON	Coa (C)	2400[d]	LT	471	0.42
Martin and McComb 2002	CON	Coa (N, C)	127,900	PF	2389	32.65
McComb et al. 1993	CON	Coa (C)	31,200	PF, ST	455	43.96
Ralph and Paton (1991)	CON	Coa (S), NW Cal	141,120	PF, ST, LT	2791	29.74
Raphael 1988	CON	NW Cal	899,431	PF	2569	26.04
Sherrell 1970	CONHDW	Coa (S)	5585	ST	332	0.60
Suzuki 1992	HDW	Coa (N, C)	19,300	PF, ST	951	1.47
Suzuki and Hayes 2003	CON	Coa (N, C)	139,600	PF	1797	44.91
Waldien 2005	CON	Coa (C)	91,200	LT	12,510	0.84

[a]CON = conifer, HDW = hardwood, MCON = mixed conifer, CONHDW = conifer hardwood.
[b]Cas = Cascades (N = north, C = central), Coa = Coast Ranges (N = north, C = central, S = South), Kla = Klamath and Siskiyou Mountains, NW Cal = northwest California.
[c]ST = snap trap, LT = live trap, PF = pitfall trap.
[d]Post hoc estimate based on data provided in publication.
[e]NR = not reported.

References

Anthony, R.G., Forsman, E.D., Green, G.A., Witmer, G., Nelson, S.K., 1987. Small mammal populations in riparian zones of different-aged coniferous forests. Murrelet 68, 94–102. http://andrewsforest.oregonstate.edu/pubs/pdf/pub1229.pdf.

Baker, D., Palmer, C., Tolle, T., 2005. Northwest Forest Plan: the first ten years (1994–2003): implementation monitoring: accomplishments and compliance with plan requirements. USDA Forest Service, Pacific Northwest Region, Portland, Oregon.

Bellinger, M.R., Haig, S.M., Forsman, E.D., Mullins, T.D., 2005. Taxonomic relationship among *Phenacomys* voles as inferred by cytochrome *b*. J. Mammal. 86, 201–210. https://www.jstor.org/stable/4094303.

Biswell, B.L., Forsman, E.D., 2010. Field trials on line transect methods to estimate abundance of trees containing nests of the red tree vole. Unpublished draft manuscript. USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, Oregon.

Bury, R.B., Corn, P.S., 1987. Evaluation of pitfall trapping in northwestern forests: trap arrays with drift fences. J. Wildl. Manage. 51, 112–119. https://www.jstor.org/stable/pdf/3801640.pdf.

Caughley, G., 1994. Directions in conservation biology. J. Anim. Ecol. 63, 215–244. https://doi.org/10.2307/5542.

Cole, E.C., McComb, W.C., Newton, M., Leeming, J.P., Chambers, C.L., 1998. Response of small mammals to clearcutting, burning, and glyphosate application in the Oregon Coast Range. J. Wildl. Mange. 62, 1207–1216. https://doi.org/10.2307/3801984.

Corn, P.S., Bury, R.B., 1991. Small mammal communities in the Oregon Coast Range. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (tech. coords.). Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service, Pacific Northwest Research Station General Technical Report PNW-GTR-285, Portland, Oregon, pp. 241–254. https://www.fs.fed.us/pnw/pubs/gtr285/.

Corn, P.S., Bury, R.B., Spies, T.A., 1988. Douglas-fir forests in the Cascade Mountains of Oregon and Washington: is the abundance of small mammals related to stand age and moisture? In: Szaro, R.C., Severson, K.E., Patterson, D.R. (tech. coord.). Management of amphibians, reptiles, and small mammals in North America. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report RM-166. Fort Collins, Colorado, pp. 340–352. https://www.fs.fed.us/rm/pubs_rm/rm_gtr166.pdf.

