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A tale of two voles: The challenge of the commonness-rarity continuum in conservation planning

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A B S T R A C T

Species rarity is often an important driver of conservation priorities in lieu of greater knowledge of extinction risk. Land management agencies often prioritize management based in part on the commonness of a species, yet identifying what constitutes where a species lies on the commonness-rarity continuum is difficult. Given limited resources, incorrect classification may have detrimental effects on species conservation. In a large area of the Northwest Forest Plan, which guides management of 9.1 million ha of federal forests in the Pacific Northwest, USA, forest management is closely tied to mitigation for the red tree vole (*Arborimus longicaudus*), a species considered uncommon due in part to its association with older forests. I explore the ability to provide insight into where a species lies along the commonness-rarity continuum by a multi-species comparison. I compared the relative distribution, abundance, and extrinsic conservation threats of red tree voles to western red-backed voles (*Myodes californicus*), a similar species considered common. Both species occur in younger forests with legacy components of older forests, but reach their greatest densities within older forests. Densities of the two vole species were qualitatively similar. If assignment of a species along a commonness-rarity continuum is a goal of species surveys, their value may be enhanced by including in the survey a set of similar species whose level of rarity is better understood. Although management of the red-tree vole was intended to be guided by adaptive management, challenging policy and legal issues have made that difficult; rarity as a criterion for prioritizing management is partly responsible.

1. Introduction

Where a species lies along the continuum from common to rare is often used to prioritize conservation efforts (Molina et al., 2006; Gaston and Fuller, 2008) because such rankings are often equated with extinction risk (Gaston, 1994; Rosenzweig and Lomolino, 1997; Toledo et al., 2014). Although it is widely recognized that in and of itself the level of rarity is not often indicative of extinction likelihoods, its use as a criterion is prevalent (Gaston, 1994; Mace and Kershaw, 1997; Gaston and Fuller, 2008). Failure to separate threats from rarity has likely led to an emphasis on rarity in natural resource management (Caughley, 1994; Flather and Sieg, 2007). Given the limited ability to differentiate where on the commonness-rarity continuum a species falls based on a species' physical, behavioral, or ecological traits (Gaston, 1994; Gaston and Kunin, 1997), it is challenging to assign a species to the oft-used classes such as common, uncommon, and rare.

Rabinowitz (1981) identified different types of rarity based on classification among three key traits placed into dichotomous categories: geographic extent of range (large/small), local population size (somewhere large/everywhere small), and habitat breadth (wide/narrow). From the possible relationships of these three traits, Rabinowitz (1981) delineated eight types, one of which represented common species: large geographic range, locally abundant and broad habitat niche. The other seven classifications identified various forms of rarity and have formed the framework for much of the theory on rarity and extinction risk (Harnik et al., 2012). Because most species are relatively numerous in some areas but are absent or sparse in others (Brown, 1984; Schoener, 1987; Magurran and Henderson, 2003), the distinction between rare and common is complex and often arbitrary. Classification of the level of rarity is usually most instructive as a relative difference between similar taxa (Preston, 1948; Reveal, 1981; Brown, 1984; Gaston, 1994; Blackburn and Gaston, 1997; Flather and Sieg, 2007) assessed on a set of core species within a geographic area of interest (Magurran and Henderson, 2003).

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Although the distinction as rare, uncommon, or common may not be indicative of extinction risk, it has been the basis for significant management direction, as demonstrated by the Northwest Forest Plan (NWFP). The NWFP was intended to provide a reasonable assurance of species persistence for plants, animals, and fungi associated with old forests and allow for timber harvest. The plan area included 9.8 million ha of lands managed by the Bureau of Land Management and U.S. Forest Service in northwestern California, western Oregon and western Washington (USDA and USDI, 1994). Population persistence under various management options was assessed through expert panels for species considered potentially associated with old forest (FEMAT, 1993). Species considered at risk were classified into six management categories which were based in large part on the species' relative rarity (USDA and USDI, 2001). To be placed in one of these categories, a species had to occur or was thought to occur within the NWFP area, be closely associated with old (≥80 years) forests, and the reserve system and other standards and guidelines of the NWFP did not provide a reasonable assurance of species persistence (USDA and USDI, 2001). Species that expert panels concluded had a ≥80% likelihood of having viable and well-distributed populations were considered to be adequately protected, whereas species with a likelihood of persistence of < 80% were considered in need of additional mitigation (FEMAT, 1993). Abundance and distribution of old forests, and dispersal potential, were important factors in the evaluation of persistence (FEMAT, 1993).

Species that were considered uncommon but for which surveys were practical were placed in a management category for which mitigation required conducting pre-disturbance surveys and avoiding habitat disturbance to high-priority sites where the species was found (USDA and USDI, 1994; Molina et al., 2006). This resulted in very different management strategies for some otherwise similar species. An excellent example is given by the divergent management approaches taken for two rodent species. The likelihood of persistence for red tree voles (*Arborimus longicaudus*) and western red-backed voles (*Myodes californicus*; hereafter red-backed vole) was evaluated under multiple forest management options (FEMAT, 1993). Under the option that ultimately became the Northwest Forest Plan, the expert panel rated red-backed voles with a 90% likelihood of having well-distributed viable populations and red tree voles with a 73% likelihood, 7% lower than the threshold value (FEMAT, 1993:IV-172).

These findings ultimately resulted in no special management for red-backed voles, but red tree voles were designated into a management category that required mitigation (USDA and USDI, 2001). When red tree vole nests were detected during pre-disturbance surveys, mitigation required a 4 ha management buffer, centered on the nest tree (USDA and USDI, 2001). These divergent management approaches were largely due to the perspective that red tree voles were uncommon, and largely restricted to old forest whereas red-backed voles were common and had a broader distribution among forest age classes (e.g., Aubrey et al., 1991). This understanding suggested that red tree voles may be potentially isolated in old forest patches ("locally restricted", FEMAT, 1993: Table IV-38), thus reducing their likelihood of persistence. Mitigation made sense from a precautionary principle, and adaptive management was intended to allow for changes to their management if warranted.

I compared the distribution and abundance of red tree voles to red-backed voles as a case study in the efficacy of a comparative species approach. Both vole species are endemic to moist coniferous forests in Oregon and northern California, most abundant in forests that contain elements of old forests, and sympatric in a large portion of their range, with red-backed voles extending farther into California and occupying higher elevations of the Cascade range than red tree voles (Verts and Carraway, 1998; Wilson and Ruff, 1999; Forsman et al., 2016). Body mass is similar at 28 g and 23 g for red tree voles and red-backed voles, respectively (Verts and Carraway, 1998). Both species have similar reproductive rates (approximately 3 young/litter, Verts and Carraway, 1998:302) and number of litters/year (approximately 3; Hamilton, 1962; Verts and Carraway, 1998). Based on the few studies conducted, both species have small home range sizes, averaging < 1 ha (Swingle and Forsman, 2009; Thompson et al., 2009). Their ecologies differ primarily in the tree vole's arboreal existence and its narrow diet, consisting of needles and twigs of several species of conifers (Kelsey et al., 2009; Forsman et al., 2016) whereas the diet of the terrestrial red-backed voles is dominated by hypogeous fungi and lichens (Alexander and Verts, 1992). Red tree voles and red-backed voles are both globally rare (sensu Rabinowitz, 1981) because of their restricted ranges but locally abundant in some locations and vegetation types (Forsman et al., 2004; Tallmon and Mills, 2004). Using the classification of Rabinowitz (1981), both species would be classified similarly among the seven forms of rarity: small geographic range but locally abundant in specific habitat.

2. Methods

I evaluated patterns of abundance for the two vole species based on published papers, unpublished reports, and an analysis I conducted from previously published data. I did not include estimates of abundance based on kill-based traps (snap traps and pit-fall traps) because red tree voles are rarely captured in these traps due to their arboreal nature (Carey et al., 1991; Swingle et al., 2004) and because of the likely overestimation of densities of red-backed voles when animals move into areas soon after removal of individuals from trapping. If densities were not reported, I computed densities based on the area of the trap grid or area searched and the number of individuals counted or estimated within those areas.

2.1. Red tree voles

Two studies estimated tree vole density based on visual observations. Maser (1966) attempted to enumerate tree voles from a 12.4 ha young (approximately 50 years) stand in the Oregon Coast Range where voles were known to occur. Between April and June 1965, Maser (1966) searched for tree voles in each nest he found within the study area. As part of a more extensive study, described below, Marks-Fife (2016) estimated minimum density of adult tree voles in the central and southern portions of the Oregon Coast Ranges by including whether or not a vole was detected in a nest as a covariate in distance-based models.

Gillesberg and Carey (1991) counted tree vole nests from large trees that were felled in a 35 ha old growth forest in the western Oregon Cascades. I computed the minimum density of trees with vole nests as the number of downed trees in which nests were detected within the entire 35 ha study area. Only a small, but unknown, proportion of trees were felled within the study area. Therefore, the density estimate represents a minimum number of trees with vole nests.

Later studies used line-transect surveys and distance-based estimation. Biswell and Forsman (unpublished manuscript; B. Biswell, personal communication, and cited in Marks-Fife [2016]) estimated densities of trees with vole nests from a stratified random sample of three tree size-classes on the eastern slope of the Oregon Coast Ranges and foothills of the Willamette Valley. Tree size-classes included pole (13–28 cm dbh, 28–61 yr), young (29–53 cm dbh, 31–73 yr), and old (> 53 cm dbh, 108–200 yr) stands. Density of nest trees was estimated by pooling observations across all stands because of the small number of observations.

In the central and southern Coast Ranges of Oregon, Marks-Fife (2016) estimated density of trees with vole nests and the density of nest trees with voles observed using line transects and distance estimation in young (25–79 years), mature (80–200 years), and old (> 200 years) forest. A total of 36 stands were sampled, and five were not included in analyses because voles were not detected and analyses were limited to stands with voles detected. Marks-Fife (2016) used two approaches to

Table 1
Estimated densities (No./ha) of red tree voles or their nest trees.