Connaughton, K., Shepard, E.W., 2011. Memorandum: 2011 settlement agreement in litigation over the survey and manage mitigation measure in Conservation Northwest et al. v. Sherman et al., Case No. 08-1067-JCC (W.D. Wash.). USDA Forest Service, USDI Bureau of Land Management BLM-Instruction Memorandum No. OR-2011-063, Portland, OR.

Cross, S.P., 1985. Response of small mammals to forest riparian perturbations. In: Johnson, R.R., Ziebell, C.D., Patton, D.R., Folliott, P.F., Hamre, R.H. (tech. coords.). Riparian ecosystems and their management: reconciling conflicting uses. USDA Forest Service, Rocky Mountain Forest and Range Experimental Station General Technical Report RM-20, Fort Collins, Colorado. https://www.fs.fed.us/rm/pubs_rm/rm_gtr120.pdf.

Dizney, L., Jones, P.D., Ruedas, L.A., 2008. Efficacy of three types of live traps used for surveying small mammals in the Pacific Northwest. Northwestern Nat. 89, 171–180. https://www.bioone.org/doi/pdf/10.1898/NWN08-18.1.

Doyle, A.T., 1985. Small mammal micro- and macrohabitat selection in streamside ecosystems, Dissertation. Oregon State University, Corvallis, Oregon.

Dunk, J.R., Hawley, J.J.V.G., 2009. Red-tree [sic] vole habitat suitability modeling: implications for conservation and management. For. Ecol. Manage. 258, 626–634.