Method	Metric	Stand age class[a]					Data type	Source
		Pole	Young	Mature	Old	Pooled		
Distance	Nest trees	0.14	0.46	0.90		0.49	All nests	Biswell and Forsman, unpublished manuscript
Distance	Nest trees		5.5	11.9	11.5	9.4	Active nests	Marks-Fife (2016)
Distance	Occupied nest trees					1.9	Voles observed	Marks-Fife (2016)
Distance	Adult voles		2.6	5.5	5.6	4.2	Estimated vole density[b]	Marks-Fife (2016)
Nests in felled trees	Nest trees				1.3[c]		All nests	Gillesberg and Carey (1991)
Capture	Voles		3.3[d]				Observations and captures	Maser (1966)

[a] Biswell and Forsman: pole = 13–28 cm dbh (28–61 y), young = 29–53 cm dbh (31–73 y), mature = > 53 cm dbh (108–200 y). Marks-Fife: young = 25–79 y, mature (80–200 y) and old growth (> 200 y) within stands known occupied. Maser: 50 y.
[b] Marks-Fife (2016) estimated the number of individuals as the number of active nest trees / number of nest trees per home range reported in Swingle (2005), including only stands with tree voles detected.
[c] Estimate is considered a minimum number because only a small proportion of trees were felled and examined for vole nests.
[d] All ages of voles; Maser (1966) estimated 1.0 adult voles/ha.

estimate density of adult tree voles. First, he estimated minimum density of adult tree voles by including whether or not a vole was detected in a nest as a covariate in distance-based models. Second, he used Swingle's (2005) mean estimate of 2.6 nest trees/adult vole to adjust nest tree densities to a proxy measure of tree vole density.

The most rigorous assessment of spatial patterns of abundance was conducted during 2001–2004 from a stratified random sample of forest plots across the species' range. Using these data, I estimated occurrence rates at multiple spatial scales to provide a broad assessment of the species' distribution across their range. Surveys were conducted on Current Vegetation Survey and Forest Inventory and Analysis plots on federal lands (Rittenhouse et al., 2002). Age stratification was based on two age classes: (1) young forest (≤80 years) and (2) old forest (> 80 years). Land-use strata included reserved lands where management is focused on maintenance and restoration of old forests (Reserve) and non-reserved lands where timber harvest is emphasized (Matrix; USDA and USDI, 1994; Molina et al., 2006). I included only plots within the species' range as depicted by Forsman et al. (2016), resulting in a total of 301 2-ha plots. Surveys for tree vole nests were conducted within two adjacent 1 ha square plots (Rittenhouse et al., 2002). I computed frequency of occurrence in the 2-ha plots based on the detection of either an active or an inactive nest because inactive tree vole nests persist for only a couple of years (Thompson and Diller, 2002), demonstrating their recent occupancy. I estimated frequency of occurrence at three different spatial scales: range-wide, physiographic provinces used in the NWFP (USDA and USDI, 1994:A-3), and geographic subregions (Forsman et al., 2016). Because relatively few young forest plots were sampled, I limited estimates at the province and subregion scales to old forest plots.

2.2. Red-backed voles

All of the studies included in my comparisons were from studies using grids of live traps. The earliest estimates of abundance of red-backed voles were from comparisons of old forests and recent clearcut harvests (Gashwiler, 1970; Hooven and Black, 1976). Gashwiler (1970) estimated densities from 1954 − 1965 in two old forests (200 years) in the western Oregon Cascades. One of the old forests was harvested after the first year and the changes in vole abundance between the harvested and the non-harvest stand were compared through time. To obtain the average estimate of density in old forest, I used the mean value of the two old forest stands prior to logging and the estimates from the one unharvested old stand for the remaining 10 years of the study. For the average red-backed vole density in the clearcut stand, I used the average estimated densities for the 10 years following harvest.

Similarly, Hooven and Black (1976) compared vole density between an old forest (125 years) and two recent clearcut stands in the western Oregon Cascades. The authors combined individuals captured during the three-day trap period across the seven-month season. Such an approach overestimates abundance by including recruitment, but ignoring mortality. Because captures per trap period were not reported, I used the average estimate for each of the three years in the two clearcut stands and the annual estimate from the single old forest stand.

Several other studies estimated red-backed vole densities in different stand age classes in the western Oregon Cascades. Rosenberg et al. (1994) sampled five old (> 400 years) and five young (30–60 years) stands. Gorman et al. (unpublished report; J. Hagar, personal communication) reported the number of individual red-backed voles captured in young (30–50 years) stands prior to thinning and Weldy (2018) sampled 6–9 old (> 200 years) stands during 2011–2016.

Two studies were conducted in the southern portion of the species' range. Tallmon and Mills (2004) compared red-backed vole densities among old forest remnants and adjacent young forests in the Siskiyou Mountains of southwestern Oregon during 1998–1999. In northeastern California, Waters and Zabel (1998) sampled old (200–400 years), mature (80–100 years), and shelterwood stands, the latter comprised of scattered large trees sampled 6–7 years after harvest.

3. Results

3.1. Red tree vole

Of the two studies that relied on visual observation of voles, Maser (1966) captured 40 animals (3.2 voles/ha), of which 30% were adults (1.0/ha; Table 1). From a larger study in the Oregon Coast Ranges, Marks-Fife (2016) estimated a minimum density of 1.9 adult voles/ha, averaged across all stand ages.

The remaining studies were based on observation of nests of tree voles. Gillesberg and Carey (1991) observed nests in 45 of the 82 (54.9%) felled trees resulting in a minimum estimate of 1.3 nest trees/ha (Table 1). In their more extensive study, Biswell and Forsman (unpublished manuscript, B. Biswell, personal communication) estimated an average density of 0.49 nest trees/ha, which ranged from 0.0 to 4.4 nest trees/ha among the 77 stands. Density of nest trees was 6.4 times greater in old forests than pole stands (13–28 cm dbh) and 2.0 times greater than in young stands (29–53 cm dbh; Table 1). However, two young stands had the highest estimated densities of nest trees, demonstrating the considerable variation among stands and the inconsistent patterns across forest age. Few trees with vole nests were detected in pole stands (13%), whereas nests were detected in 33% and 59% of young and old stands, respectively.

From a survey of transects within 36 forest stands in the Oregon Coast Ranges, Marks-Fife (2016) estimated a density of 5.5 to nearly 12 nest trees/ha in young and old age-classes, respectively (Table 1). The density of adult tree voles, using his proxy metric based on estimates of

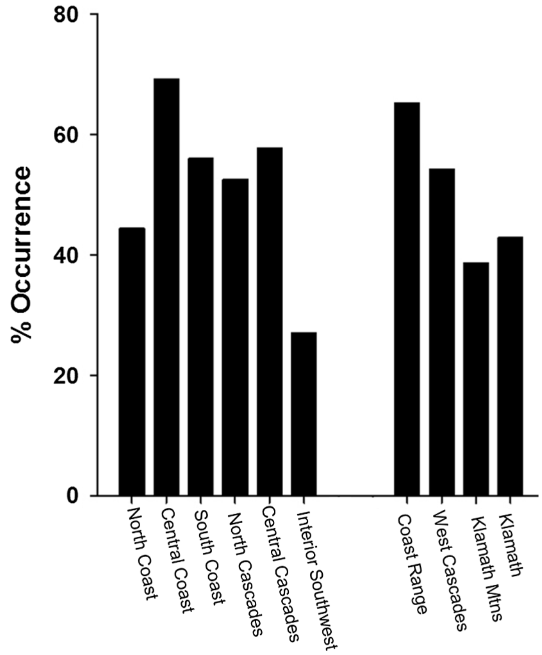

Fig. 1. Percent occurrence of red tree vole nests in old forest plots within lands managed by the Bureau of Land Management and the U.S. Forest Service. Occurrence in old forest plots was computed as the percent of 2-ha plots in which ≥1 red tree vole nest was detected during the 2002–2004 stratified random survey (Rittenhouse et al., 2002) in sub-regions (left) and physiographic provinces (right). Red tree vole nests were detected in a high percent of 2-ha plots, particularly in the Coast Ranges and Cascade Mountains.

the number of nest trees/vole, were 2.6, 5.5, and 5.6 voles/ha in young, mature, and old forest, respectively (Table 1).

Based on my analysis of the Rittenhouse et al. (2002) data, occurrence of red tree voles was highly variable across the species range and was over twice as high in old (51.5%, n = 237 plots) than in young forest plots (21.9%, n = 64 plots). Across physiographic provinces, occurrence within old forest ranged from 38.7% in the Klamath Mountains to 65.3% in the Coast Ranges (Fig. 1). Within subregions, occurrence in old forest was lowest within the Interior Southwest (27.1%) and highest in the Central Coast (69.2%; Fig. 1). There were few North Coast plots in old forest (n = 9 plots) and thus the estimate of 44% occurrence may not be representative.

3.2. Red-backed vole

The two early comparisons of red-backed vole densities in recently harvested and old forest reported similar results. Red-backed voles were either absent or rare in recent clearcut harvests, and in these stands they were only trapped at the edges between clearcut harvests and old forests (Gashwiler, 1970; Hooven and Black, 1976). Densities of red-backed voles in mature and old growth forests averaged approximately 7.0 voles/ha (Table 2).

In the study comparing young and old stands, red-backed voles had low densities in most young stands, and in some years they were absent in stands that originated from clearcut harvest (Rosenberg et al., 1994). Only the young stand that was fire-regenerated had densities (1.3 voles/ha) that were similar to those in old forests (1.4/ha; D. Rosenberg, unpublished data). Although red-backed vole densities were higher in old than in young stands (Table 2), densities were highly variable in old stands both across years and stands (Rosenberg et al., 1994).

Two other studies live-trapped red-backed voles in young and old stands in the western Oregon Cascades. The density of voles from 16 young stands in Gorman's (unpublished report; J. Hagar, personal communication) study ranged from 0 to 9.0 voles/ha among stands and years, and averaged 1.7 voles/ha (Table 2). Weldy (2018; personal communication) found high variation of red-backed vole densities in old forests, ranging from 0 to 36 voles/ha among stands and years with a mean of 10.8 voles/ha over all 9 sites and 3 years (Table 2). Annual and spatial variation was high with average vole densities ranging from 3.0 to 18.3 voles/ha among years with one grid having almost consistently the highest density.

Among old forest fragments in the Siskiyou Mountains, estimated densities ranged from 4.9 to 16.5 voles/ha and averaged 10.2 voles/ha. Voles were rarely captured, and nearly absent, in the young stands that resulted from clearcut harvests (Mills, 1995; Tallmon and Mills, 2004; Table 2).

In the only comparison of red-backed vole abundance outside of Douglas-fir forests of which I am aware, Waters and Zabel (1998) rarely captured voles in shelterwood harvests, had extremely low densities in mature stands, and their densities in old forest (0.45 voles/ha) were among the lowest of all reported densities in old forest stands (Table 2).