https://doi.org/10.1016/j.foreco.2009.04.041.
Flather, C.H., Sieg, C.H., 2007. Species rarity: definition, causes, and classification. In: Raphael, M.G., Molina, R. (Eds.), Conservation of rare or little-known species: biological, social, and economic considerations. Island Press, Covelo, California, pp. 40–66.
Fontaine, J.B., 2007. Influences of high severity fire and postfire logging on avian and small mammal communities of Siskiyou Mountains, USA. Dissertation. Oregon State University, Corvallis. Oregon.
Forsman, E.D., Swingle, J.K., Davis, R.J., Biswell, B.L., Andrews, L.S., 2016. Tree voles: an evaluation of their distribution and habitat relationships based on recent and historical studies, habitat models, and vegetation change. USDA Forest Service, Pacific Northwest Research Station General Technical Report PNW-GTR–948. https://www.fs.fed.us/pnw/pubs/pnw_gtr948.pdf.
Gashwiler, J.S., 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology 51, 1018–1026. https://www.jstor.org/stable/1933628?seq=1#metadata_info_tab_contents.
Gilbert, F.F., Allwine, R., 1991. Small mammal communities in the Oregon Cascade Range. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (tech. coord.). Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service, Pacific Northwest Research Station General Technical Report, PNW-GTR-285, Portland, Oregon, pp. 256–267. https://www.fs.fed.us/pnw/pubs/gtr285/.
Gillesberg, A.-M., Carey, A.B., 1991. Arboreal nests of *Phenacomys longicaudus* in Oregon. J. Mammal. 72, 784–787. https://www.fs.fed.us/pnw/pubs/journals/pnw_1991_gillesberg001.pdf.
Gitzen, R.A., West, S.D., Maguire, C., Halpern, C.B., 2007. Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in the Pacific Northwest. For. Ecol. Manage. 251, 142–155. https://doi.org/10.1016/j.foreco.2007.05.028.
Gomez, D.M., Anthony, R.G., 1998. Small mammal abundance in riparian and upland areas of five seral stages in western Oregon. Northwest Sci. 72, 293–302. https://research.wsulibs.wsu.edu/xmlui/bitstream/handle/2376/1209/v72%20p293%20Gomez%20and%20Anthony.PDF?sequence=1.
Gomez, D.M., Anthony, R.G., Lowe, R.W., 1997. Small mammal and amphibian abundance at Cape Meares National Wildlife Refuge. Unpublished report on file at USDI Fish and Wildlife Service, Oregon Coastal Refuges. Hatfield Marine Science Center, Newport, Oregon.
Hayes, J.P., Adam, M.D., Anthony, R.G., Witt, J.W., 1996. Comparison of the effectiveness of Sherman and modified Fitch live-traps for capture of small mammals. Northwestern Nat. 77, 40–43. https://doi.org/10.2307/3536617.
Hooven, E.F., 1971. Effects of clearcutting a Douglas-fir stand upon small animal populations in western Oregon, Dissertation. Oregon State University, Corvallis, Oregon.
Hooven, E.F., Black, H.C., 1976. Effects of some clearcutting practices on small-mammal populations in western Oregon. Northwest Sci. 50, 189–208.
Huff, R., 2016. High-priority site management recommendations for the red tree vole. Version 1.0. USDA Forest Service Regions 5 and 6, and USDI Bureau of Land Management, Oregon/Washington, Portland, Oregon.
Johnston, A.N., 2006. Relative abundance and habitat associations of small mammals in two forest types in southern Oregon. Thesis. Oregon State University, Corvallis, Oregon.
Manning, J.A., 2002. Small mammal responses to silvicultural fuels treatments in southwest Oregon. Thesis. Oregon State University, Corvallis, Oregon.
Manning, J.A., Edge, W.D., 2004. Small mammal survival and downed wood at multiple scales in managed forests. J. Mammal. 85, 87–96. https://doi.org/10.1644/1545-1542(2004) 085<0087:SMSADW>2.0.CO;2.
Marks-Fife, C.A., 2016. Estimation of population age structure, detection probability, and density of red tree voles in Oregon. Thesis. Oregon State University, Corvallis, Oregon.
Martin, K.J., McComb, W.C., 2002. Small mammal habitat associations at patch and landscape scales in Oregon. For. Sci. 48, 255–264. https://academic.oup.com/forestscience/article/48/2/255/4617448.
Maser, C., 1966. Life histories and ecology of *Phenacomys albipes, Phenacomys longicaudus, Phenacomys silvicola*. Thesis. Oregon State University, Corvallis, Oregon.
Maser, C., 1968. Personal communication to senior author regarding establishment of tree vole population study area, Corvallis, Oregon.
Maser, C., 1988. Mammals of the Pacific Northwest: From the Coast to the High Cascades. Oregon State University Press, Corvallis, Oregon.
Maser, C., Trappe, J.M., Nussbaum, R.A., 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59, 799–809. https://doi.org/10.2307/1938784.
McComb, W.C., McGarigal, K., Anthony, R.G., 1993. Small mammal and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, western Oregon. Northwest Sci. 67, 7–15. http://hdl.handle.net/2376/1573.
Meslow, E.C., 2018. Personal communication regarding criteria used by Thomas et al. (1993b) to evaluate likelihood of persistence of small mammals, Corvallis, Oregon.
Musser, G.G., Carlton, M.D., 2005. Genus *Myodes*. In: Wilson, D.E., Reeder, D.M. (Eds.), Mammal species of the world: a taxonomic and geographic reference, 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
Olson, D.H., Van Norman, K.J., Huff, R.D., 2007. The utility of strategic surveys for rare and little-known species under the Northwest Forest Plan. USDA Forest Service, Pacific Northwest Research Station General Technical Report, PNW-GTR-708, Portland, Oregon.
Oregon Department of Forestry, 2010. Northwest Oregon state forests management plan. Revised plan April 2010. http://www.oregon.gov/ODF/Documents/AboutODF/2010FMPNorthwestOregon.pdf.
Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62, 3–135. https://www.webpages.uidaho.edu/wlf448/2011/lab/otis%20etal%201978.pdf.