4. Discussion

Evaluation of species rarity has been an important component of prioritizing conservation efforts despite the recognition that extinction risk is much more complex than where a species lies on the commonness-rarity continuum (Caughly, 1994; Gaston, 1994; Molina et al., 2006; Gaston and Fuller, 2008; Harnik et al., 2012). Although much of the discussion revolves around biological factors contributing to rarity and methods to assign rarity (e.g., Gaston, 1994; Dobson et al., 1995; Kunin and Gaston, 1997), where a species lies along the commonness-rarity continuum has important implications to policy and management. Indeed, many large scale conservation planning efforts target species that are considered uncommon or rare.

The vastly different approaches federal agencies have taken on red tree vole and red-backed vole management resulted from the tree vole's initial inclusion as a species in the Survey and Manage Program (hereafter, survey and manage species) in the Northwest Forest Plan (Molina et al., 2006), and demonstrates how the classification of a species as common, uncommon, or rare matters in practical applications (Marcot et al., 2018). Although the distribution of potential suitable habitat and the species' dispersal abilities were used in identifying survey and manage species, the perceived level of rarity of the species within the planning area and among habitats was an important element in the decision process (USDA and USDI, 2001:6, Marcot et al., 2018).

The red-backed vole was considered common despite its association with old forests (FEMAT, 1993; IUCN, 2008a) whereas the red tree vole was considered uncommon (USDA and USDI, 2001:49) or "near-threatened" (IUCN, 2008b). The lack of data on red tree vole and red-backed vole abundance at the time the species were evaluated (FEMAT, 1993) may have contributed to over estimating commonness and rarity for red-backed voles and red tree voles, respectively. The two vole species are largely sympatric within their narrowly defined range. Forest age is an important determinant of occupancy and density for both species, likely related to characteristics of forest floor components in the case of red-backed voles (Doyle, 1987; Alexander and Verts, 1992; Rosenberg et al., 1994; Tallmon and Mills, 1994; Thompson et al., 2009) and tree structure (Gillesberg and Carey, 1991; Swingle, 2005; Forsman et al., 2016; Johnston and Moskal, 2017; Linnell et al., 2017, 2018) or nearby suitable habitat or older forests (Dunk and Hawley, 2009; Price et al., 2015; Rosenberg et al., 2016; Linnell et al., 2017) in the case of red tree voles.

The different intensities and breadth of sampling throughout the species' ranges and the different estimation approaches used by investigators made comparisons less than ideal. The methods of estimating relative abundance of both species often lacked rigor due to the unknown and likely non-constant detection probability across studies as well as the difficulty in interpreting indices of abundance (Hallett et al.,

Table 2
Mean density estimates of California red-backed voles (No./ha) based on number captured (NC) or model-based estimated density (ED).

Metric	Area method[b]	Stand age class[a] (No./ha)				Source
		Clearcut	Young	Mature	Old	
NC	MMDM	0			6.8	Gashwiler (1970)
NC	GRID	0		7.5		Hooven and Black (1976)
NC	GRID		0.3		1.4	Rosenberg et al. (1994)
NC	GRID	0[b]		0.1	0.5	Waters and Zabel (1998)
ED	GRID	rare[c]			10.2	Tallmon and Mills (2004)
NC	GRID				13.1	M. Weldy (personal communication) and Weldy (2018)
NC	MMDM		1.7			S. Garman (unpubl. report); J. Hagar (personal communication)

[a] Gashwiler: clearcut: 0–11 y, old: > 200 y; Hooven and Black: clearcut < 5 yr, mature = 125 y; Rosenberg et al.: young < 80, old > 400 y; Waters and Zabel: clearcut = shelterwood (low density of > 200 y trees), mature = 80–100 y, old = 200–400 y; Tallmon and Mills: Clearcut = 1–30 y; Old > 80 y; Weldy: old: > 200 y; Garman/Hagar: young = 40 y.

[b] Method used to estimate the effective area trapped, and from which densities were computed, included one-half of the mean maximum distance moved (MMDM) added to the perimeter of the trap grid or the area of the trap grid (GRID) with no adjustment for movement.

[c] < 1/20th of the relative densities in old forests; estimated densities not reported.

2003), such as the density of trees with vole nests. An additional difficulty in making range-wide comparisons is that only red tree voles were sampled throughout most of their range. The lack of a broad survey of the distribution of red-backed voles leads to greater uncertainty in interpreting differences between the two species' relative abundance in many parts of their ranges, particularly in the northern portion of Oregon. In the north coast, red tree voles are considered a distinct population segment and a Federal Candidate under the Endangered Species Act (USFWS, 2011), the latter consistent with threats to the population from extensive areas of intensively managed young forests that are outside of federal lands (Price et al., 2015; Forsman et al., 2016; Linnell et al., 2017).

Despite these challenges, my evaluation of studies related to the distribution and abundance of these two species provide a qualitative understanding of how these metrics differ between them. Based on the breadth of studies I examined, densities of red tree voles in old forest likely fall into the typical range of red-backed voles (1–13 voles/ha; Table 2). Both species achieved their highest densities, as evidenced by either animal density or frequency of occurrence, within older forests but both species occurred with reasonable frequency in younger forests as well, presumably those stands that retained components of old forests.