Pechman, M.J., 2006. Northwest Ecosystem Alliance et al. v. Mark E. Rey: Case No. C04-844-P stipulation and (proposed) order RE: injunction. US District Court, Western District of Washington, Seattle, Washington.
Price, A.L., Mowdy, J.S., Swingle, J.K., Forsman, E.D., 2015. Distribution and abundance of tree voles in the northern Coast Ranges of Oregon. Northwestern Nat. 96, 37–49. https://doi.org/10.1898/NWN14-04.1.
Ralph, C.J., Paton, P.W.C., Taylor, C.A., 1991. Habitat association patterns of breeding birds and small mammals in Douglas-fir/hardwood forests in northwestern California and southwestern Oregon. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (tech. coord.). Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service, Pacific Northwest Research Station General Technical Report, PNW-GTR-285, Portland, Oregon, pp. 378–393. https://www.fs.fed.us/pnw/pubs/gtr285/.
Raphael, M.G., 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests in northwestern California. In: Szaro, R.C., Severson, K.E., Patterson, D.R. (tech. coord.). Management of amphibians, reptiles, and small mammals in North America. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report RM-166. Fort Collins, Colorado, pp. 22–31. https://www.fs.fed.us/rm/pubs_rm/rm_gtr166.pdf.
Rittenhouse, B., Breckle, R., Alegria, J., Max, T., Edwards, T.C., 2002. Survey protocol for conducting red tree vole strategic survey on randomly selected CVS/FIA plots. Unpublished report USDA Forest Service and USDI Bureau of Land Management, Portland, Oregon.
Rosenberg, D.K., 2019. A tale of two voles: the challenge of the commonness-rarity continuum in conservation planning. For. Ecol. Manage. 434, 165–171. https://doi.org/10.1016/j.foreco.2018.12.010.
Rosenberg, D.K., Swindle, K.A., Anthony, R.G., 1994. Habitat associations of California red-backed voles in young and old-growth forests in western Oregon. Northwest Sci. 68, 266–272. http://hdl.handle.net/2376/1561.
Rosenberg, D.K., Swindle, K.A., Anthony, R.G., 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. Canadian J. Zool. 81, 1715–1725. https://doi.org/10.1139/z03-167.
Rosenberg, D.K., Davis, R.J., Van Norman, K.J., Dunk, J.R., Forsman, E.D., Huff, R.D., 2016. Patterns of red tree vole distribution and habitat suitability: implications for surveys and conservation planning. Ecosphere 7, 1–21. https://doi.org/10.1002/ecs2.1630.
Sherrell, P.E., 1970. An annotated checklist of the land mammals of Curry County, Oregon. Thesis. Central Washington State College, Ellensburg, Washington.
Suzuki, N., 1992. Habitat classification and characteristics of small mammal and amphibian communities in beaver-pond habitats of the Oregon Coast Range. Thesis. Oregon State University, Corvallis, Oregon.
Suzuki, N., Hayes, J.P., 2003. Effects of thinning on small mammals in Oregon coastal forests. J. Wildl. Manage. 67, 352–371. https://www.doi.org/10.2307/3802777.
Swingle, J.K., 2005. Daily activity patterns, survival, and movements of red tree voles (*Arborimus longicaudus*) in western Oregon. Thesis. Oregon State University, Corvallis, Oregon.
Swingle, J.K., Forsman, E.D., 2016. Annotated bibliography of the red tree vole (*Arborimus longicaudus*), Sonoma tree vole (*A. pomo*), and white-footed vole (*A. albipes*). USDA Forest Service, Pacific Northwest Research Station General Technical Report PNW-GTR–948. https://www.fs.usda.gov/treesearch/pubs/52322.
Swingle, J.K., Forsman, E.D., Anthony, R.G., 2010. Survival, mortality, and predators of red tree voles (*Arborimus longicaudus*). Northwest Sci. 84, 255–265. https://doi.org/10.3955/046.084.0305.
Swingle, J.K., Forsman, E.D., Sovern, S.G., 2004. A method for live-trapping tree voles. In: Northwestern Nat. 85. pp. 134–135.
Thomas, J.W., Raphael, M.G., Meslow, E.C., et al., 1993a. Forest ecosystem management: an ecological, economic, and social assessment: report of the Forest Ecosystem Management Assessment Team. USDA Forest Service, USDI Bureau of Land Management, and USDI Fish and Wildlife Service, Portland, Oregon.
Thomas, J.W., Raphael, M.G., Anthony, R.G., Forsman, E.D., Gunderson, A.G., Holthausen, R.S., Marcot, B.G., Reeves, G.H., Sedell, J.R., Solis, D.M., 1993b. Viability assessments and management considerations for species associated with late-successional and old-growth forests of the Pacific Northwest: the report of the Scientific Analysis Team. USDA Forest Service, Portland, Oregon.
Ure, D.C., Maser, C., 1982. Mycophagy of red-backed voles in Oregon and Washington. Can. J. Zool. 60, 3307–3315. https://doi.org/10.1139/z82-419.
USDA Forest Service, USDI Bureau of Land Management, 1994. 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, Oregon. https://www.blm.gov/or/plans/nwfpnepa/FSEIS-1994/newsandga.pdf.
USDA Forest Service, USDI Bureau of Land Management, 2001. Record of decision and standards and guidelines for amendment to the survey and manage, protection buffer, and other mitigation measures standards and guidelines, Portland Oregon https://www.blm.gov/or/plans/surveyandmanage/files/rd-rod_s_and_g-2001-01.pdf.
USDA Forest Service, USDI Bureau of Land Management, 2004. Record of Decision to remove or modify the survey and manage mitigation measure standards and guidelines in Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owls, Portland, Oregon.
USDI Bureau of Land Management, 2007. Record of decision to remove the survey and manage mitigation measure standards and guidelines from Bureau of Land Management land and resource management plans within the range of the northern spotted owl, Portland, Oregon. https://www.blm.gov/or/plans/surveyandmanage/files/01-2007_fs_record_decision.pdf.
USDI Bureau of Land Management, 2016a. Northwestern and coastal Oregon record of