I view Marks-Fife's (2016) density estimate (5.5 voles/ha) as the most reliable estimate of the density of red tree voles in old forest because of his rigorous statistical approach that included estimating the detection probability of nests along the transect line and from a relatively large number of stands that were sampled. This estimate of vole density, however, is based on a proxy measure (Marks-Fife, 2016) which applied the number of nest trees used by individual voles in a previous study (Swingle, 2005) to estimate the number of individual voles. Despite the ad-hoc nature of such an estimate, it does provide a first approximation. Marks-Fife's (2016) modeled estimate of the minimum densities of 1.9 voles/ha provides further support for a density > 1 vole/ha. The very high frequency of occurrence of vole nests from other studies in older forests support these results over a broad area. Biswell and Forsman (unpublished manuscript; B. Biswell, personal communication) assumed all nest tees were detected along the transect line, a false assumption based on Marks-Fife's finding that locating a nest on the transect line is difficult. This suggests underestimation by Biswell and Forsman's study. Marks-Fife's (2016) density estimates were based on only stands that were known occupied by red tree voles during the study and from only the central and south coast regions. Applying Marks-Fife's (2016) results beyond occupied stands would lead to positively biased average densities. Given the high frequency of occurrence in old conifer forests (51%) at the small spatial scale of 2 ha from the random sample of old stands (see Results), it is very likely that Marks-Fife's (2016) estimates are more robust than the sampling methodology suggests. Even in young stands, the frequency of occurrence in 2-ha stratified random plots was moderately (21.9%) high (see Results), lessening the potential bias in broader application of Marks-Fife's (2016) estimates within the central and southern portion of the Oregon Coast Ranges.

Red tree vole studies generally corroborate density estimates of > 1 per ha in old forests and in some young stands. For example, Maser's (1966) enumeration of all tree voles in a 35-ha young stand resulted in estimates of ≥1 vole per ha, demonstrating that at least in some young stands they can be relatively abundant. Gillesberg and Carey's (1991) finding that 54.9% of felled trees contained nests would equate to a density much greater than 1 vole/ha given the low proportion of trees that were sampled and the number of nest trees used by individual voles. This is consistent with the 1.0–1.9 voles/ha that Linnell et al. (2017) assumed occupied old forest patches. In areas of suitable habitat, red-backed voles and red tree vole densities were above the median value of 1 animal/ha for small mammals in a synthesis of rarity of New World mammals, and consistent with what the authors considered "common" (Yu and Dobson, 2000). Further, model-based suitable habitat for red tree voles included approximately 1.6 million ha and was generally well distributed in a large portion of their range (Forsman et al., 2016).

The rationale for the dichotomous management policy for these two species was based on data available during the initial evaluations (FEMAT, 1993). Surveys conducted on red tree voles since its designation as a survey and manage species demonstrates that this species is much more abundant and well distributed than initially believed, at least for populations outside of the northern portion of their range. The Annual Species Review process of the NWFP (https://www.blm.gov/or/plans/surveyandmanage/species.php) was intended to review updated information and recommend changes to management. Although federal agencies have updated their management in response to new information on red tree voles, such as restricting where surveys are required and designating high priority sites (Huff, 2016), changes have been limited due in large part to legal rulings (https://www.blm.gov/or/plans/surveyandmanage/history.php). The difficulty of incorporating updated information to public policy that has important political, economic and social considerations may be one reason adaptive management has not been as successful as once envisioned (Allen and Gunderson, 2011). Once a species has been included as one deserving special management, it may be difficult to remove due to court challenges, such as occurred with the red tree vole. Updating the scientific basis for a species to be listed for special management should be the first step in modifying management, and the approach I used here facilitates ways to address the rarity criterion that is part of the Northwest Forest Plan and many other conservation assessments and planning documents.

5. Conclusions

Prioritizing conservation actions based on where a species lies along the commonness-rarity continuum is fraught with challenges. Estimating abundance and distribution of a single species is inadequate to address rarity because ultimately it is a relative measure among species, populations, or through time (Preston, 1948; Reveal, 1981; Brown, 1984; Gaston, 1994; Blackburn and Gaston, 1997; Flather and Sieg, 2007). Species surveys to assess rarity are often conducted, yet placing the results in a broader context is difficult, and most such survey data may be uninformative despite the often high cost in collecting it. If assignment of a species along a commonness-rarity continuum is a goal of surveys, their value may be enhanced by including in the survey a set of species whose level of rarity is better understood. The Northwest Forest Plan is not unique in its use of rarity as a criterion for targeting conservation efforts, nor in its desire to use adaptive management. To evaluate population viability and how management can intervene to improve species persistence requires a much more comprehensive evaluation than assessment of rarity alone. Using a precautionary principle, such as was used with the initial assignment of the red tree vole as a survey and manage species, in the often data-challenged circumstances that are typical in species conservation was an important first step. Given the better understanding of the ecology of both species since red tree voles were included as a survey and manage species, adaptive management must allow for a more effective and efficient strategy for managing red tree voles.

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Declarations of interest

None.

References

Alexander, L.F., Verts, B.J., 1992. Clethrionomys californicus. Mammalian Species 406, 1–6.
Allen, C.R., Gunderson, L.H., 2011. Pathology and failure in the design and implementation of adaptive management. J. Environ. Manage. 92, 1379–1384.
Aubrey, K.B., Crites, J.J., West, S.D., 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service General Technical Report, PNW-GTR-285, Portland, Oregon, pp. 285–294.
Blackburn, T.M., Gaston, K.J., 1997. Who is rare? Artefacts and complexities of rarity determination. In: Kunin, W.E., Gaston, K. (Eds.), The Biology of Rarity: Causes and Consequences of Rare—Common Differences. Chapman and Hall, London, pp. 48–60.
Brown, J.H., 1984. On the relationship between abundance and distribution of species. Am. Nat. 124, 255–279.
Carey, A.B., Biswell, B.L., Witt, J.W., 1991. Methods for measuring populations of arboreal rodents. General Technical Report PNW-GTR-273. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.
Caughley, G., 1994. Directions in conservation biology. J. Anim. Ecol. 215–244.
Dobson, F.S., Yu, J., Smith, A.T., 1995. The importance of evaluating rarity. Conserv. Biol. 9, 1648–1651.
Doyle, A.T., 1987. Microhabitat separation among sympatric microtines, *Clethrionomys californicus, Microtus oregoni and M. richardsoni*. Am. Midl. Nat. 118, 258–265.
Dunk, J.R., Hawley, J.J., 2009. Red-tree vole habitat suitability modeling: implications for conservation and management. For. Ecol. Manage. 258, 626–634.
FEMAT [Forest Ecosystem Management Assessment Team], 1993. Forest Ecosystem Management: An Ecological, Economic, and Social Assessment. Report of the FEMAT. U.S. Government Printing Office, Washington, District of Columbia.
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.
Forsman, E.D., Anthony, R.G., Zabel, C.J., 2004. Distribution and abundance of red tree voles in Oregon based on occurrence in pellets of Northern Spotted Owls. Northwest Sci. 78, 294–302.
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. General technical report GTR-938. U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, Portland, Oregon.
Gashwiler, J.S., 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology 51, 1018–1026.
Gaston, K.J., 1994. Rarity. Chapman and Hall, London, United Kingdom.
Gaston, K.J., Fuller, R.A., 2008. Commonness, population depletion, and conservation biology. Trends Ecol. Evol. 23, 14–19.
Gaston, K.J., Kunin, W.E., 1997. Rare-common differences: an overview. In: Kunin, W.E., Gaston, K. (Eds.), The Biology of Rarity: Causes and Consequences of Rare—Common Differences. Chapman and Hall, London, United Kingdom, pp. 12–29.
Gillesberg, A.-M., Carey, A.B., 1991. Arboreal nests of *Phenacomys longicaudus* in Oregon. J. Mammal. 72, 784–787.
Hallett, J.G., O'Connell, M.A., Maguire, C.C., 2003. Ecological relationships of terrestrial small mammals in western coniferous forests. In: Zabel, C.J., Anthony, R.G. (Eds.), Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America. Cambridge University Press, Cambridge, United Kingdom, pp. 120–156.
Hamilton III, W.J., 1962. Reproductive adaptations of the red tree mouse. J. Mammal. 43, 486–504.
Harnik, P.G., Simpson, C., Payne, J.L., 2012. Long-term differences in extinction risk among the seven forms of rarity. Proc. Royal Soc. London B: Biol. Sci. 279, 4969–4976.
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. U. S. Department of Agriculture Forest Service Regions 5 and 6, and U.S. Department of the Interior Bureau of Land Management, Oregon/Washington, Portland, OR.
IUCN [Linzey, A.V. and NatureServe (Hammerson, G.)], 2008a. Myodes californicus. The IUCN Red List of Threatened Species: e.T42616A10730310. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T42616A10730310.en.
IUCN [Linzey, A.V., and NatureServe (Scheuering, E. and Hammerson, G.)], 2008b. Arborimus longicaudus. The IUCN Red List of Threatened Species 2008: e.T42615A10729936. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T42615A10729936.en.
Johnston, A.N., Moskal, L.M., 2017. High-resolution habitat modeling with airborne LiDAR for red tree voles. J. Wildl. Manage. 81, 58–72.
Kelsey, R.G., Forsman, E.D., Swingle, J.K., 2009. Distribution of terpenoid resins in conifer needles and their implications for Red Tree Vole, *Arborimus longicaudus*, foraging. Can. Field-Naturalist 123, 12–18.
Kunin, W.E., Gaston, K. (Eds.), 1997. The Biology of Rarity: Causes and Consequences of Rare—Common Differences. Chapman and Hall, London, United Kingdom.
Linnell, M.A., Davis, R.J., Lesmeister, D.B., Swingle, J.K., 2017. Conservation and relative habitat suitability for an arboreal mammal associated with old forest. Forest Ecol. Manage. 402, 1–11.
Linnell, M.A., Lesmeister, D.B., Bailey, J.D., Forsman, E.D., Swingle, J.K., 2018. Response of arboreal rodents to increased availability of nest substrates in young forests. J. Mammal. 99, 1174–1182.
Mace, G.M., Kershaw, M., 1997. Extinction risk and rarity on an ecological timescale. In: Kunin, W.E., Gaston, K. (Eds.), The Biology of Rarity: Causes and Consequences of Rare—Common Differences. Chapman and Hall, London, United Kingdom, pp. 130–149.
Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422 (6933), 714–716.
Marcot, B.G., Pope, K.L., Slauson, K., Welsh, H.H., Wheeler, C.A., Reilly, M.J., Zielinski, W.J., 2018. Other species and biodiversity of older forests. In: Spies, T.A., Stine, P.A., Gravenmier, R., Long, J.W., Reilly, M.J. (Eds.), MJ, tech. coords. Synthesis of Science to Inform Land Management within the Northwest Forest Plan area. Gen. Tech. Rep. PNW-GTR-966. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, pp. 371–459.
Marks-Fife, C.A., 2016. Estimation of Population Age Structure, Detection Probability, and Density of Red Tree Voles in Oregon. Oregon State University, Corvallis, Oregon Thesis.
Maser, C., 1966. Life Histories and Ecology of Phenacomys Albipes, Phenacomys longicaudus, Phenacomys Silvicola. Thesis, Oregon State University, Corvallis, Oregon.
Mills, L.S., 1995. Edge effects and isolation: red-backed voles on forest remnants. Conserv. Biol. 9, 395–403.
Molina, R., Marcot, B.G., Lesher, R., 2006. Protecting rare, old-growth, forest-associated species under the survey and manage program guidelines of the Northwest Forest