decision and resource management plan. Portland, Oregon. https://www.blm.gov/or/plans/rmpswesternoregon/files/rod/Northwestern_and_Coastal_Oregon_ROD_RMP.pdf.

USDI Bureau of Land Management, 2016b. Southwestern Oregon record of decision and resource management plan. Portland, Oregon. https://www.blm.gov/or/plans/rmpswesternoregon/files/rod/SWO_ROD_RMP.pdf.

USDI Fish and Wildlife Service, 2011. Endangered and threatened wildlife and plants; 12-month finding of a petition to list a distinct population segment of the red tree vole as endangered or threatened. Fed. Reg. 76, 63720–63762. https://www.federalregister.gov/documents/2011/10/13/2011-25818/endangered-and-threatened-wildlife-and-plants-12-month-finding-on-a-petition-to-list-a-distinct.

Verts, B.J., Carraway, L.N., 1998. Land Mammals of Oregon. The University of California Press, Berkeley, California.

Waldien, D.L., 2005. Population and behavioral responses of small mammals to silvicultural and downed wood treatments in the Oregon Coast Range. Dissertation. Oregon State University, Corvallis, Oregon.

Waters, J.R., Zabel, C.J., 1998. Abundance of small mammals in fir forests in northeastern California. J. Mammal. 79, 1244–1253. https://doi.org/10.2307/1383015.

Weldy, M.J., Epps, C.W., Lesmeister, D.B., Manning, T., Linnell, M.A., Forsman, E.D., 2019. Abundance and ecological associations of small mammals. J. Wildl. Manage. Early online version. https://doi.org/10.1002/jwmg.21641.

White, G.C., Anderson, D.R., Burnham, K.P., Otis, D.L., 1982. Capture-recapture and removal methods for sampling a closed population. Los Alamos National Laboratory Report LA-8787-NERP, Washington D.C.

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