Plan. Conserv. Biol. 20, 306–318.
Preston, F.W., 1948. The commonness, and rarity, of species. Ecology 29, 254–283.
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 Naturalist 96, 37–49.
Rabinowitz, D., 1981. Seven forms of rarity. In: Synge, H. (Ed.), The Biological Aspects of Rare Plant Conservation. John Wiley and Sons, New York, pp. 205–217.
Reveal, J.L., 1981. The concepts of rarity and population threats in plant communities. In: Morse, L.E., Henefin, M.S. (Eds.), Rare Plant Conservation. New York Botanical Garden, Bronx, New York, pp. 41–46.
Rittenhouse, B., Breckel, R., Alegria, J., Max, T., Edwards, T.C., Jr., 2002. Survey protocol for conducting red tree vole strategic survey on randomly selected CVS/FIA plots. Unpublished report. U.S. Department of Agriculture Forest Service and U. S. Department of the Interior Bureau of Land Management, Portland, Oregon.
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.
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 (12) e01630.
Rosenzweig, M.L., Lomolino, M.V., 1997. Who gets the short bits of the broken stick? In: Kunin, W.E., Gaston, K. (Eds.), The Biology of Rarity: Causes and Consequences of Rare—Common Differences. Chapman and Hall, London, United Kingdom, pp. 63–90.
Schoener, T.W., 1987. The geographical distribution of rarity. Oecologia 74, 161–173.
Swingle, J.K., 2005. Daily Activity Patterns, Survival, and Movements of Red Tree Voles (*Arborimus longicaudus*) in Western Oregon. Oregon State University, Corvallis, Oregon Thesis.
Swingle, J.K., Forsman, E.D., 2009. Home range areas and activity patterns of red tree voles (*Arborimus longicaudus*) in western Oregon. Northwest Sci. 83, 273–286.
Swingle, J.K., Forsman, E.D., Sovern, S.G., 2004. A method for live-trapping tree voles. Northwestern Naturalist 85, 134–135.
Tallmon, D., Mills, L.S., 1994. Use of logs within home ranges of California red-backed voles on a remnant of forest. J. Mammal. 75, 97–101.
Tallmon, D.A., Mills, L.S., 2004. Edge Effects and Isolation: Red-backed voles revisited. Conserv. Biol. 18, 1658–1664.
Thompson, J.L., Diller, L.V., 2002. Relative abundance, nest site characteristics, and nest dynamics of Sonoma tree voles on managed timberlands in coastal northwest California. Northwestern Naturalist 83, 91–100.
Thompson, R.L., Chambers, C.L., McComb, B.C., 2009. Home range and habitat of western red-backed voles in the Oregon Cascades. Northwest Sci. 83, 46–56.
Toledo, L.F., Becker, C.G., Haddad, C.F., Zamudio, K.R., 2014. Rarity as an indicator of endangerment in neotropical frogs. Biol. Conserv. 179, 54–62.
USDA and USDI [USDA Forest Service, and 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.
USDA and USDI [USDA Forest Service, and USDI Bureau of Land Management], 2001. Record of decision and standards and guidelines for amendments to the survey and manage, protection buffer, and other mitigation measures standards and guidelines, Portland, Oregon.
USFWS [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.
Verts, B.J., Carraway, L.N., 1998. Mammals of Oregon. University of California Press, Berkeley, California.
Waters, J.R., Zabel, C.J., 1998. Abundances of small mammals in fir forests in northeastern California. J. Mammal. 79, 1244–1253.
Weldy, M., 2018. Spatiotemporal Associations of Abundance and Vital Rates of Co-occurring Small Mammals in a Late Successional Forest. Oregon State University, Corvallis, Oregon Thesis.
Wilson, D.E., Ruff, S., 1999. North American Mammals. Smithsonian Institute, Washington, District of Columbia.
Yu, J., Dobson, F.S., 2000. Seven forms of rarity in mammals. J. Biogeogr. 27, 131–139.